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Top-down effects on rocky reef ecosystems in north-eastern New Zealand: a historic and qualitative modelling approach

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A.B. MacDiarmid,
A. McKenzie,
E. Abraham

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Since New Zealand was first settled, humans have had a profound impact on the abundance of many of the larger predatory marine species including white sharks (*Carcharodon carcharias*), killer whales (*Orcinus orca*), hapuku or groper (*Polyprion oxygenios*), sea lions (*Phocarctos hookeri*), and small and medium sized sharks such as school sharks (*Galeorhinus galeus*) and bronze whaler (*Carcharhinus brachyurus*). In this study, we explored the potential impact of the removal of these top predators on rocky reef ecosystems in the Hauraki Gulf in order to determine the critical interactions amongst species and other ecosystem components, and identify those that should be a priority for future research. We used an existing qualitative model of a present day rocky reef ecosystem and included each top predator sequentially in the model by applying a positive or negative perturbation to the abundance of one or more of the existing groups in the model to simulate the effects of predation impact or release. In essence, using this approach, we worked from the present day situation back in time in four steps, at each step adding another group of top predators that were previously abundant in the Hauraki Gulf. For each step or iteration of the model, system stability was examined, and where necessary negative feedback loops were added to ensure that the system was stable.

The inclusion of small and medium sized sharks in the qualitative model had the most predictable impacts with highly certain negative impacts on the abundance of small and large lobsters, and highly certain increases in the abundance of large predatory invertebrates, such as snake stars and sea stars, and macro-invertebrate predatory fish, such as snapper. In the model none of these groups are directly preyed upon by small and medium sized reef sharks, indicating that the effect of shark predation propagates through the food web indirectly via linkages of prey groups to the affected groups in a complex manner.

Subsequent and sequential addition of white sharks and orca, hapuku, and sea lions to the model system had a variety of positive and negative impacts, but all interactions had predictability values of 0.32 or less indicating that the probability of obtaining the correct direction of impact on groups in the modelled ecosystem was moderate to low. This uncertainty indicates that more information than the direction of the first order interactions (i.e. a positive or negative impact on the abundance of a modelled group) is required to successfully explore the impact of these predators on reef ecosystems in northern New Zealand. Such additional information may be about the intensity of interactions which are likely to be density or encounter rate dependent as these larger predators range over very large distances revisiting the same area only intermittently or seasonally. The uncertainty in the outcome of modelling the impact of white sharks and orca, hapuku, and sea lions underscores the limitation of qualitative models. While they require less information to setup and run than mass-balance models, for example, they may also leave out potentially critical information.

The qualitative modelling undertaken in this study suggests that historically higher school shark and bronze whaler populations in the Hauraki Gulf were very likely to increase the abundance of reef fish, such as snapper, that prey upon macro-invertebrates, but depress rock lobster abundance. That more sharks may mean more snapper is an unexpected finding. It suggests that it may be fruitful to undertake a field sampling programme to examine changes in reef community structure across a gradient of small and medium shark population abundance in northern New Zealand, that the diet of these sharks should be investigated in greater detail, and the relationships between these predators and other components of the reef ecosystem should be remodelled once further data are available.

1. INTRODUCTION

1.1 Background

New Zealand was the last major land mass to be settled by humans, occurring around 1250 AD (Wilmshurst et al. 2011). Consequently, New Zealand has a short and reasonably complete archaeological, historical and contemporary record of human exploitation of marine resources compared to most other places where the earliest evidence of human impacts on marine ecosystems is difficult to discern because of climate fluctuations and changes in sea level (MacDiarmid et al. 2016). The collaborative multi-disciplinary Taking Stock project (ZBD200505), commissioned by the Ministry for Primary Industries, has the overall objective of determining the effects of climate variation and human impact on the structure and functioning of New Zealand shelf ecosystems over the timescale of human occupation since about 1250. While Māori rapidly explored and settled all the main islands, the Chatham Islands to the east and as far south as the sub-Antarctic Auckland Islands, the main centre of settlement and growth was the northern half of the North Island, including the Hauraki Gulf region, where a more benign climate allowed the cultivation of a greater range of tropically derived crops (King 2003). The Hauraki Gulf was chosen as a case study of the broader New Zealand wide changes as the available prehistoric, historic and modern information about marine resource use allowed the pattern and magnitude of human impacts on the marine environment to be usefully explored (Smith 2011, Smith 2013, MacDiarmid et al. 2016). This report details part of that story; specifically the ecological consequences of sequential depression in the numbers of the larger marine predators by humans either directly via hunting and fishing, or indirectly through depression of prey species on which the larger predators were dependent.

1.2 Impacts of humans on top predators

Since New Zealand was first settled, humans have had a profound impact on the abundance of many of the larger predatory marine species. In north-eastern New Zealand Māori encountered significant populations of New Zealand fur seals (*Arctocephalus forsteri*) on rocky headlands, and New Zealand sea lions (*Phocarctos hookeri*) on sandy beaches (Childerhouse & Gales 1998, Smith 2005). Smith (2011) has calculated a high reliance by early Māori on seals which contributed about 61% of their marine diet in the Hauraki Gulf region. This equated to an annual removal of about 4000 fur seals and about 560 sea lions from the Greater Hauraki Gulf. This level of exploitation gradually removed seal populations southwards from North Cape to the southern shores of the South Island over a period of 500 years with both species eliminated from northern New Zealand before 1500 (Smith 2005). European sealers in the late 18th century and early 19th century hunted fur seals and sea lions to extinction around the New Zealand mainland and nearly eliminated them from the sub-Antarctic Islands (Lalas & Bradshaw 2001; Ling 2002). New genetic research on ancient sea lion DNA extracted from midden derived bones indicates that the sea lions that once inhabited northern New Zealand were distinct (possibly a separate species) from the surviving populations of sea lions in southern New Zealand and the sub-Antarctic Islands (Collins et al. 2014). This suggests that human harvesting caused an extinction event, not just a range retraction.

Fish became more important in the diet of Māori as seals, moa and some marine and coastal birds ceased to be available (Smith 2011). At about 1400 the best estimate of the total annual fish harvest by Māori in the Hauraki Gulf was about 130 ± 45tonnes, increasing to 2330 ± 700 t by about 1550, and 2600 ± 780 t by about 1750 (Smith 2011). Commercial fisheries for a range of marine fish and invertebrates became established in the Hauraki Gulf in the 1860s (Paul 2014). For many of the principal exploited species, noticeable declines in abundance occurred in the late 19th century and early 20th century (MacDiarmid et al. 2015). The historical narratives indicate that the declines were first evident in species such as oysters, grey mullet and flat fishes in sheltered, shallow, easily accessed areas, but later progressed to species with a wider inshore distribution such as snapper (*Pagrus auratus*) and blue cod (*Parapercis colias*), or a deep water refuge such as hapuku or groper

(*Polyprion oxygenios*) (MacDiarmid et al. 2015). McKenzie & MacDiarmid (2012) have estimated that the combined biomass of exploited species in the Hauraki Gulf is now about 41% of the biomass present in 1930.

Hapuku were formerly abundant along reef edges at depths of 10–30 m on exposed coasts in the Hauraki Gulf (MacDiarmid et al. 2015). These were caught by Māori and although fished commercially starting in the 1860s, continued to be available in small numbers around Great Barrier Island and the Coromandel Peninsular until the 1950s (Maxwell & MacDiarmid 2015). Hapuku fisheries are now confined to the outer half of the continental shelf and upper slope at depths of 100–300 m (Ministry for Primary Industries 2014). Prior to European settlement and in the 19th century school sharks (*Galeorhinus galeus*), rig (*Mustelus lenticulatus*) and northern spiny dogfish (*Squalus mitsukurii*) were important sources of food and oil for Māori, while larger sharks including white sharks (*Carcharodon carcharias*) were prized for their teeth (Francis 1998, Smith 2011, 2013). The annual commercial catch of school sharks in the Hauraki Gulf is currently around 100–150 t (Paul 2014). Since 1992, most of the larger sharks cannot be targeted in commercial fisheries (Francis 1998, Ministry for Primary Industries 2014). However, commercial by-catch, and recreational and sport fisheries for sharks such as mako (*Isurus oxyrinchus*), blue (*Prionace glauca*), hammerhead (*Sphyrna zygaena*), thresher (*Alopias vulpinus*), and bronze whaler (*Carcharhinus brachyurus*) continue (Francis 1998, Ministry for Primary Industries 2014, NIWA unpublished data). From 2007, white sharks have been completely protected from fishing although they are still caught incidentally each year in set nets and other fishing gear (see http://www.niwa.co.nz/our-science/oceans/research-projects/all/white-sharks).

Captain James Cook commented on the abundance of whales and dolphins around the New Zealand coast in the journal from his first voyage to New Zealand (Beaglehole 1955). Jackson et al. (2016) estimated that about 27 000 (95% confidence interval of 22 000 to 32 000) southern right whales occurred in New Zealand waters at this time. Carroll et al. (2014) have estimated that about 40 000 southern right whales were removed from the waters surrounding New Zealand during the nineteenth century by the combined efforts of pelagic whalers, bay whalers and shore-based whaling stations, though the majority were taken during the 1830s and 1840s. The New Zealand and southern hemisphere distribution of the pelagic catch of southern right whales over the period has recently been described by Smith et al. (2012). These combined shore whaling, bay-whaling and pelagic catches had a devastating impact on the New Zealand population of southern right whales which Jackson et al. (2016) have calculated came close to extinction with perhaps fewer than 100 individuals surviving into the early twentieth century. During the nineteenth and twentieth centuries, sperm whales and humpback whales were also taken from New Zealand waters (Jackson et al. 2016, Smith et al. 2012), and pelagic whaling in the Southern Ocean and the Antarctic removed vast numbers of humpback, blue and fin whales (Baker & Clapham 2004, Berzin 2008, Clapman & Ivashchenko 2009, Clapman et al. 2009), some of which would have migrated through New Zealand waters on their way to and from winter calving and breeding grounds in the tropics. Pinkerton et al. (2015) has estimated that, in combination, these historic whaling activities reduced present day whale biomass in the Hauraki Gulf study region by about 70%.

The greatly reduced biomass of marine mammals around New Zealand, with the consequent reduction in the annual production of pups, calves and placentas, and more modest declines in fish stocks described above may have had important consequences for top predators such as white sharks and killer whales (*Orcinus orca*) which prey upon a variety of fish, seals and cetaceans (Corte´s 1999, Visser 1999a and b, Visser 2000, Heithaus 2001, Estrada et al. 2006, Mehta et al. 2007, Carlisle et al. 2012). Marine mammals are an energy rich food source for white sharks, in particular. (Fallows et al. 2013, Semmens et al. 2013). Depletion of prey species has been identified as a threat to white shark populations worldwide (Wildlife Conservation Society 2004) and some populations of killer whales (Ainley & Ballard 2012, Ayres et al. 2012).

1.3 Study Objectives

This report pertains to Objective 5 of Project ZBD200505: To use qualitative modelling techniques to determine the critical interactions amongst species and other ecosystem components in order to identify those that should be a priority for future research.

The New Zealand Ministry for Primary Industries is working towards an ecosystem-based approach to the management of marine resources and is funding several inshore and offshore projects to investigate the functional ecology of different ecosystems (Ministry for Primary Industries 2012). The complexity of interactions amongst species and the impacts of exploitation, and other human activities, as well as environmental fluctuations (Edgar & Shaw 1995, Dayton et al. 1998, Shears & Babcock 2003, Gagnon et al. 2004, Thrush et al. 1998 and 2004, Langlois et al. 2005, Connell 2007a), means that a coherent understanding of how marine ecosystems function is only just emerging (Loreau et al. 2001, Estes et al. 2004, Shears & Babcock 2004, Connell 2007b, Pinkerton et al. 2010).

While complex quantitative models can be used to study specific processes within simple systems (e.g. Abraham 2007, Pinkerton et al. 2010), the task of quantifying each of the interactions for larger systems is difficult and time consuming (e.g. Okey et al. 2004, Brose et al. 2005). A further difficulty is that as a model's complexity increases, its predictability will generally decrease (May 1974). In principle, even if model parameters can be measured accurately, the predictions may be poor. This lack of predictability is exemplified by systems such as weather forecasting models, where even though the physics is well understood, and the models are supported by extensive quantitative data, huge resources are needed to make accurate predictions beyond a few days and predictions are decreasingly accurate with increasing period no matter what the resources.

Rather than demanding detailed measurements for a plethora of variables, loop analysis or qualitative modelling takes a different approach (Levins 1974, Dambacher et al. 2002, 2003a, 2003b). It aims to identify the relationships between a subset of species (or groups of species), and to determine what consequences flow from that structure. Interactions are classified as positive or negative, and no further information is required. This has the advantage of requiring less information than mass balance modelling, for example, but the disadvantage of leaving out potentially critical information about the nature or intensity of interactions. Qualitative analysis gives a prediction of how a perturbation in the biomass of one species affects the biomass of others in the community and may be useful in determining which interactions may be most fruitful in investigating further. Qualitative modelling is similar to the analysis of interactions in food webs (e.g. Whipple et al. 2000), but also allows other non-trophic interactions (such as competition and provision of habitat) to be included. Once the qualitative model has been built, it can be used to explore different scenarios, and assess the likely effects of external pressures, such as increased fishing or greater sedimentation.

We used qualitative modelling to explore the impact of predation by small to medium sized sharks (such as school sharks and bronze whalers), white sharks, orca, hapuku, and sea lions that previously were more abundant in the Hauraki Gulf, on rocky reef ecosystems. We chose rocky reef ecosystems to investigate as they are an important subcomponent of the Hauraki Gulf ecosystem (Pinkerton et al. 2015), supporting important commercial and recreational fisheries for snapper and rock lobsters now and in the past (Smith 2011, Paul 2014, MacDiarmid et al. 2015, Maxwell & MacDiarmid 2015).

2. METHODS

2.1 Rocky reef qualitative model

Beaumont et al. (2011) developed a qualitative model of a rocky reef ecosystem in the Leigh Marine Reserve, Hauraki Gulf. The initial model structure resulted from a review of 211 published and unpublished literature sources that summarised the details of 104 first order or direct trophic interactions amongst twenty-seven reef components. The review suggested a model comprised of 18 groups or components (Figure 1; Table 1).

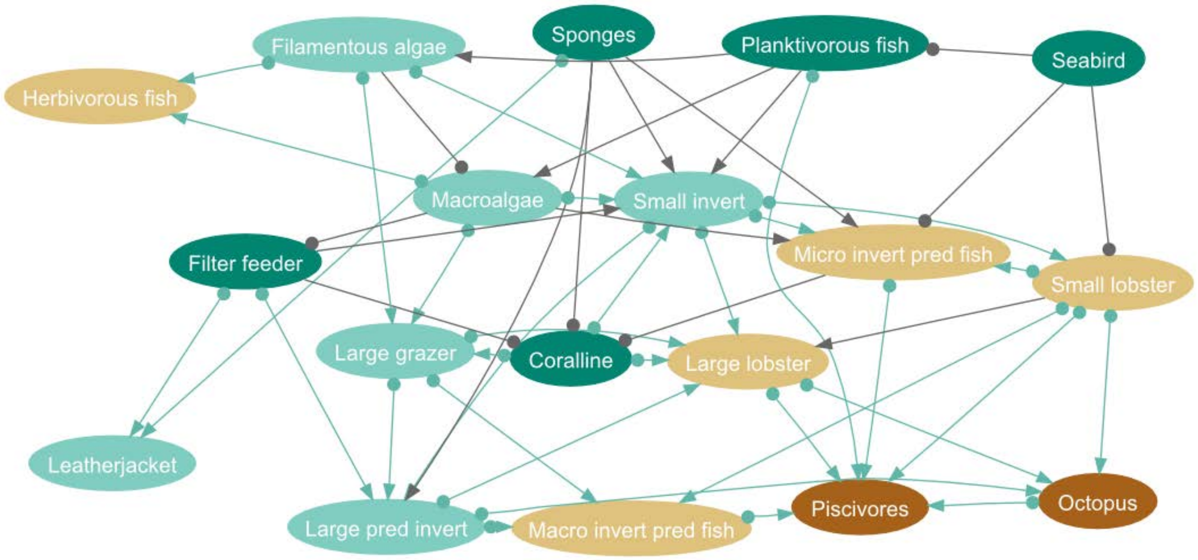

Figure 1. The qualitative model including all interactions. An arrow head indicates a positive interaction and a dot shows a negative interaction. Predator-prey interactions between two species are coloured in aqua-blue. The colour of each group is determined by following positive interactions through the system. Dark green groups, have no positive interactions leading to them. If the model was purely hierarchical, the colours would correspond to trophic level, with dark green at the bottom and dark brown at the top. All subsequent similar figures use the same format.

Table 1: The groups used in the qualitative model.

Group Name	Example
Sea birds	Shags or cormorants
Piscivorous fish	Kingfish (*Seriola lalandi*), John dory (*Zeus faber*), kahawai (*Arripis trutta*), scorpion fish (*Scorpaena cardinalis*), large snapper (*Pagrus auratus*) (> 400 mm TL)
Macro-invertebrate predatory fish (feed on large crustaceans, molluscs, and echinoderms found on reefs and around reef margins)	Snapper (< 400 mm TL), blue cod (*Parapercis colias*), conger eel (*Conger wilsoni*), eagle ray (*Myliobatis tenuicaudatus*), sting rays (Dasyatis spp.), larger tarakihi (*Nemadactylus macropterus*)
Micro-invertebrate predatory fish (feed on small crustaceans, molluscs, and echinoderms found in algal turf and surficial sediments)	Red moki (*Cheilodactylus spectabilis*), porae (*Nemadactylus douglasii*), cryptic fish, wrasses, goatfish (*Upeneithys porosus*), sea perch (*Helicolenus percoides*), triplefins, smaller tarakihi, mado (*Atypicthys latus*), giant boarfish (*Paristiopterus labiosus*), hiwihiwi (*Chironemus marmoratus*), yellow moray eel (*Gymnothorax prasinus*)
Planktivorous fish	Maomao (*Scorpis violacea*), demoiselle (*Chromis dispilus*), trevally (*Pseudocaranx georgianus*), koheru (*Decapterus koheru*), sweep (*Scorpis lineolata*), big-eye (*Pempheris adspersa*), butterfly perch (*Caesioperca lepidoptera*), slender roughy (*Optivus elongatus*), golden or red snapper (*Centroberyx affinis*), oblique swimming blennies (*Fosterygion maryannae*)
Leatherjacket (only sponge and tunicate feeder)	Leatherjacket (*Meuschenia scaber*)
Herbivorous fish	Butterfish (*Odax pullus*), silver drummer (*Kyphosus sydneyanus*), parore (*Girella tricuspidata*), marblefish (*Aplodactylus arctidens*),
Large lobster	Red rock lobster (*Jasus edwardsii*), packhorse lobster (*Sagmirasus verreauxi*)
Small lobster	Red rock lobster, packhorse lobster
Octopus	Octopus (*Pinnoctopus cordiformis*)
Large predatory invertebrates	Crabs, asteroids, large ophiuroids
Filter feeders	Hydroids, bryozoans, tunicates, mussels, clams, brachiopods, polychaetes
Sponge	Finger sponges, encrusting sponges,
Large grazing invertebrates	Sea urchins, abalone, large limpets and other large grazing gastropods such as *Cookia sulcata, Trochus spp.*
Small mobile invertebrates	Chitons, small gastropods, amphipods, isopods, hermit crabs, sea cucumber
Macroalgae	Large foliose brown algae
Filamentous algae	Red algae, green algae
Coralline	Turfing coralline, mound forming coralline

Because of the number of groups in this system, and the extent to which they are connected, the degree of predictability for the direction of a response was very low with no predictability value greater than 0.026 (see appendix 4 in Beaumont et al. 2011). A predictability of at least 0.5 is required to give approximately a 90% probability of the predicted direction of response being correct (Dambacher et al. 2003b). Consequently, for the complete system, none of the predicted directions of response to perturbations could be relied upon to be correct with only the sign of the interaction among groups in an ecosystem specified. In other words, the strength of the interactions may be critical to understanding the role of the group in the ecosystem. For this reason Beaumont et al. (2011) obtained expert opinion about the likely strength of interactions among the groups specified in Table 1 independently from each of six rocky reef ecologists. The median value of the strength of each interaction was then used to refine the model by progressively eliminating the weaker interactions, as well as those groups connected only by a single or small number of negative interactions going from them to the rest of the system (Beaumont et al. 2011). Also dropped were sub-systems of interacting groups that, after elimination of weak and small strength interactions, were no longer connected to the main system. This process of progressive elimination helped Beaumont et al. (2011) to discern which were the most important groups and interactions for the system and identified a simplified system for which the predictability of the direction of response (as given by the weighted predictions matrices) was high.

Not defined in the initial model setup was negative feedback on groups. Negative feedback, such as density dependent self-shading, growth, predation, and cannibalism, limits the growth in numbers or biomass for a group and at modest levels can be important for system stability (Dambacher et al. 2003b). Two guiding criteria used by Beaumont et al. (2011) when adding negative feedback were: (1) it is most likely to occur at lower trophic levels, and (2) the system must be stable to be a realistic model. Negative feedback was first added by Beaumont et al. (2011) to all groups for this system, this giving a stable system, and then progressively removed from the higher trophic levels, eventually leaving it on a minimal number of groups, for which any further removal of negative feedback gave an unstable system. These were taken as the essential groups in the system in which there should be negative feedback (Beaumont et al. 2011).

The procedures described above enabled Beaumont et al. (2011) to produce a minimal negative feedback trimmed medium and higher strength interaction model with 12 groups and 135 direct and indirect interactions in which the predictability for the direction of response was 1.0 for about 24% of interactions and 0.5 or greater for 40% of interactions (Figure 2) which is acceptable for this type of model (Dambacher 2003a and b). Of note in this system was the presence of the well documented (e.g., Shears & Babcock 2003) rock lobster – sea urchin – macroalgae cascade (or in the system labels: large lobster – large grazer – macroalgae) (see Figure 3), although the predictability of this interaction was modest.

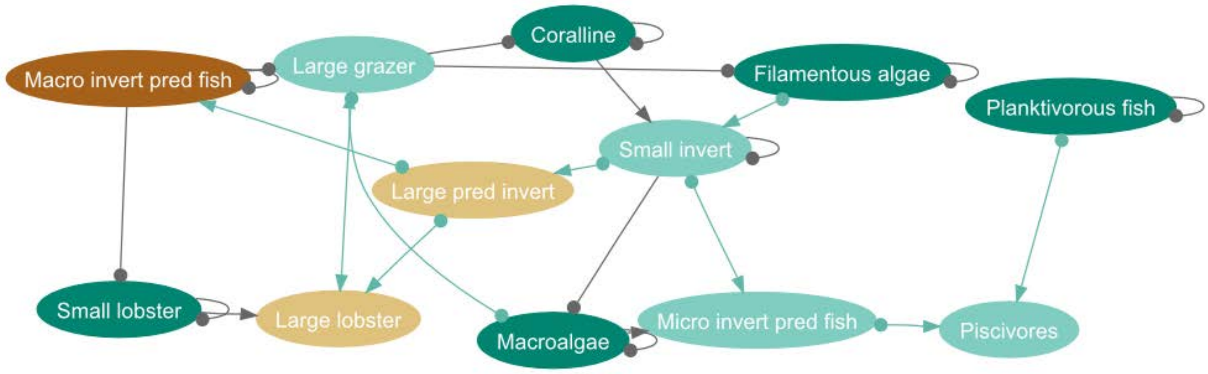

Figure 2: The trimmed qualitative model with minimal negative feedback and retaining only medium and stronger interactions.

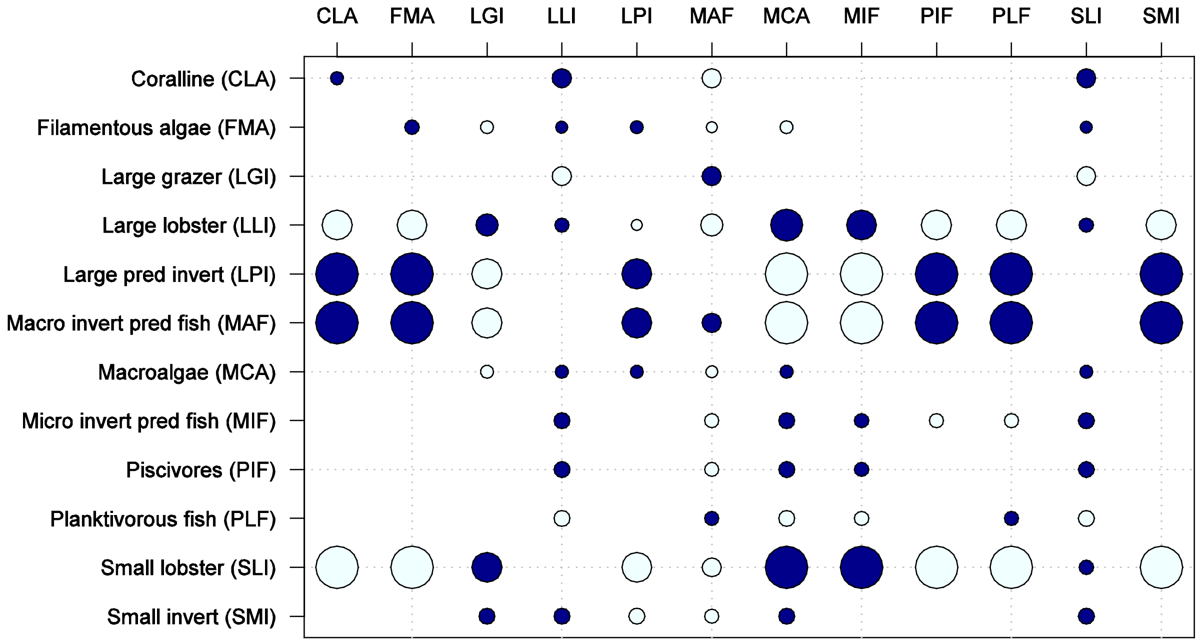

Figure 3: Minimal negative feedback trimmed medium and stronger interaction strength qualitative model: direction of response. The dark shaded circles represent positive response values, the lightly shaded circles negative response values. The area of the circles is proportional to the prediction strength, with the largest circle representing a value of 1.0. The response of large lobsters to a positive perturbation in coralline algae abundance is, reading down the CLA column, negative with a predictability of 0.5. Note that the effects of changes in the abundance of a group on other groups are listed down the column while the response of a group to changes in the abundance of other groups is listed across a row.

2.2 Sequential inclusion of mega-predators

We used the model described above to explore the impact of sequentially including in the system small to medium sized sharks (such as bronze whalers), white sharks and orca, hapuku, and sea lions which historically were more abundant in the Hauraki Gulf (Table 2).

Each top predator was included in the model by applying a positive or negative perturbation to the abundance of one or more of the existing groups in the model to simulate the effects of predation impact or release. In essence, using this approach, we worked from the present day situation back in time in four steps, at each step adding another group of top predators that were previously abundant in the Hauraki Gulf. For each iteration of the model, system stability was examined and where necessary negative feedback loops were added to ensure that the system was stable.

Small and medium sharks

The available information for bronze whaler indicates that their diet comprises 79% fish including reef fish, and 19% octopus, while school shark diet comprises predominately fish including many reef associated species, as well as some squid and octopus (Ayling & Cox 1982, Russell 1983, Olsen 1984, Francis 2012). As there are no octopus or squid in the minimal trimmed model, and they are a relatively small proportion of shark diet, the shark – octopus interaction was ignored. Assuming that the diet of these sharks is similar to that of reef piscivores (i.e. they preyed upon micro- invertebrate predatory fish such as red moki, porae, goatfish, and tarakihi, as well as planktivorous fish such as blue maomao, sweep, and butterfly perch), a simple way to model the impact of including small and medium sharks was to apply a positive perturbation to the abundance of the piscivore group (Table 3).

White sharks and Orca

The diet of white shark diet comprises 34% small pelagic fish, 36% sharks and rays, 18% cetaceans, and 2% planktivorous fish (Estrada et al. 2006, Carlisle et al. 2012, Malcolm Francis, NIWA, pers. comm.). Neither small pelagic fish nor cetaceans are included in the rocky reef model, so interactions with these groups are not considered further. Rays are part of the macro-invertebrate predatory fish group in the model, while small and medium sharks are included above as a positive perturbation to the piscivores group. This suggested that white sharks should be included in the model as negative perturbations to the abundance the piscivorous fish, macro-invertebrate predatory fish, and planktivorous fish groups (Table 3).

Orca have a varied diet of finfish, rays, sharks, seals and cetaceans (Fertl et al.1996, Constantine et al. 1998, Ford et al. 1998, Ford & Ellis 1999, Pyle et al. 1999, Visser 1999a and b, Visser et al. 2000, Fallows et al. 2013, Semmens 2013). Orca predation on seals in New Zealand is not confirmed (Visser 2000). Visser (2000) noted that the North-Island exclusive sub-population of orca foraged only for rays, fin-fish, and sharks, therefore predation on cetaceans is ignored in this model. All but one of the fin fish species preyed upon by orca in New Zealand are hooked fish on fishing lines (Visser 2000) and so are ignored in this model. Orca predation on fish-eating sharks is included as a positive perturbation to the abundance of piscivores fish group. Predation on rays are already included in the model as a negative perturbation on the macro-invertebrate predatory fish group as for the white sharks (Table 3).

Hapuku

The present diet of hapuku on deep (more than 100 m) reefs includes red cod, blue cod, tarakihi, hoki, and squid (Francis 2012, Ministry for Primary Industries 2014). Historically, on coastal reefs hapuku probably preyed upon snapper of less than 400 mm total length (TL) and lobster, the most abundant reef associated fish and invertebrate respectively in the Hauraki Gulf (Shears & Babcock 2003, 2004). Around Otago coasts, lobster 18–28 cm long were common in the guts of hapuku (Graham 1956). In the model hapuku were included as negative perturbations on the abundance of macro invertebrate predatory fish (which includes snapper less than 400 mm TL, blue cod, red cod and larger tarakihi), small lobsters and large lobsters (Table 3). Hapuku predation on squid and hoki was ignored as these species do not occur on Hauraki Gulf coastal reefs.

Sea lions

We base the historical diet of sea lions on reefs in the Hauraki Gulf on data from southern New Zealand where sea lions target cephalopods and teleost fishes (Childerhouse et al. 2001; Meynier et al. 2008, 2009, 2010, Chilvers et al. 2011). We substituted similar species occurring on northern reefs. Ignoring prey items that comprised 5% or less of sea lion diet in the above studies, likely prey groups include piscivorous fish and macro-invertebrate predatory fish, and a negative perturbation was applied to the abundance of both these groups to model sea lion predation (Table 3). Due to their relatively weak interaction with other reef groups octopus are excluded from the model outlined in Figure 2, and are not considered further.

Table 2: Mega-predators in the Hauraki Gulf. The year denotes the nominal year in which the mega-predator was last of high ecological significance.

Mega-predator	Nominal year of high ecological significance	Rationale/ Evidence
Small to medium reef sharks	1965	Medium size sharks such as bronze whalers were commonly observed on inshore reefs until about the mid-1960s despite being subject to by-catch in commercial fishing and directed spear fishing (Russell 1983), and big game fishing (Francis 1998). At reefs near Goat Island apparently resident bronze whalers were speared in the late 1960s (Russell 1983) but have not been recorded since. The annual catch of school sharks in the Hauraki Gulf by pre-European Māori was 960 ± 288 t (Smith 2011), about 8 or 9 times the present commercial catch (Paul 2014). The current biomass of school shark in the Hauraki Gulf is poorly known (McKenzie & MacDiarmid 2012).
White shark and orca	1850	White sharks were fished by pre-European Māori for their teeth (Francis 1998). There is no evidence for directed fishing for orca by Māori or by European settlers. Seal prey were hunted to extinction in this region by 1500 (Smith 2005), but all whale species that migrated close inshore (southern rights and humpbacks) were still seasonally available till about 1845. Shore and bay whaling for southern right and humpback whales may have increased carcass availability to white sharks and orca through to the peak of shore whaling in 1835–45 (Fallows et al. 2013, Carroll et al. 2014). Small numbers of orca were hunted in New Zealand waters in the twentieth century (Mikhalev et al. 1981, Visser 2000). Despite current protection, both white shark and orca probably experience low to moderate mortalities, or lowered rates of reproduction, through the combined effects of human competition for prey species, ship strikes, accumulation of toxic pollutants, entanglement in bather protection nets, ingestion of plastics, disturbance, and incidental by-catch (Hofman 1995, Slooten & Dawson 1995, Francis 1998, Visser 1999c, Ross et al. 2000, Visser & Fertl 2000, Williams et al. 2006, Green et al. 2009).
Hapuku	1700	Hapuku were seasonally exploited by pre-European Māori and subject to a growing commercial fishery from 1860 (MacDiarmid et al. 2015), but were present in small numbers along reef edges around outer Hauraki Gulf islands until the 1950s (Maxwell & MacDiarmid 2015). Current annual commercial catch in the Hauraki Gulf is about 100 t (Paul 2014) but the biomass is poorly known (McKenzie & MacDiarmid 2012). The year 1700 for high ecological significance is nominal and indicates a pre-European date at which hapuku stocks were close to pre-exploitation levels.
Sea lions	1400	Sea lions were hunted to local extinction in northern New Zealand by 1500 AD (Smith 2005). There has been no recovery in the region to date.

Table 3: Perturbation applied to the abundance of groups in the qualitative model to account for the sequential inclusion of each mega-predator. The perturbations accumulate the earlier the period considered: the total perturbation applied in 1400 due to the combined effects of all top predators is given by the last column.

	Nominal Year				
	1965	1850	1700	1400	Total
Mega predator	Small and medium sharks	White shark and orca	Hapuku	Sea lions	All mega-predators combined
Model group					
Planktivorous fish (PLF)	0	-1	0	0	-1
Macro-invertebrate predatory fish (MAF)	0	-1	-1	-1	-3
Small lobster (SLI)	0	0	-1	0	-1
Large lobster (LLI)	0	0	-1	0	-1
Piscivorous fish (PIF)	+1	-1/+1	0	-1	0

3. RESULTS

3.1 System stability

The only iteration of the model that did not require additional negative feedback loops to remain stable was the inclusion of small and medium sized sharks. In all other iterations negative feedback loops on all model groups was required producing the model shown in Figure 4.

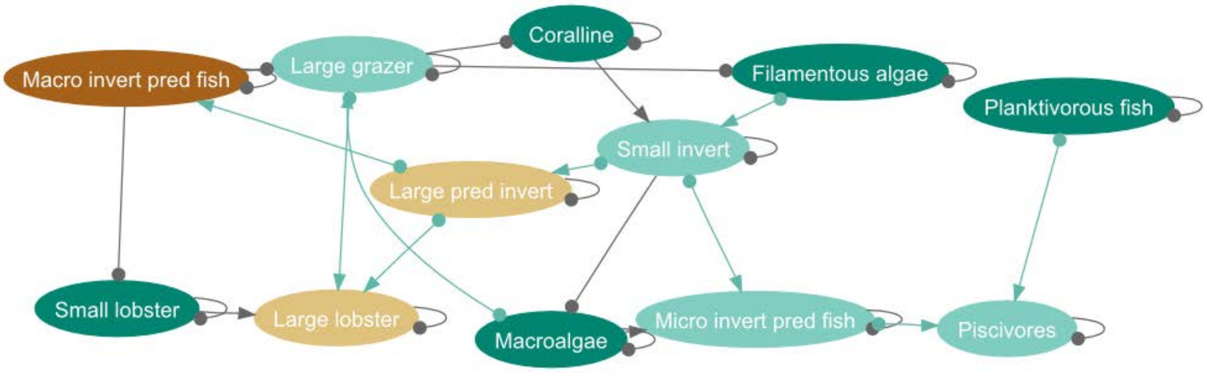

Figure 4: The trimmed qualitative model with negative feedback on all groups and retaining only medium and stronger interactions.

3.2 Effects of adding mega-predators

The impact of including predation by small and medium sized sharks in the qualitative model of a Hauraki Gulf rocky reef ecosystem (1965 column in Table 4 and Figure 5) was highly certain negative impacts on the abundance of small and large lobsters, and highly certain positive impacts on the populations of large predatory invertebrates, such as snake stars and sea stars, and macro-invertebrate predatory fish, such as snapper. Simulation studies by Dambacher et al. (2003b) indicate that values in a weighted predictions matrix that are greater than or equal to 0.5 indicate an approximately 90% probability of obtaining the correct direction of change.

The addition of white sharks and orca to the model, in combination with smaller sharks (see 1850 column in Table 4), reversed the impact on small and large lobsters and macro-invertebrate predatory fish to increase their abundance, neutralised the impact on large predatory invertebrates and micro-invertebrate predatory fish, and depressed the abundance of planktivorous fish. Combined, small and medium sized sharks, white sharks, orca and hapuku (see 1700 column in Table 4) had negative impacts on the abundance of coralline, filamentous, and macro-algae, small mobile invertebrates, micro-invertebrate predatory fish, piscivorous fish, planktivorous fish, and macro-invertebrate predatory fish, as well as increasing the abundance of lobsters, large grazing invertebrates, and large predatory invertebrates. The combined effects of all the mega-predator groups (see right-most column in Table 4) had only one effect; reversing the impact on piscivorous fish populations. However, all the values in the weighted predictions matrix for the inclusion of white shark and orca, hapuku, and sea lions were less than 0.32 indicating a low probability of obtaining the correct direction of change in abundance of the affected groups.

Table 1: Inclusion of mega-predators: weighted predictions matrix. The effects of changes in the abundance of a group on other groups are listed down the column. For example, in the period "1850" when white sharks and orca were abundant in the Hauraki Gulf, their combined impact along with small and medium sized sharks is an increase in large lobsters with a predictability of 0.28. Note: simulation studies indicate that entries in the matrix that are greater than or equal to 0.5 (bolded) give approximately 90% probability of obtaining the correct direction of change (Dambacher et al. 2003b).

				Year
	1965	1850	1700	1400
Mega-predator	Small and medium sharks	White shark and orca	Hapuku	Sea lions
Model group				
Coralline (CLA)	0.00	0.00	-0.12	-0.08
Filamentous algae (FMA)	0.00	0.00	-0.01	-0.01
Large grazing invertebrates (LGI)	0.00	0.00	+0.12	+0.08
Large lobster (LLI)	**-0.50**	+0.28	+0.08	+0.13
Large predatory invertebrate (LPI)	**+1.00**	0.00	+0.03	+0.04
Macro-invertebrate predatory fish (MAF)	**+1.00**	-0.32	-0.22	-0.25
Macro-algae (MCA)	0.00	0.00	-0.01	-0.02
Micro-invertebrate predatory fish (MIF)	-0.11	0.00	-0.04	-0.05
Piscivorous fish (PIF)	0.00	0.00	-0.02	+0.01
Planktivorous fish (PLF)	0.00	-0.09	-0.06	-0.07
Small lobster (SLI)	**-1.00**	+0.32	+0.07	+0.12
Small mobile invertebrates (SMI)	0.00	0.00	-0.10	-0.06

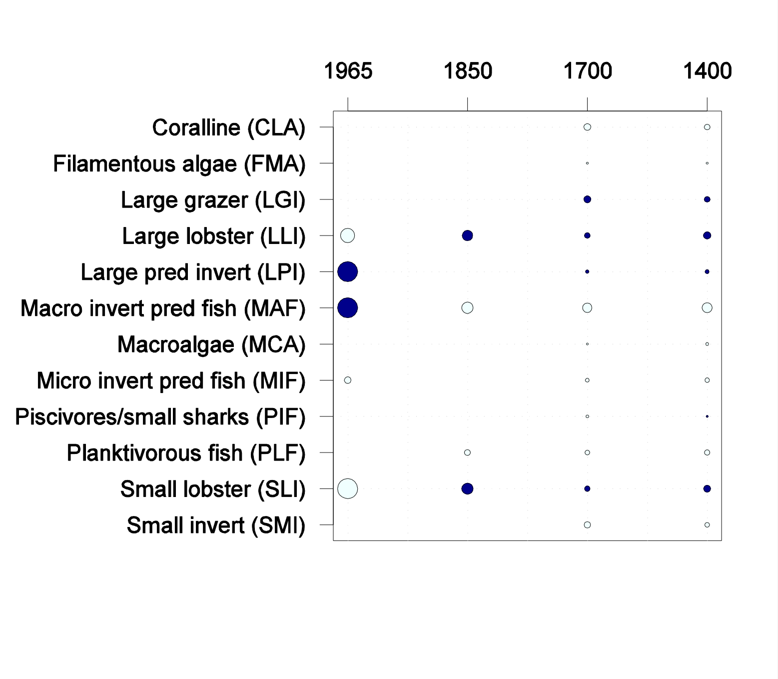

Figure5: Addition of mega-predators: direction of response and weighted predictability (see Table 1). The dark shaded circles represent positive response values, the lightly shaded circles negative response values. The area of the circles is proportional to the prediction strength, with the largest circle representing a value of 1.0.

4. DISCUSSION

The qualitative modelling undertaken in this study suggests that historically higher populations of small to medium sized sharks, such as school sharks and bronze whalers, are very likely to have had positive and negative effects on the populations of key components of rocky reef ecosystems in the Hauraki Gulf. Large predatory invertebrates such as crabs, asteroids, and ophiuroids, and macro-invertebrate predatory fish, such as snapper, would have been more abundant, while spiny lobster populations would have been depressed. In the model none of these groups are directly preyed upon by small and medium sized reef sharks, indicating that the effect of shark predation propagates through the food web indirectly via linkages of prey groups to the affected groups in a complex manner. Similar conclusions about the important role of sharks in reef ecosystems were reached by Stevens et al. (2000) in their global review of the effects of fishing on sharks, and more generally by Heithaus et al. (2007) in their review of the role of top marine predators. Key roles of reef sharks have recently been identified in empirical studies of fished and unfished coral reefs off north-west Australia (Ruppert et al. 2013), on coral reefs in the Pacific (Friedlander & De-Martini 2002, De-Martini et al. 2008), and in the temperate north-western Atlantic (Myers et al. 2007).

It is interesting to note that as more of the mega-predators were included in the rocky reef ecosystem model, the abundances of larger invertebrates, including grazers such as sea urchins, predatory asteroids and ophiuroids, and lobsters increased, while the populations of algal groups, most fish groups and small mobile invertebrates were depressed. However, the reliability of the ultimate direction of these strings of interactions was moderate to low indicating that more information than the direction of the first order interactions (i.e. predator-prey or algae-grazer) is required to successfully model the impact of white sharks, orca, hapuku and sea lions on reef ecosystems in northern New Zealand. Such additional information may be about the intensity of interactions which could be density or encounter rate dependent as these larger predators range over very large distances revisiting the same area only once or a few times a year (Visser 2000, see http://www.niwa.co.nz/our-science/oceans/research-projects/all/white-sharks) or move inshore seasonally, as was the case for hapuku historically (Maxwell & MacDiarmid 2015, MacDiarmid et al. 2016).

Beaumont et al. (2011) modelled the impact of protecting snapper, lobsters and piscivorous fish (in marine reserves, for example) by simultaneously applying a positive perturbation to the abundance of macro-invertebrate predatory fish, lobster, and piscivorous fish groups. Their model results agreed with field observations in the Cape Rodney-Okakari Point (Leigh) Marine Reserve, where an increase in the abundance and size of lobsters and macro-invertebrate predatory fish has coincided with a gradual decrease in grazing sea urchin density and an increase in macro-algae percentage cover (Shears & Babcock 2003, 2004). But, the modelling undertaken by Beaumont et al. (2011) also found that the effects of increasing the abundance of these reef predators on kina and macroalgae were highly uncertain (i.e., the weighted prediction values were no more then 0.20). It is noteworthy that this apparently uncertain trophic cascade has been the subject of a great deal of research activity over the last 20 years (reviewed in Babcock 2013, Schiel 2013), while a potentially more certain cascade involving reef sharks has been overlooked.

5. PRIORITIES FOR FUTURE RESEARCH

If the role of small and medium sized sharks in New Zealand rocky reef systems is investigated further, three lines of inquiry could yield useful information:

1. Undertake a field sampling programme to examine changes in reef community structure across a gradient of small and medium shark population abundance in northern New Zealand Inclusion of marine reserves will be critical in this sampling design to help overcome the confounding effects of fishing which will tend to depress the abundance of snapper and lobsters. However, sampling in these protected environments will require the use of non-destructive approaches, such as baited underwater video, to establish shark relative abundance. A key metric for inclusion in a sampling programme may be the relative abundance of large predatory invertebrates such as crabs, asteroids, and ophiuroids. The qualitative modelling undertaken in this study suggests that these groups show a clear indirect response to predation by small and medium sized sharks on reef fish, but are not subject to fishing.
2. Gather better data on the diet and trophic status of sharks in reef environments, through stomach content analysis and stable isotope analysis of shark tissue. The dietary preferences of school sharks and bronze whaler sharks provided in Section 2.2 were compiled from a variety of sources, including studies of sharks feeding in pelagic environments. More detailed data on shark diet collected from reef associated sharks would provide more precise evidence of their feeding preferences on reef species, while stable isotope analysis of shark tissue could provide an estimate of the time spent in coastal reef and pelagic environments (Graham et al. 2010, Lorrain et al. 2013). As stable isotope analysis requires small amounts of tissue, it is likely that plugs of shark muscle tissue could be sampled from live animals.
3. Rerun the rocky reef ecosystem qualitative model once further data are available on shark diet and abundance to determine whether the results reported in this study are upheld.

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