

Regional differences in kelp forest interaction chains are influenced by both diffuse and localized stressors

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Abstract. On temperate rocky reefs, overexploitation of high-trophic-level omnivores can result in the decimation of kelp forest habitats by releasing sea urchin population networks from top-down control. However, the local dynamics of the resulting trophic cascades are context-dependent. Here, we investigate the community-wide patterns associated with both diffuse stressors and localized protection of high-trophic-level omnivores in kelp forest ecosystems by comparing communities among marine reserves and fished areas in two contrasting regions in terms of fishing intensity and land-based stressors, Fiordland and the Marlborough Sounds, New Zealand. We find higher densities of the potential sea urchin predators, red rock lobsters (*Jasus edwardsii*) and banded wrasse (*Notolabrus fucicola*), in the Fiordland region, and larger effect sizes of fishing on the exploited fish communities in the Marlborough Sounds. Patterns in sea urchin density were consistent with the idea that high-trophic-level species, such as large fish and rock lobsters, regulate sea urchin population density, with lower densities of *Evechinus chloroticus* observed inside marine reserves, in both regions. Nevertheless, densities of *E. chloroticus* were generally high (>3 m²) in the Marlborough Sounds, likely above a grazing threshold in both fished and reserve sites. The proportion of habitat where sea urchins were absent was 29% in Marlborough Sounds and 90% in Fiordland. Consequently, we observe 49% barren habitat in Fiordland vs. 70%, and a larger effect of fishing on kelp community structure, in the Marlborough Sounds, where fishing effect sizes and land-based stressors were more severe. We propose that a combination of diffuse stressors including regional overexploitation of important sea urchin predators, sedimentation, and warming of coastal waters likely contributed to regional differences in the responses of trophic interaction chains to localized reductions in fishing within marine reserves. The present study highlights how physiologically stressed and modified kelp forest ecosystems are more susceptible to detrimental phase shifts at a regional spatial scale.

Key words: alternate stable states; generalized additive models for location, scale, and shape; kelp forest; marine reserve; multiple stressors; regime shift; trophic cascade.

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INTRODUCTION

Growing evidence demonstrates that declines in biomass and truncation of size distributions of high-trophic-level fish and invertebrates wrought from overexploitation can alter the structure and

function of entire marine ecosystems (Pinnegar et al. 2000, Gascuel 2005, Myers et al. 2007). Removal of target species by fishing can affect the relative abundance of other species in the community by altering predator–prey and competitive interactions (Willis and Anderson 2003,

Langlois and Ballantine 2005). High-trophic-level multichannel omnivores, including large fish and lobsters, feed across multiple organic matter channels and trophic levels in food webs. In some cases, through trophic interaction chains, the removal of these high-trophic-level omnivores can result in a detrimental phase shift of the ecosystem, generally to a less productive state (e.g., Filbee-Dexter and Scheibling 2014). An improved understanding of how fishing pressure induces phase shifts, and the environmental factors that contribute to the likelihood of fishing inducing a trophic cascade, is vital for implementing effective management of marine ecosystems (Pikitch et al. 2004, Marzloff et al. 2016).

Kelp forests are a vital component of the temperate reef ecosystem, providing habitat structure and an important organic matter source to coastal fishes and invertebrates (Steneck et al. 2003, Graham et al. 2007, Udy et al. 2019a, b). The exploitation of top predators in rocky reef habitats can reduce top-down control on the structure of marine communities (Frank et al. 2006, Leleu et al. 2012). For example, on many temperate reefs worldwide, a reduction in algal cover due to an increase in herbivorous sea urchins has been linked to fisheries-induced declines in key sea urchin predators (e.g., Sala et al. 1998, Shears and Babcock 2002, 2003). Nevertheless, these observed multi-trophic-level effects of fishing on interaction chains are decidedly context-dependent (Shears et al. 2008, Salomon et al. 2010). The magnitude of the effects of fishing on trophic interaction chains may be influenced by various abiotic and biotic factors including predator diversity, system productivity, and the amount and distribution of fishing pressure on the community (Finke and Denno 2004, Salomon et al. 2010). In addition to the indirect effects of fishing and broad-scale removal of predatory species, kelp communities are increasingly being affected by a range of diffuse stressors including disease, proliferation of introduced species, nutrient pollution, increasing sea surface temperatures, modified subtidal light environments, and smothering linked to coastal sedimentation (Allison et al. 1998, Sala et al. 1998, Airolidi 2003, Schiel 2013). Understanding how fishing affects kelp communities is critical to maintaining diversity and productivity of temperate reef ecosystems, particularly in the context of the

intensifying array of diffuse anthropogenic stressors.

The presence of kelp has a dominant influence on the composition of reef fish assemblages, with distinct fish communities associated with kelp beds vs. those observed within barren rocky reef habitats (Choat and Ayling 1987, Jones 1988, Anderson and Millar 2004, Pérez-Matus and Shima 2010). Thus, there exists a potential feedback loop where in addition to the presence of kelp beds influencing the composition of fish assemblages, changes in fish community structure may simultaneously modify the structure and composition of kelp communities through their control on the proliferation of grazers.

No-take marine reserves protect whole communities from exploitation within a defined area, making them a useful tool for investigating the ecosystem-level consequences of the localized effects of fishing (Quinn et al. 1993, Tegner and Dayton 2000, Leleu et al. 2012). In New Zealand, the majority of marine reserves are relatively small and are focused on protecting the local dynamics of coastal reef communities (Thrush et al. 2011, Schiel 2013). As many reef-associated fishes and large rock lobsters have limited home ranges, they typically respond well to spatial management (Barrett 1995), as evidenced by widespread increases in abundance and size structure of otherwise exploited species within New Zealand's marine reserves (Willis and Anderson 2003, Pande and Gardner 2012, Jack and Wing 2013, Costello 2014). Marine reserves have been shown to have positive long-term effects on kelp forest community structure in northern New Zealand (Babcock et al. 1999, Shears and Babcock 2002, 2003). However, this relationship has not been as extensively studied in southern New Zealand, primarily because of a scarcity of marine reserves, with the exception of studies in Stewart Island and Fiordland, where there is a network of marine reserves (Schiel 2013, Wing and Jack 2013, Wing et al. 2015).

Evechinus chloroticus is a dominant grazer within kelp forest habitats, being the only shallow water sea urchin on rocky reefs around New Zealand (Lamare et al. 2002). Although sea urchins have a patchy distribution at the mesoscale on the South Island, they can occur at high density under some conditions creating local reproductive sources connecting population networks

along the coast (Perrin et al. 2003, Wing et al. 2003). These high-density aggregations typically result in a sea urchin barren habitat, where habitat-forming kelps have been removed by grazing (Villouta et al. 2001, Wing 2009, Wing and Wing 2015). In southern New Zealand, the primary predators of sea urchins, large blue cod (*Parapericis colias*) and the red rock lobster (*Jasus edwardsii*), are targeted by intensive commercial and recreational fisheries (Dix 1970, Schiel 2013). However, there are other non-exploited predators, such as the banded wrasse (*Notolabrus fucicola*), which can also strongly influence sea urchin densities (Denny and Schiel 2001, Davis and Wing 2012).

The present study investigated the effects of fishing on the trophic structure of kelp forest communities within two important regions in southern New Zealand. The objective was to determine whether the abundance of important predators of sea urchins varied between marine reserve and fished areas, and to examine whether changes in the density of exploited fish species covaried with changes in the non-exploited fish community, sea urchin density, and the structure and composition of the community of large brown algae.

These relationships were investigated in two coastal waterway systems on the South Island, New Zealand: Marlborough Sounds and southern Fiordland. Both regions were characterized by extensive wave-sheltered rocky reef habitats at the entrances of the Sounds, harboring kelp forests with similar reef fish and benthic invertebrate communities (Shears and Babcock 2007, Wing and Jack 2014). Nevertheless, there were considerable regional differences in anthropogenic stressors, with evidence for land-based stressors, influence of invasive species, frequency of warming events, and intensity of fishing pressure each more prevalent in the Marlborough Sounds (Handley 2016). The Marlborough Sounds have long been inhabited by the Māori people, with European settlers arriving in the mid- to late 19th century, clearing large areas of the catchment and exploiting a wide range of marine species (Handley 2016). In comparison, the catchments in Fiordland are covered in undisturbed native forest, as reflected by the Te Wahipounamu UNESCO World Heritage Area

status, and limited access due to the remote location restricts fishing pressure (Wing and Jack 2014). Analyzing the ecosystem effects of fishing in these two regions provided a unique example of the context dependence of trophic interaction chains in temperate reef ecosystems. Here, we rely on counts data from subtidal surveys to resolve evidence of strong interactions in the relationships among: density of sea urchins, kelp, and potential predators on sea urchins.

Comparison of density distributions in ecological studies using counts data is often hampered by a high number of zeros, which violates the basic distribution assumptions of many common statistical models (Martin et al. 2005, Clark et al. 2008). As an alternative, modeling the factors that affect the number of zeros in a stratified survey aids in understanding the likely processes influencing density distributions. Excess true zeros are generally the result of contiguous distribution patterns linked to important ecological processes, such as the presence of sea urchin barren habitat. For the present study, we used a two-part modeling approach that resolved the factors that best explained the probability of a species presence, in addition to the factors that best explained the density of those species when present. This approach provided a robust method for resolving distribution patterns of sea urchin barren habitats and kelp forest habitats with sea urchins absent, across our study systems.

The specific aims of the present study were as follows: (1) to estimate the effect that marine reserve status and presence of kelp forest habitat had on the probability of a fish species being present, and its density when present, for the 22 most common reef fish species in Fiordland and in the Marlborough Sounds; (2) to estimate the effect of marine reserve status and presence of kelp forest habitat, on the structure of the exploited and non-exploited fish communities in Fiordland and in the Marlborough Sounds; (3) to determine whether marine reserve status affects the probability of *E. chloroticus* being present, and the density of *E. chloroticus* when present; and (4) to determine whether marine reserve status affects the probability of barren habitat, the density of holdfasts when kelp is present, or the composition of kelp communities.

METHODS

Study sites

In order to compare the effects of fishing and presence of kelp forest habitat, our study sites were stratified in a factorial design among wave-exposed (generally higher kelp density) and wave-sheltered sites (generally lower kelp density) and within fished and non-fished (marine reserve) areas within each region (Fig. 1).

Diving surveys in the Marlborough Sounds were conducted during January 2017 (eight sites) and February 2018 (four sites) from the RV *Polaris II*. In the Sounds, our twelve sites were distributed around the Kokomohua Marine Reserve, established in 1993. Sites were chosen using data and charts from reports on macroalgae assemblages (Shears and Babcock 2007) to guide our orthogonal distribution of sampling. Within the study, fished sites were also partially managed to reduce fishing effort, with the Sounds being closed to commercial fishing from 1 September till 20 December each year, reduced recreational take limits for blue cod (*P. colias*) within the inner Marlborough Sounds effective year around, and periodic closures of recreational fishing during blue cod spawning season October–December (MPI 2018b). Each of these specific management actions was implemented as a response to regional declines in *P. colias* stocks (Ministry of Primary Industries 2018b).

Diving surveys in Fiordland were conducted during November 2015 (11 sites) and May 2017 (seven sites) from the RV *Polaris II* and RV *Typhoon*. In order to sample wave-exposed and wave-sheltered sites within both fished and unfished areas, study sites in Fiordland were spread throughout the network of marine reserves in the southern Fiordland Marine Area. Site selection in Fiordland was based on kelp density data from previous monitoring reports (Wing and Jack 2014) and information on habitat types from a Fiordland wide habitat classification system (Wing et al. 2007). The Fiordland network of marine reserves was established in 2005, though the Te Awaatu Channel reserve in Doubtful Sound has been established since 1993. The inner waters of Fiordland were closed to commercial fishing as a part of the Fiordland Marine Management Act—2005, and further recreational restrictions were put in place for catch of red

rock lobsters (*J. edwardsii*) and blue cod (*P. colias*) in the inner fjords (Ministry of Primary Industries 2018b). Here, we group sites as fished or reserve based on whether they are located within a no-take marine reserve or elsewhere, as fishing effects were still observed between commercial exclusion zones and no-take marine reserves (Wing and Jack 2013).

Surveys of reef fish, invertebrate, and kelp density

Non-cryptic reef fish species and the red rock lobster (*J. edwardsii*) were enumerated at each site by divers using SCUBA along multiple belt transects (50 m long × 5 m wide × 2.5 m high). *J. edwardsii* were included in the surveys due to their important ecological role as sea urchin predators on rocky reefs. Fifty meter long transects provided a balance between statistical power and spatial resolution of patterns in the sampling design (Samoilys and Carlos 2000). Sampling was depth-stratified with transects centered at 5 and 15 m. In cases where the bottom of the reef was shallower than 15 m, the deep transect was centered just above the bottom of the reef on rocky substratum. Four independent replicate transects were surveyed at each depth for each site. At some sites, only three replicate transects were completed if the dive team had exhausted their air supply. The composition of diver teams identifying and counting fishes was kept constant between sites and regions for the duration of the study.

At each site, and during each year of the surveys, water column structure was recorded before each dive survey using a SeaBird SBE 25 conductivity, temperature, and depth profiler with an attached Wetstar fluorometer used to estimate the concentration of Chl *a* (mg/m³) as a proxy for phytoplankton concentration. The resolution of Chl *a* was restricted to conditions at the time of each survey, so were limited in terms of resolving regional averages of phytoplankton distribution. In order to characterize the density and species composition of the kelp and macro-invertebrate community at each site, 2-m² quadrats were randomly placed along the belt transects described above, to achieve 5–10 quadrats per depth stratum (<5, 10–15 m) per transect. The density of errant invertebrate species, such as gastropods, sea urchins, sea stars, and brittle stars, and the number of holdfasts of each kelp species

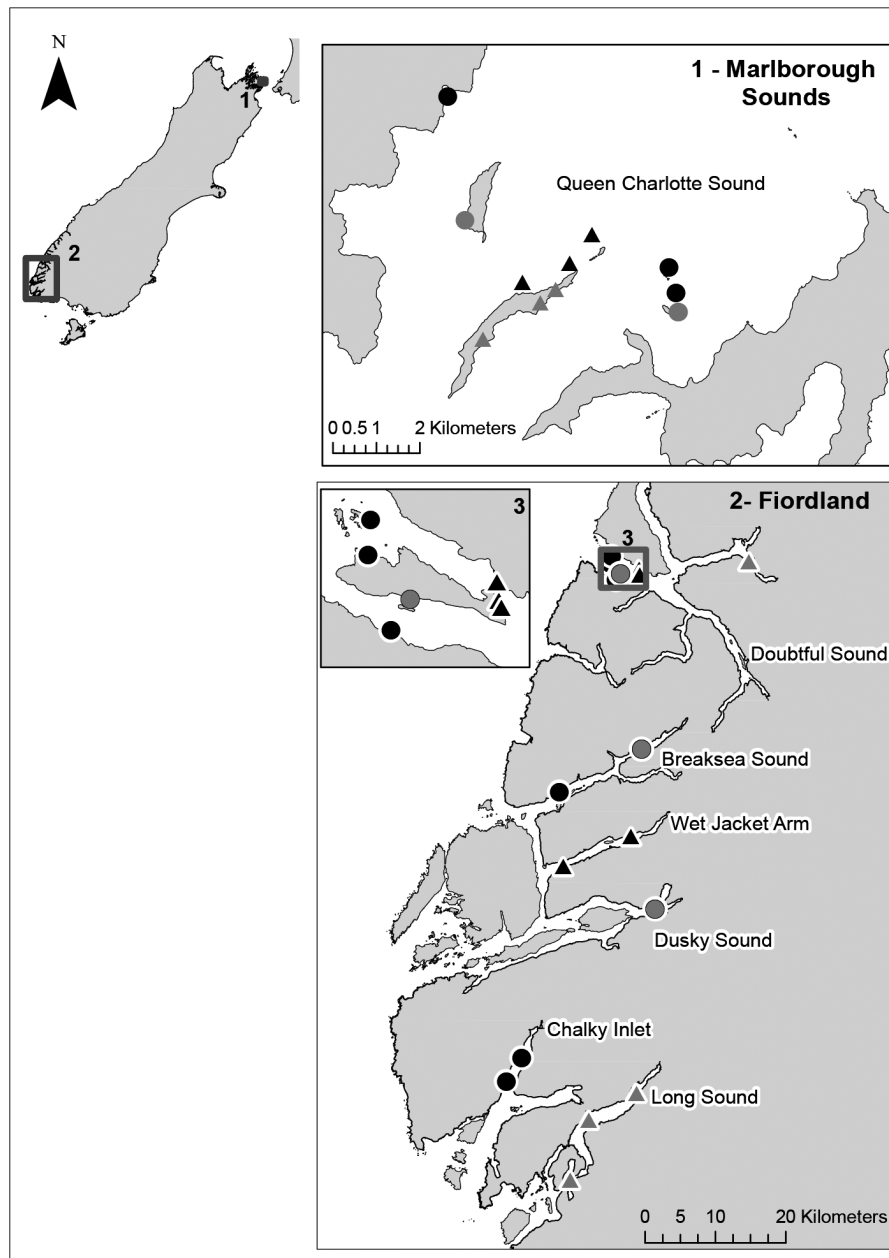


Fig. 1. Map showing the location of survey sites in the Marlborough Sounds and Fiordland Marine Area, New Zealand. Symbols within each region represent sites in marine reserves (triangles) and fished areas (circles). Shading in each figure represents kelp bed sites (black) or barren areas (gray).

were recorded. The native kelp species enumerated during the surveys were *Lessonia variegata*, *Ecklonia radiata*, *Cystophora* spp., *Carpophyllum maschalocarpum*, *Carpophyllum flexuosum*, *Margaritiella urvilliana*, *Sargassum sinclairii*, and *Macrocystis*

pyrifera. The density of the invasive seaweed *Undaria pinnatifida* was also recorded.

We grouped kelp species for our analysis of the coincidence of kelp beds with fish density under the assumption that presence or absence

of large stipitate or canopy-forming kelp, rather than the species identity, would be correlated most strongly with temperate reef fish assemblage structure (Pérez-Matus and Shima 2010). Further, if the average kelp density for a site was >1 holdfast per 2 m^2 , the site was classed as a kelp bed habitat. Alternatively, if kelp density was <1 holdfast per 2 m^2 , the site was classed as barren habitat. This threshold approximated the observed antimode in the observed bimodal distribution of holdfast densities in both regions. Although some sites classed as barren had a few scattered holdfasts, an average kelp density below 1 holdfast per 2 m^2 was likely to have negligible effects on provision of habitat for reef fish compared to a site with no kelp holdfasts (Holbrook et al. 1990).

Statistical analysis

Drivers of reef fish abundance.—Like many data sets comprising discrete counts from ecological studies, our survey data on fish density per transect were zero-inflated and the distribution of counts differed between the different explanatory variables. Hence, the assumptions of normality of data distributions for generalized linear models were not met. To allow for this fact, we fitted generalized additive models for location, scale, and shape (GAMLSS) using the GAMLSS package in R to test for potential drivers of species density (Rigby and Stasinopoulos 2005). Generalized additive models for location, scale, and shape is based on regression-type models and uses maximum likelihood for parameter estimation. However, in contrast to conventional regression models, which only model the location (e.g., mean), GAMLSS allows for the simultaneous modeling of all distribution parameters including the scale (e.g., variance) and the shape (e.g., skewness or kurtosis) in a supervised machine learning framework (Stasinopoulos and Rigby 2007). Unlike conventional generalized linear models which are based on exponential family distributions, GAMLSS allows for distributions that are not in the exponential family. For the present study, models for all species were run using the zero-adjusted inverse Gaussian distribution family.

A key feature of the GAMLSS models is the separation of fish, sea urchin, and kelp counts

into the mean of the nonzeros (μ), the scale parameter (σ), and the probability of zero (v ; Hernandez et al. 2009). The resulting division of the variance structure overcomes the issue of zero inflation and allows the factors associated with each component of species density to be identified. The μ coefficient enabled us to calculate the ratio effect of each factor (e.g., mean of nonzeros [fished]/mean of nonzeros [reserve]), and the v coefficient enabled calculation of the odds ratio of the co-variability of each factor with presence or absence of each species (e.g., sea urchin barren habitat, or kelp bed free of sea urchins). The σ parameter estimates how an independent factor affects the variability in the data (e.g., Is the variation in densities of fish, sea urchins or kelp greater in reserve compared to fished areas?)

Generalized additive models for location, scale, and shape models were used to test how a series of environmental factors within the two different regions covaried with density for the most commonly observed fish species, blue cod (*P. colias*), tarakihi (*Nemadactylus macropterus*), blue moki (*Latridopsis ciliaris*), spotty (*Notolabrus celidotus*), banded wrasse (*N. fucicola*), scarlet wrasse (*Pseudolabrus miles*) butterfly perch (*Caesiooperca lepidoptera*), and, the important sea urchin predator, the red rock lobster (*J. edwardsii*). To determine which factors best statistically explained the mean densities of fish and rock lobsters, we compared different models using the generalized Akaike information criterion (GAIC). The initial models included SITE (random), REGION (two levels, fixed), FISHING (two levels, fixed), KELP (two levels, fixed), average Chl *a* (mg/m^3) concentration (continuous), and average INVERTEBRATE density (continuous). The interaction of REGION with KELP and FISHING was significant for most species, and thus, in order to investigate the effect of FISHING and KELP within each region, we separated data for the two regions and ran models for each independently. Here, we define FISHING as either a site contained in a marine reserve or a site in a region open to fishing. KELP is defined as either a site with a mean frond density of >1 holdfast per 2 m^2 or a site with mean frond density of <1 holdfast per 2 m^2 .

Within each region, removing SITE improved GAIC, indicating that the variation among sites

was small relative to that explained by other environmental factors. The average Chl *a* (mg/m³) concentration and INVERTEBRATE density at each site did not significantly covary with the density of any fish species, and thus, these factors were also removed from the models. While our estimates of Chl *a* concentration were restricted to a limited number of dive survey time periods, the values were within the ranges reported by previous more systematic surveys in the two regions (Ogilvie et al. 2000, Goebel et al. 2005). The final models used to test for explanatory factors for species density included FISHING (two levels, fixed), KELP (two levels, fixed), and their interaction. Further, GAIC testing was used to determine whether FISHING, KELP, or both factors best statistically explained the μ (mean of nonzeros), σ (variability of densities), and v (probability of zero) distributions of each species. These tests were done on each species independently; hence, the effect of FISHING and KELP on the σ and v parameters was only calculated for species where each factor had an effect. Residuals were plotted for each model to check that the assumptions of each model were valid. Where the interaction between FISHING and KELP was significant, we used the model coefficients to calculate the predicted mean densities for each factor level combination of FISHING and KELP to interpret the interaction. Predicted means are the GAMLSS equivalent of least squares means and combine the different parameters (μ , σ , and v) into an overall mean. Bootstrapping was used to obtain 95% confidence intervals for the overall means of each group. Here, significant differences between groups are inferred from the 95% confidence intervals.

Effect of FISHING and KELP on fish community assemblages.—To summarize the direct and indirect effects of fishing on fish community assemblages, the fish species and the red rock lobster were grouped into exploited and non-exploited species. Butterfish (*Odax pullus*), sea perch (*Helicolenus percoides*), red cod (*Pseudophycis bachus*), trumpeter (*Latris lineata*), tarakihi (*N. macropterus*), red moki (*Cheilodactylus spectabilis*), copper moki (*Latridopsis forsteri*), kahawai (*Arripis trutta*), blue cod (*P. colias*), blue moki (*Latridopsis ciliaris*), and leatherjacket (*Meuschenia scaber*) as well as the red rock lobster (*J. edwardsii*) were the only exploited species observed on the transects. All other

species observed were classed as non-exploited (Table 1).

To test for differences in community structure (exploited and non-exploited), resemblance matrices were constructed from square-root-transformed count data using the Bray-Curtis similarity index. Differences in community structure were tested among the factors FISHING and KELP using permutational multivariate analysis of variance (PERMANOVA, Primer-*e* version 6). PERMANOVA tests are robust to deviations from a normal distribution of data by being permutation-based to recreate the underlying distribution in the sample data. Principal coordinates analysis (Primer-*e* version 6) was used to calculate the distance between centroids for each pair of management zones (reserve vs. fished) within each habitat for each region. The centroid distance is a measure of the difference between the mean positions of the communities in multivariate community similarity space, and hence provides a metric for differences in community structure associated with the factor FISHING.

Effect of FISHING on Evechinus chloroticus and kelp density.—Here, we use GAMLSS models, run in R, to test for effects of FISHING (two levels, fixed) and SITE (random, Fiordland: 18 levels, Marlborough: 12 levels) on *E. chloroticus*, *E. radiata*, *Carpophyllum* spp., *U. pinnatifida*, and total kelp holdfast density in Fiordland and the Marlborough Sounds. *Evechinus chloroticus* was the only sea urchin species encountered in our study.

RESULTS

Fiordland had higher fish species richness than the Marlborough Sounds, with 20 fish species observed in Fiordland compared to 13 in the Marlborough Sounds (Table 1). The most common species were present in both regions; however, regional differences occurred in the presence of some of the less common species, as well as the frequency at which species occurred (Table 1).

Effect of FISHING and KELP on fish density

Density of individual species covaried with both FISHING and KELP, with large variation among species in the magnitude and direction of their response to each factor. In contrast, the direction of the effect of FISHING and KELP was

Table 1. Frequency of occurrence of species on transects in Fiordland and the Marlborough Sounds.

Common name	Scientific name	Fiordland (%)	Marlborough Sounds (%)
Spotty	<i>Notolabrus celidotus</i>	71.9	97.4
Blue Cod†	<i>Parapercis colias</i>	64.9	80.5
Scarlet Wrasse	<i>Pseudolabrus miles</i>	75.4	24.7
Butterfly perch	<i>Caesioperca lepidoptera</i>	72.8	11.7
Banded Wrasse	<i>Notolabrus fucicola</i>	44.7	46.8
Tarakihi†	<i>Nemadactylus macropterus</i>	28.1	16.9
Rock Lobster†	<i>Jasus edwardsii</i>	28.94	2.59
Marblefish	<i>Aplodactylus arctidens</i>	26.3	3.9
Blue Moki†	<i>Latridopsis ciliaris</i>	7.0	29.9
Girdled Wrasse	<i>Notolabrus cinctus</i>	27.2	
Sea Perch†	<i>Helicolenus percoides</i>	21.9	
Leatherjacket†	<i>Meuschenia scaber</i>	15.8	5.2
Telescope Fish	<i>Mendosoma lineatum</i>	12.2	
Red Banded Perch	<i>Hypoplectrodes huntii</i>	11.4	
Butterfish†	<i>Odax pullus</i>	5.3	11.7
Splendid Perch	<i>Callanthias allporti</i>	5.3	
Red Lined Perch	<i>Lepidoperca tasmanica</i>	4.4	
Trumpeter	<i>Latris lineata</i>	4.4	
Cm Roughy	<i>Paratrachichthys trailli</i>	3.5	
Yellow-eyed mullet	<i>Aldrichetta forsteri</i>		2.5
Red Cod†	<i>Lotella rhacinus</i>	2.6	
Red Moki†	<i>Cheilodactylus spectabilis</i>		5.2
Copper Moki†	<i>Latridopsis forsteri</i>	1.7	
Kahawai†	<i>Arripis trutta</i>		2.6

Note: Species ordered by frequency of observation across both regions.

†Exploited species.

generally the same within a species between the two different regions, with interspecific regional differences in the effect sizes observed (Tables 2 and 3). Despite individual species effects, there was no overall effect of FISHING or KELP on the total density in either region (Fig. 2d).

Parapercis colias (blue cod) was the only exploited species that was consistently found more frequently and at higher density under reserve protection, with higher probability of being present within reserves in both regions (Marlborough Sounds, $P = 0.048$; Fiordland,

$P = 0.007$). In addition, when present, *P. colias* occurred at 2.03 times greater density within reserves than in fished areas in the Marlborough Sounds ($P = 0.019$; Table 3). There was a dramatically larger total effect size of FISHING on *P. colias* occurrence and density in the Marlborough Sounds than in Fiordland (Fig. 2a). In addition, when *P. colias* was present, there was a significant interaction between FISHING and KELP on species density for the Marlborough Sounds ($P = 0.02$; Table 3), with the largest fishing effect observed in barren habitats (Fig. 2a).

Table 2. Key for interpretation of effect sizes from generalized additive models for location, scale, and shape models, for μ , σ , and v parameters.

Parameter	Pa fishing	Kelp
μ	Higher density in fished <1> Higher density in reserve	Higher density in kelp <1> Higher density in barren
σ	Higher variance in fished <1> Higher variance in reserve	Higher variance in kelp <1> Higher variance in barren
v	Higher prop (0) in fished <1> Higher prop (0) in reserve	Higher prop (0) in kelp <1> Higher prop (0) in barren

Table 3. Results from generalized additive models for location, scale, and shape models for each species, for the effect size of FISHING, KELP, and FISHING × KELP interaction on μ (mean density when species is present), σ (amount of variation in fish density), and v parameters (probability of a species being present).

Species	Variable	FISHING Effect size (95% CI)	KELP Effect size (95% CI)	F × K Effect size
Fiordland				
<i>Parapercis colias</i> (blue cod)	μ	0.86 (0.52, 1.41)	0.65 (0.35, 1.20)	2.32.
	σ	...	1.22 (1.22, 1.22)	...
	v	0.33 (0.11, 0.98)**	0.11 (0.03, 0.33)	...
<i>Nemadactylus macropterus</i> (tarakihi)	μ	3.62 (2.01, 6.51)***	1.26 (0.75, 2.12)	0.31*
	σ	1.30 (1.30, 1.30)
	v	0.27 (0.09, 0.77)*	0.63 (0.17, 2.35)	9.98*
<i>Latridopsis ciliaris</i> (blue moki)	μ	0.53 (0.29, 0.98)*	0.40 (0.18, 0.87)*	0.12
	σ	0.93 (0.93, 0.93)
	v	...	4.42 (0.24, 81.1)	...
<i>Jasus edwardsii</i> (rock lobster)	μ	1.50 (0.72, 3.13)	0.70 (0.19, 2.65)	1.44
	σ	0.80 (0.45, 1.41)	1.14 (0.40, 3.24)	0.07***
	v	1.86 (0.69, 4.97)	5.71 (1.14, 28.7)*	0.20
<i>Notolabrus celidotus</i> (spotty)	μ	5.70 (2.16, 15.1)***	1.85 (0.68, 5.06)	0.58
	σ	0.76 (0.76, 0.76)
	v	0.10 (0.03, 0.34)***	0.10 (0.02, 0.50)**	26.67**
<i>Notolabrus fucicola</i> (banded wrasse)	μ	0.59 (0.31, 1.14)	0.47 (0.23, 0.97)*	1.05
	σ	1.49 (1.49, 1.49).
	v	3.00 (1.11, 8.14)*	1.06 (0.29, 3.79)**	2.95
<i>Pseudolabrus miles</i> (scarlet wrasse)	μ	0.75 (0.40, 1.39)	0.78 (0.26, 2.30)	0.27.
	σ	...	1.47 (1.47, 1.47)*	...
	v	$1.1 \times 10^4 (3.9 \times 10^{-100}, 2.9 \times 10^{109})$	$2.1 \times 10^5 (7.6 \times 10^{-100}, 5.6 \times 10^{109})$	5.8×10^{-5}
<i>Caesioperca lepidoptera</i> (butterfly perch)	μ	1.44 (0.50, 4.12)	0.97 (0.15, 6.52)	0.18
	σ	...	2.06 (2.06, 2.06)***	...
	v	5.67 (1.13, 28.5)*	...	11.40.
Marlborough Sounds				
<i>Parapercis colias</i> (blue cod)	μ	2.03 (1.14, 3.61)*	1.72 (0.97, 3.06).	2.49*
	σ	1.02 (1.02, 1.02)	1.10 (1.10, 1.10)	0.27*
	v	0.21 (0.05, 0.96)*	0.21 (0.05, 0.96)*	1.2×10^{-4}
<i>Nemadactylus macropterus</i> (tarakihi)	μ	0.05 (0.01, 0.22)***	0.03 (0.01, 0.10)***	75.66***
	σ	1.70 (1.70, 1.70)
	v	2.69 (0.75, 9.65)
<i>Latridopsis ciliaris</i> (blue moki)	μ	1.05 (0.66, 1.66)	1.73 (0.85, 3.53)	0.86
	σ	...	1.64 (1.64, 1.64)	...
	v	...	2.53 (0.92, 6.96)	...
<i>Jasus edwardsii</i> (rock lobster)	μ
	σ
	v
<i>Notolabrus celidotus</i> (spotty)	μ	1.21 (0.48, 3.03)	3.34 (1.44, 7.70)**	0.90
	σ	-	0.47 (0.47, 0.47)***	...
	v	$3.3 \times 10^{-5} (1.4 \times 10^{-105}, 7.5 \times 10^{95})$
<i>Notolabrus fucicola</i> (banded wrasse)	μ	0.99 (0.50, 1.98)	0.58 (0.27, 1.26)	1.18
	σ	0.92 (0.92, 0.92)
	v	-	8.18 (2.94, 22.76)***	...
<i>Pseudolabrus miles</i> (scarlet wrasse)	μ	1.18 (0.52, 2.67)	1.06 (0.61, 1.84)	0.10
	σ	1.41 (0.64, 3.08)
	v	4.17 (1.01, 17.31).	3.11 (0.79, 12.14)	17089.1
<i>Caesioperca lepidoptera</i> (butterfly perch)	μ	0.12 (0.03, 0.43)**	0.86 (0.03, 24.0)	0.49
	σ	$2.2 \times 10^{-16} (2.2 \times 10^{-16}, 2.2 \times 10^{-16})$ ***
	v	10.12 (1.10, 93.1)*	10.12 (1.10, 93.1)*	2867.2

Notes: Ellipses indicate that factor was not included in model. No models would run for *J. edwardsii* in Marlborough due to lack of observations.

* $P < 0.1$, ** $P < 0.05$, *** $P < 0.01$, **** $P < 0.001$.

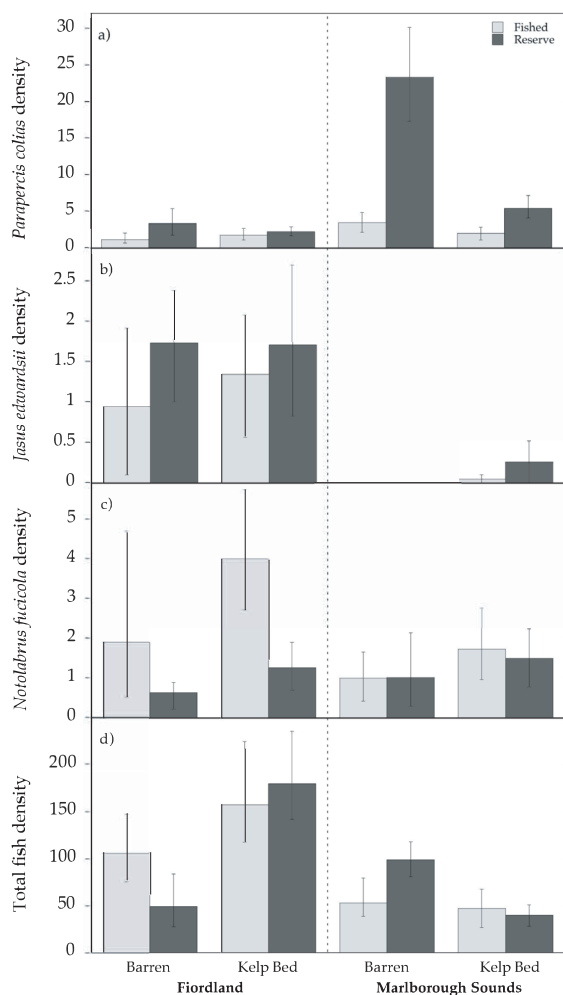


Fig. 2. Overall mean density (250 m^{-2}) of (a) *Paraperis colias*, (b) *Jasus edwardsii*, (c) *Notolabrus fucicola*, and (d) all fish species combined, for the fished (light gray) and reserve (dark gray) transects within kelp bed and barren habitat. Error bars indicate 95% confidence intervals. Predict means are calculated from generalized additive models for location, scale, and shape models, and 95% confidence intervals are from bootstrapping to combine effect parameters.

In Fiordland, *N. fucicola* (banded wrasse) were observed most frequently in fished areas ($P = 0.033$; Table 3). In the Marlborough Sounds, *P. miles* (scarlet wrasse) tended to be present most frequently in fished areas ($P = 0.053$; Table 3). *Caesioperca lepidoptera* (butterfly perch) were less frequently observed in marine reserves in Fiordland ($P = 0.037$) and in the Marlborough Sounds

($P = 0.041$), and less abundant when present in the Marlborough Sounds ($P = 0.002$; Table 3).

In cases where positive effect sizes were observed for the factor KELP, most fish species were more likely to be present, or present in higher densities in kelp bed habitats (Table 3). *P. colias* and *N. celidotus* (spotty) were the exception, with higher densities when present in barren areas in the Marlborough Sounds (Table 3). *Notolabrus celidotus* were also more likely to be present in barren habitat in Fiordland ($P = 0.006$; Table 3).

The effect of fishing on *P. colias* density when present was greater in barren areas (Fiordland, $P = 0.067$; Marlborough Sounds, $P = 0.022$; Fig. 2a). The presence of kelp also altered the effect of FISHING on density when present for *N. macropterus* (Tarakihi; both regions) and *P. miles* (Fiordland; Table 2). In Fiordland, there was a significant KELP \times FISHING interaction for the probability of *N. macropterus*, *N. celidotus*, and *C. lepidoptera* being present (Table 2).

Differences in fish community structure

For both regions, FISHING was significantly correlated with both the exploited, (Fiordland $F_{1, 110} = 2.71$, $P = 0.033$; Marlborough Sounds $F_{1,73} = 8.29$, $P < 0.001$) and non-exploited, fish community structure (Fiordland $F_{1, 110} = 15.21$, $P < 0.001$; Marlborough Sounds $F_{1,73} = 3.85$, $P = 0.007$). The non-exploited fish community structure was significantly correlated with KELP in both regions (Fiordland $F_{1, 110} = 14.60$, $P < 0.001$; Marlborough Sounds $F_{1,73} = 12.55$, $P < 0.001$); however, KELP was only significantly correlated with the exploited fish community in the Marlborough Sounds ($F_{1,73} = 7.94$, $P < 0.001$). There was a significant interaction between FISHING \times KELP for the non-exploited fish community in Fiordland ($F_{1, 110} = 4.11$, $P = 0.003$), with a larger FISHING effect in barren areas (Fig. 3b). For the exploited fish community, there was significant FISHING \times KELP interaction in both regions, but the direction of the interaction varied. In Fiordland, there was a greater effect of FISHING in the kelp bed habitat, whereas in the Marlborough Sounds, there was a larger FISHING effect within the barren habitats (Fig. 3a).

In both barren and kelp bed habitats, the factor FISHING best explained differences in exploited fish community structure in the Marlborough

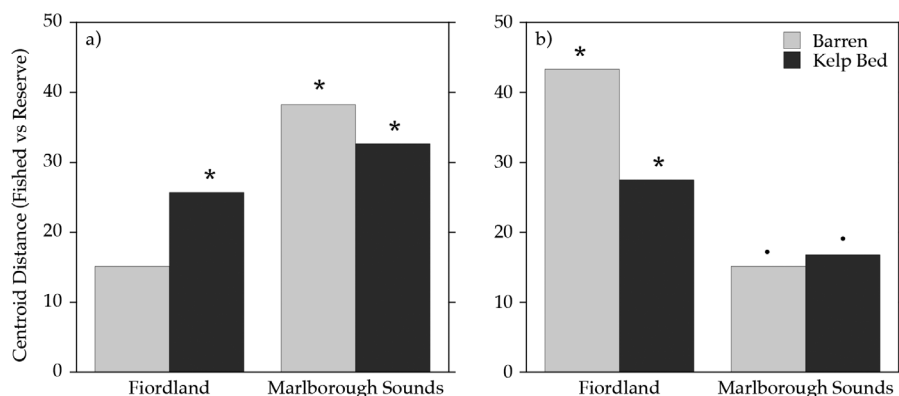


Fig. 3. Fish community dissimilarity between fished and reserve sites as indicated by multivariate centroid distances calculated using Bray-Curtis index based on square root of relative abundance for the (a) exploited fish community and (b) the non-exploited fish community. Significant community differences ($P < 0.05$) are indicated by asterisks as determined by PERMANOVA.

Sounds compared to those differences observed for the exploited fish community in Fiordland (Fig. 3a). Contrastingly, the best statistical explanation for differences in non-exploited fish community structure was given by the factor FISHING in Fiordland (Fig. 3b).

FISHING effect on *E. chloroticus* and kelp density

Evechinus chloroticus density, when present, was significantly lower in marine reserves in Fiordland ($t = 3.95$, $P < 0.001$) and in the Marlborough Sounds ($t = 1.996$, $P = 0.047$). In addition, there

was higher variability in *E. chloroticus* densities in fished areas in Fiordland ($t = 4.1$, $P < 0.001$) and a lower probability of *E. chloroticus* being present in reserves in the Marlborough Sounds ($t = 1.945$, $P = 0.054$; Fig. 4).

The factor FISHING was not associated with differences in mean kelp holdfast density or overall kelp community structure in Fiordland (Fig. 5). However, when present, *Carpophyllum* spp. occurred at higher densities in fished areas in Fiordland (Table 4). In the Marlborough Sounds, the kelp community differed between fished and reserve sites ($P = 0.038$; Fig. 6), with a higher total

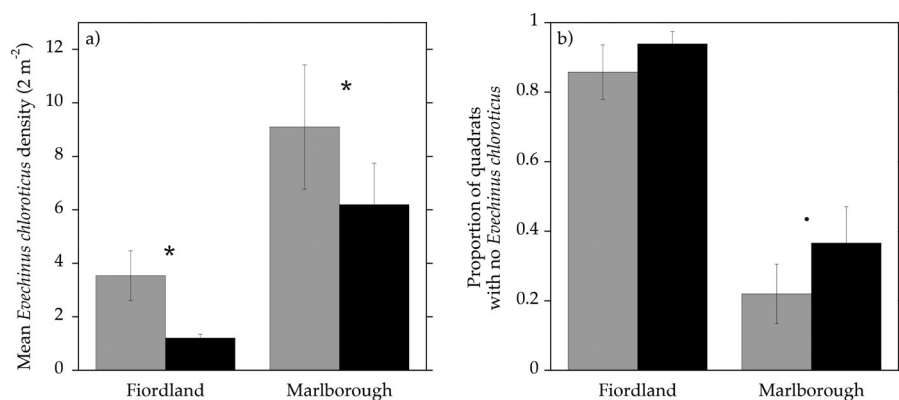


Fig. 4. (a) Mean density of *Evechinus chloroticus* for the quadrats where *E. chloroticus* are present \pm SE and (b) the proportion of quadrats where *E. chloroticus* are absent, for fished (gray bars) and reserve (black bars) areas. Significance ($P < 0.05$) is indicated by asterisks as determined from generalized additive models for location, scale, and shape model.

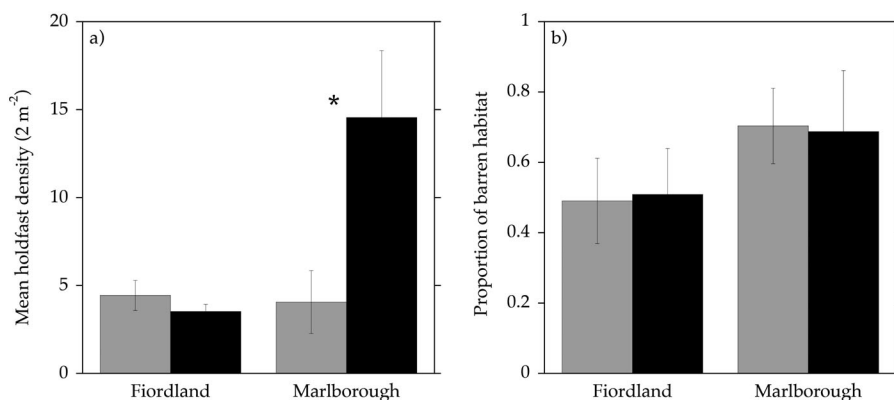


Fig. 5. (a) Mean density of holdfasts for the quadrats where kelp is present \pm SE and (b) the proportion of barren quadrats, for fished (gray bars) and reserve (black bars) areas. Significance ($P < 0.05$) is indicated by asterisks as determined from generalized additive models for location, scale, and shape model.

Table 4. Results from generalized additive models for location, scale, and shape models for each kelp species, for the effect size (95% CI) of FISHING on μ (mean density when species is present), σ (amount of variation in holdfast density), and ν parameters (probability of a species being present).

Species	μ	σ	ν
Fiordland			
<i>Ecklonia radiata</i>	0.94 (0.75, 1.17)	1.23 (0.97, 1.56)	1.66 (0.89, 3.09)
<i>Carpophyllum</i> spp.	0.65 (0.44, 0.95)*	0.36 (0.15, 0.87)*	2.94 (0.68, 12.6)
<i>Undaria pinnatifida</i>
Marlborough Sounds			
<i>Ecklonia radiata</i>	3.78 (2.27, 6.32)***	0.74 (0.43, 1.26)	0.53 (0.18, 1.56)
<i>Carpophyllum</i> spp.	3.63 (2.16, 6.08)***	0.81 (0.47, 1.40)	0.36 (0.13, 0.95)*
<i>Undaria pinnatifida</i>	1.22 (0.98, 1.53)	0.23 (0.11, 0.50)***	2.43 (0.76, 7.70)

Note: Ellipses indicate species not present.
 $P < 0.1$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

holdfast density, when kelp was present, in reserves ($t = 7.454$, $P < 0.001$). There was also a greater variability in kelp holdfast density in fished areas ($t = -2.717$, $P = 0.0074$). The density of *E. radiata* and *Carpophyllum* spp. was best explained by FISHING; however, there was also a slight statistical effect of FISHING on *U. pinnatifida* density in the Marlborough Sounds (Table 4).

DISCUSSION

The results of the present study demonstrate that selective removal of a few high-trophic-level multichannel omnivorous species can indirectly alter the structure of temperate reef ecosystems. We found higher densities of potential sea urchin predators, the red rock lobster (*J. edwardsii*) and

banded wrasse (*N. fucicola*) in the Fiordland region, where total fish density and diversity, particularly in kelp forests, were also highest. In both the Marlborough Sounds and Fiordland, a higher density of *P. colias* (blue cod), another potential sea urchin predator when large, inside marine reserves appeared to have altered predator-prey and competitive interactions within the kelp forest communities. Yet, we found distinct regional variability in the signatures of important trophic interaction chains within kelp forest communities, linking declines in the density of sea urchin predators, abundance of sea urchins, and prevalence of barren habitats to regional-scale effects of fishing and other diffuse stressors on kelp forest ecosystem structure.

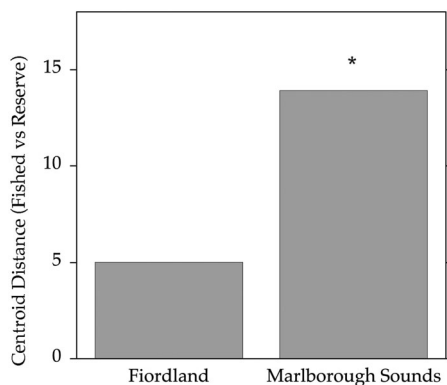


Fig. 6. Macroalgae community dissimilarity between fished and reserve sites as indicated by multivariate centroid distances calculated using Bray-Curtis index based on square root of relative abundance for the macroalgae community. Significant community differences ($P < 0.05$) are indicated by asterisks as determined by PERMANOVA.

In both regions, fishing likely influenced the composition and structure of the exploited reef fish community. Here, *P. colias* exhibited the largest differences in density between reserve and fished sites, consistent with observations of their responses to fishing closure in other reserves across New Zealand (Willis and Anderson 2003, Pande and Gardner 2012). *Parapercis colias* are the primary target species of recreational fishers in southern New Zealand, as well as being part of a large commercial fishery (MPI 2018a). Size distributions of *P. colias* were severely truncated, consistent with higher fishing pressure, in the Marlborough Sounds compared to those in Fiordland (S. Kolodzey, unpublished data). Here, maintenance of old-growth size distributions of important sea urchin predators such as rock lobsters and large fish can be as important to ecosystem function as density (Jack and Wing 2010, 2011, 2013). The observed patterns among reserve and fished regions in the present study corroborate similar investigations that concluded the most heavily exploited species are the most likely to respond to reserve protection (Nardi et al. 2004, Edgar and Barrett 2012). The resident nature and relatively limited adult movement patterns of *P. colias* likely contributed to their positive responses to reserve protection (Cole et al. 2000).

Variable responses to marine reserve protection observed for the other exploited species may be a reflection of lower fishing pressure, a result of the home ranges of these species having been greater than the spatial area protected by isolated marine reserves (Dugan and Davis 1993), or alternatively the influence of environmental conditions on reserve efficacy (Edgar et al. 2017). The effect sizes of marine reserve protection on both incidence and abundance of the whole exploited community, particularly *L. ciliaris* (blue moki) and *P. colias* (blue cod), were much larger in the Marlborough Sounds than in Fiordland (Figs. 2a, 3a, Table 3). Each of these patterns likely reflected large-scale differences in fishing pressure between the two regions (Cote et al. 2001). Due to more accessible rocky reef habitats and proximity to a much larger human population, rocky reef habitats in the Marlborough Sounds were likely subject to higher recreational fishing pressure than those in the Fiordland region. Alternatively, underlying regional differences in population productivity or habitat complexity may have affected the magnitude of the communities' responses to fishing (Pace et al. 1999, Aburto-Oropeza et al. 2011).

In association with the observed impacts of fishing on the exploited community, we found evidence that marine reserve protection was associated with differences in the structure of the non-exploited fish community. For example, *C. lepidoptera* (butterfly perch), a common prey species of large fish, were less likely to be present in reserves in both regions and were less abundant when present in reserves in the Marlborough Sounds. Decreased density of *C. lepidoptera* was likely associated with increased predation pressure by large fishes inside reserves (Wing and Jack 2013). In addition to altering predation pressure, it was possible that fishing may have affected interspecific competition for food and space within the reef fish community (Denny et al. 2003). For example, the wrasses *N. fucicola* and *P. miles* occupy similar trophic levels to several species in the exploited reef fish group including *P. colias* (Denny and Schiel 2001, Russell 2010) and were observed less frequently inside marine reserves, particularly where *P. colias* were present in higher densities.

Benthic surveys revealed that density of the sea urchin *E. chloroticus*, when present, was

lower inside marine reserves than in fished areas for both regions. The observed lower densities of sea urchins in marine reserves were coincident with high densities of the important sea urchin predator *P. colias* within marine reserves. In addition, in the Marlborough Sounds, *E. chloroticus* were more likely to be present in heavily fished areas. These results are consistent with the idea that across our study sites, overexploitation of important sea urchin predators has led to regional increases in the abundance of sea urchins, whose populations can be locally regulated by predation from high-trophic-level omnivores such as large fish and rock lobsters in kelp forest ecosystems (Sala and Zabala 1996, Shears and Babcock 2002).

Although *E. chloroticus* density varied with marine reserve protection in both regions, variation in kelp holdfast density was only explained by reserve protection in the Marlborough Sounds. Ayling (1981) demonstrated that high sea urchin densities approaching six individuals per m² can result in rapid formation of barren ground habitats. In the Marlborough Sounds, the mean sea urchin densities both inside and outside marine reserves approached this threshold; hence, small reductions in predation pressure on sea urchins would be likely to initiate a trophic cascade resulting in declines in kelp forest habitats. It is important to note here that sea urchin populations form networks that cover large spatial scales along the coast (>100 km) and high levels of sea urchin recruitment within marine reserve habitats are likely sourced from heavily fished areas with abundant sea urchins within each region (Wing 2011). *Evechinus chloroticus* were recorded at densities greater than six individuals per m² in some quadrats at two fished sites in Fiordland; however, the mean regional abundance was significantly lower than this important threshold density. In addition, *E. chloroticus* were present in approximately 70% of quadrats in the Marlborough Sounds compared to approximately 10% in Fiordland. Hence, although sea urchins may be present in high enough densities in some localized areas to affect kelp abundance in Fiordland, they do not appear to be common enough to have an overall regional effect on the kelp forest community. In contrast, in the Marlborough Sounds, the high regional abundance of sea urchins appears to

have resulted in large regional patterns in prevalence of sea urchins and barren habitats (Figs. 4b, 5b).

Sea urchins are generally less abundant in southern New Zealand than in the north (Schiel 2013), with southern *E. chloroticus* populations at wave-exposed sites typically comprised of adults larger than 100 mm (Shears and Babcock 2007). The lack of abundant juvenile sea urchins in populations with high larval settlement is consistent with high post-settlement mortality from predation (Quinn et al. 1993, Wing et al. 1998). Consequentially, in Fiordland, where sea urchin larval retention and high sea urchin settlement are observed in the inner fjords (Wing et al. 2003, Wing 2009), we observed, in the present study, relatively high densities of important sea urchin predators such as *J. edwardsii* (rock lobster) and *N. fucicola* (banded wrasse). These predators are more likely to be present and occur in greater densities in kelp forest habitats. The patterns observed here highlight the potential for a trophic feedback loop or interaction chain, where in healthy kelp ecosystems higher diversity of multichannel omnivores, which are important sea urchin predators, helps maintain density and composition of habitat-forming kelp species (Filbee-Dexter and Scheibling 2014).

In agreement with previous studies (Choat and Ayling 1987, Holbrook et al. 1990, Levin and Hay 1996), we found that the assemblage structure of fish communities was correlated with the presence of high-density kelp bed habitats. Kelp beds provide refuge from predators and are often associated with increased food availability (Steneck et al. 2003, Graham et al. 2007, Pérez-Matus and Shima 2010); hence, macroalgae-dominated reefs often support more abundant small forage fishes (Choat and Ayling 1987). As differences in species composition, density, or height of kelp beds influence fish aggregations (Holbrook et al. 1990, Carr 1991, Levin and Hay 1996), the observed intraspecific variability in responses to presence of kelp bed habitat between regions further supports a regional difference in the kelp community observed in the present study. For example, despite orthogonal sampling across fished and unfished sites, we found a higher proportion of barren quadrats in the Marlborough Sounds, with higher variability in kelp holdfast density when present.

Regional variability in kelp communities may have been due to natural variation in environmental conditions between the two regions; however, evidence suggests that there have been substantial losses of kelp forests in the Marlborough Sounds in recent years (Hay 1990, Handley 2016). Suggested mechanisms for the decline in macroalgae in the Sounds include warming of the ambient sea surface temperature and increase in the frequency of marine heat wave events (Hay 1990), and increases in the amount of fine sediment released into the Sounds as a result of land clearing (Handley 2016). If kelp density and depth distributions have already been reduced by other stressors, and the remaining kelps are physiologically stressed, increases in sea urchin abundance would be more likely to initiate a trophic cascade (Foster and Schiel 2010). In healthy kelp forests with high algae abundance, sea urchins subsist primarily on drift algae, but when algae abundances are low, sea urchins switch to active grazing on attached kelp (e.g., Dean et al. 1984, Harrold and Reed 1985). Hence, the observed evidence for trophic cascades in the Marlborough Sounds may have been the result of synergistic effects of multiple stressors acting at a regional spatial scale.

Although we observed a strong correlation between higher sea urchin abundance and lower kelp abundance in fished compared with the marine reserve areas in the Marlborough Sounds (Figs. 4a, 5a) and a higher proportion of barren habitat in the Marlborough Sounds region overall (Fig. 5b), within the Sounds marine reserve protection did not correspond with a higher proportion of barren habitat (probability of zero kelp) outside of marine reserves. In the Marlborough Sounds, kelp beds had a high proportion of *C. flexuosum*. *C. flexuosum* is less palatable than *E. radiata* to *E. chloroticus* (Cole 2001), so its density was less likely to have been reduced by an increase in *E. chloroticus* abundance. Here, we observe larger differences in kelp community structure between fished areas and marine reserves in the Marlborough Sounds than in Fiordland, with larger effect sizes for both abundance and incidence of the palatable species *E. radiata* than the less palatable kelp *C. flexuosum* (Fig. 6, Table 4). Further, in the Marlborough Sounds, density of *U. pinnatifida* was the stipitate kelp species least

linked to differences in marine reserve protection. In contrast, we observe the largest positive effect size of marine reserve protection on incidence of *U. pinnatifida* of the three kelp species considered (Table 4). As an invasive kelp, with distinctive early-season sporophyte production, an increase in space occupied by *U. pinnatifida* has been associated with declines in abundance and productivity of the native kelp forest communities (Jiménez et al. 2015, South et al. 2017). These results highlight the potential for increases in *E. chloroticus* density above specific threshold levels to alter both the composition and productivity of kelp forest ecosystems, creating rapid shifts to an alternate state of the system. The observed patterns are consistent with the idea that herbivory is just one of a suite of interacting factors that affect the distribution, density, and species composition of kelp forests (Graham et al. 2007). For example, the observed high densities of *Carpophyllum* spp. holdfasts in fished areas in Fiordland highlight how natural variation in wave exposure and light availability influence kelp community structure (Wing et al. 2007).

The exploited reef fish and the red rock lobster populations considered in the present study have been extensively targeted by line or pot fishing. Therefore, within our study regions, biogenic habitat structure has not been subject to direct disturbances due to fishing. Here, the use of an orthogonal design for sampling between wave-exposed and wave-sheltered locations was used to account for the effects of the primary abiotic factors influencing kelp abundance in these regions (Shears and Babcock 2007, Wing et al. 2007). Additionally, a survey of the benthic habitat in Queen Charlotte Sound revealed that the kelp forest communities were comparable between reserve and control sites before marine reserve establishment (Grange 1993). Hence, we concluded that the large differences in holdfast density and kelp diversity observed between marine reserve and fished sites in the Marlborough Sounds were likely a response of the trophic interaction chain to the removal of fishing pressure since the establishment of the marine reserves. Nevertheless, we are unable to conclude whether the higher density of kelp holdfasts within the marine reserves represented a recovery or a halt of kelp forest degradation.

Regardless, the results give further support to the conclusion that marine reserves can be an effective tool for protecting localized ecosystem function and trophic structure in kelp forest systems, but in isolation are not sufficient to manage regional patterns of degradation. Our data support the idea that networks of marine reserves are necessary to account for the spatial scales over which population dynamics of key species operate in kelp forest systems, in order to match the scale of fishing pressure with effects on regional population dynamics (Quinn et al. 1993, Wing 2011, Jack and Wing 2013).

The results of the present study demonstrate that the effects of localized removal of fishing pressure on kelp forest interaction chains likely vary as a result of diffuse stressors that predispose kelp forests to habitat degradation. We propose that a combination of differences in sea urchin predator diversity and size distributions and diffuse environmental stressors on kelp physiology are likely to have contributed to the regional difference in effect sizes to marine reserve protection we observe within kelp forest trophic interaction chains. The observed higher densities of kelp within marine reserves in the Marlborough Sounds and high prevalence of kelp forest habitats in the Fiordland marine reserve network demonstrate that marine reserves can be an effective management option for locally maintaining healthy kelp forests subject to multiple stressors. Nevertheless, our results indicate that under intensified diffuse stressors, such as sedimentation and heat stress, even kelp forest communities within marine reserves can be vulnerable to the regional effects of fishing, associated with large-scale release of sea urchin population networks from regulation by predators. These results corroborate previous studies that highlight how networks of marine reserves can build resilience under an array of diffuse environmental stressors including nutrient pollution, sedimentation, and warming events within kelp forest ecosystems (Lubchenco et al. 2003, Filbee-Dexter and Scheibling 2014, Marzloff et al. 2016). The presence of kelp bed habitats coincided with the presence and density of the majority of fish species observed in the present study. Here, the presence of kelp forest habitats was associated with a more diverse and trophically complex fish community structure, highlighting how maintenance of a healthy kelp forest community is

essential to maintain community structure and ecosystem functioning in our coastal seas. Regional differences in the consequences of fishing pressure, observed in the present study, highlight the need for targeted management policies that consider the vulnerability of individual kelp forest communities in the context of multiple diffuse environmental stressors.

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