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Original Article

Trade-offs between invertebrate fisheries catches and ecosystem impacts in coastal New Zealand

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Invertebrate catches are increasing globally following the depletion of many finfish stocks, yet stock assessments and management plans for invertebrates are limited, as is an understanding of the ecosystem effects of these fisheries. Using an ecosystem modelling approach, we explored the trade-offs between invertebrate catches and their impacts on the associated ecosystem on the south coast of Wellington, New Zealand. We simulated exploitation of lobster (*Jasus edwardsii*), abalone (*Haliotis australis*, *H. iris*), and sea urchin (*Evechinus chloroticus*) over a range of depletion levels—from no depletion to local extinction—to estimate changes in target catches and associated effects on other species groups, trophic levels, and benthic and pelagic components. Exploitation of lobster showed the strongest ecosystem effects, followed by abalone and urchin. In all three fisheries, the current exploitation rate exceeds that which produces maximum sustainable yield, with considerable ecosystem effects. Interestingly, a reduced exploitation rate is predicted to increase target catches (and catch-per-unit-effort), thereby strongly reducing ecosystem effects, a win–win situation. Our results suggest that invertebrate exploitation clearly influences ecosystem structure and function, yet the direction and magnitude of responses depend on the target group and exploitation rate. An ecosystem-based fisheries management approach that includes the role of invertebrates would improve the conservation and management of invertebrate resources and marine ecosystems on broader scales.

Keywords: ecological indicators, Ecopath with Ecosim, ecosystem effects, ecosystem-based fisheries management, fisheries exploitation, low-trophic level fishery.

Introduction

Over the past 60 years, invertebrate fisheries have expanded substantially around the world, with global catches having increased sixfold, the number of target species doubled, and 50% more countries actively fishing invertebrates (Berkes *et al.*, 2006; Anderson *et al.*, 2011a, b). This includes an expansion of existing fisheries for bivalves (mussels and oysters) and crustaceans (lobster, shrimp, and crabs), as well as the emergence of new fisheries for cephalopods (squids and octopus) and echinoderms (sea urchins and sea cucumbers). Many of these species fetch high market prices and demand is increasing, yet for many populations there are no formal stock assessments or management plans in place and the broader effects of invertebrate exploitation on other species and the ecosystem as a whole are largely unknown (Perry *et al.*, 1999; Anderson *et al.*, 2011a). Additionally, traditional fisheries stock assessment methods developed for finfish species may not be appropriate for invertebrates due to differential life histories and ecology (Perry *et al.*, 1999).

Many invertebrate species fulfil important roles in the ecosystem that contribute to overall foodweb structure, functioning and resilience, and almost all invertebrates are prey for higher trophic level (TL) species (Anderson *et al.*, 2011a; Coll *et al.*, 2013). The direct or indirect (e.g. bycatch or seabed trawling) harvesting of these lower TL species removes a proportion of prey biomass with potential direct effects on higher TLs (Smith *et al.*, 2011). This can affect the productivity and recovery of species higher in the foodweb

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(Cury *et al.*, 2011; Smith *et al.*, 2011; Garcia *et al.*, 2012). High levels of exploitation can also affect ecosystem complexity, stability, and resilience (Coll *et al.*, 2008; Lotze *et al.*, 2011).

Understanding the impacts of fisheries on the population dynamics of targeted species has long been a goal of fisheries science and management (e.g. Walters and Martell, 2004). More recently, increasing attention is being paid to fisheries impacts on non-targeted species and the structure and functioning of the ecosystem, either through bycatch, habitat alteration, or foodweb linkages (Pikitch *et al.*, 2004). This approach, known as ecosystem-based fisheries management (EBFM), has been broadly adopted as a fisheries management policy (Pikitch *et al.*, 2004; Jennings *et al.*, 2014); however, its implementation has been difficult and slow, and a global evaluation indicated that no country received a "good" implementation score (Pitcher *et al.*, 2009). The aim of EBFM is to sustain healthy ecosystems and the fisheries that they support (Pikitch *et al.*, 2004). It is possible that a species can be managed sustainably from a single-species perspective, while concurrently being considered overfished from an EBFM perspective, or contributing to the decline of other species (Murawski, 2000; Pikitch *et al.*, 2004; Walters *et al.*, 2005).

Ecosystem modelling is one tool that can be used to evaluate the ecosystem effects of exploitation, and has been used to understand the trade-offs between the level of exploitation of individual and multiple species and the magnitude of resulting ecosystem effects (Walters *et al.*, 2005; Worm *et al.*, 2009; Collie *et al.*, in press), the ecosystem effects of fisheries for forage fish (Smith *et al.*, 2011), and balanced harvesting (Garcia *et al.*, 2012). Yet to date, little effort has been made to model the exploitation of invertebrate species (but see Coll *et al.*, 2013 for an example on squids) to understand their ecosystem effects. This is in part because of the paucity of information on invertebrate populations and ecology, with few fisheries carrying out assessments on such species. New Zealand is one location where available information is sufficient to begin an analysis of the ways in which exploitation of invertebrates may reshape marine foodwebs.

The managing authority of fisheries in New Zealand is the Ministry of Primary Industries (MPI), with the single goal to have "New Zealanders maximising the benefits from the use of fisheries within environmental limits" (MPI, 2014). Supporting this goal is the desired environmental outcome that "The capacity and integrity of the aquatic environment, habitats and species are sustained at levels that provide for current and future use, including (among others) that biodiversity and the function of ecological systems, including trophic linkages are conserved" (MPI, 2014). As with many other countries around the world (Anderson *et al.*, 2011a), New Zealand has also seen strong increases in the number of invertebrate groups being commercially fished and their level of catch over the past 40 years (Figure 1).

The purpose of this study is to utilize a recently published Ecopath with Ecosim (EwE) model for a coastal region in New Zealand (Eddy *et al.*, 2014) to analyse the consequences of differing exploitation rates of three commercially fished invertebrate groups (lobster, abalone, and urchin) on catches and ecosystem structure and functioning. Our approach provides information that can be used by fisheries managers and policy makers to inform sustainable and ecosystem-based management of invertebrate fisheries as well as conservation of higher TL species.

Methods

Study area and ecosystem model

An EwE model (Christensen and Walters, 2004) that was developed for the temperate, south coast of Wellington, New Zealand (Eddy *et al.*, 2014), was employed to run a series of ecological simulations. This model was developed for a well-studied and representative ecosystem with its associated fisheries using extensive ecological and fisheries survey data from the model area to answer fisheries exploitation related questions. Details on the study area and the model, including key assumptions and uncertainties, can be found in Eddy *et al.* (2014). Commercial, recreational, and customary fisheries for finfish and shellfish that occur in this area are included in the ecosystem model. The primary invertebrate species that are harvested include lobster (locally referred to as "crayfish"; *Jasus edwardsii*), abalone ("paua"; *Haliotis australis* and *H. iris*), and sea urchin ("kina"; *Evechinus chloroticus*).

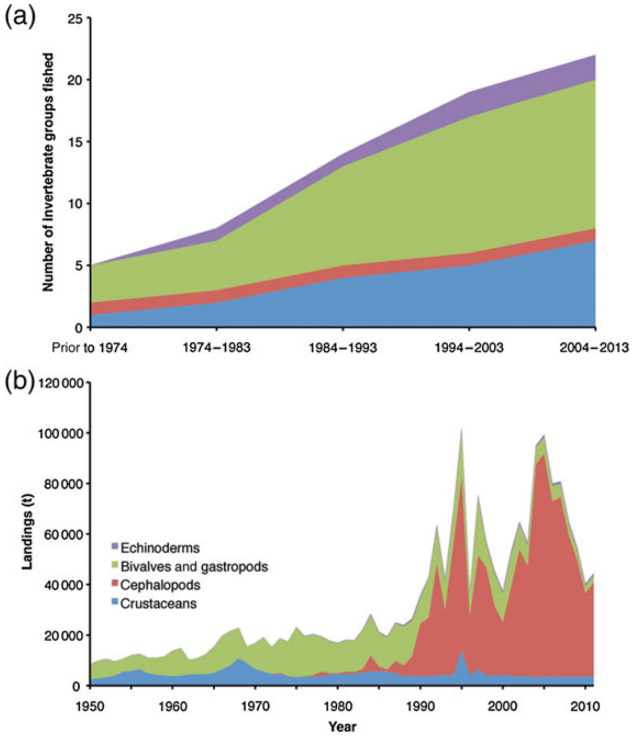

Figure 1. Invertebrate fisheries in New Zealand. (a) Number of invertebrate species or groups commercially harvested in New Zealand (Ministry for Primary Industries, 2014). Only invertebrate groups that are included in the Quota Management System are shown. (b) Reported landings of invertebrate groups commercially harvested in New Zealand (FAO, 2014). Note that the echinoderm catch is small relative to that of the other species.

Modelling strategy

We used the temporal dynamic module Ecosim (Christensen and Walters, 2004) to simulate exploitation of the three invertebrate groups for levels of depletion (LODs) from 0 to 100% by varying fishery mortality (F) values for the target group (by trial and error), while holding F values for all other exploited trophic groups constant at their most recent (2008) levels. LODs for exploited groups were calculated as the proportion of available biomass for a specific fishery simulation compared with the biomass of that group during a simulation where there was no exploitation of the species (i.e. B_i/B_0), which is the opposite of unfished biomass (B_0) (100% depletion = 0% of unfished biomass and *vice versa*; *sensu* Smith *et al.*, 2011).

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During each simulation, the *F* value of only one invertebrate trophic group was manipulated. The historical time series was run from 1945 to 2008, after which fishing mortality on the invertebrate group in question was forced at a constant level previously found to achieve the desired LOD for the target species, and all other fisheries were forced with *F* values from 2008. Simulations were run for 100 years to allow the model to reach equilibrium (a standard ecosystem modelling practice to achieve a desired LOD at equilibrium conditions, not to predict for 100 years in the future, *sensu* Smith *et al.*, 2011). As the fishing methods for these three groups are very selective and have minimal impact on habitat, we have not included bycatch or habitat impacts in our simulations.

Ecosystem effects and ecological indicators

We calculated several indicators to interpret the ecosystem effects of invertebrate fisheries, based on EwE output for biomass, catches, TLs, and other ecological indicators (e.g. connectance, keystoneness, and omnivory) that may explain the magnitude of ecosystem effects.

First, to determine the impacts of varying invertebrate LOD on ecosystem structure, we determined the proportion of trophic groups that were impacted by differing levels of biomass change: ± 20%; ± 40%. These levels were chosen to compare with previous studies on ecosystem impacts (e.g. Smith *et al.*, 2011). We then related these ecosystem effects at each LOD to the maximum sustainable yield (MSY) for each invertebrate fishery. MSY is a metric used to estimate the maximum catch as a function of fishing exploitation (often expressed as *F*), historically a major target for fisheries management. MSY was defined here as the equilibrium catch level of the simulation producing the greatest catches.

Second, we analysed fishery impacts on different TLs of the ecosystem as an indication of changes in top predators, low-TL groups (such as forage fish), and primary producers. Impacts were calculated by determining the change in biomass by TL at a particular LOD compared with when the target invertebrate was unexploited. Individual trophic groups were assigned to a TL based on their TL from the Ecopath model under an unfished level of exploitation (Table 1). This was done so that if a species group changed from one TL to another during simulations of fisheries exploitation, due to a shifting prey base, it did not unduly influence observed changes in the biomasses of TLs. We recognize that dynamically changing TLs are the reality, but this simple handling of TL facilitates cleaner interpretations of potential ecosystem changes. Apart from changes in individual TLs, we also calculated changes in the mean TL of the community (*mTLco*) for all TLs greater than one (i.e. consumers) across the varying LODs. *mTLco* was calculated as a weighted mean of the biomass contributions from trophic groups with TLs greater than one.

Third, individual trophic groups were assigned to either benthic or pelagic compartments of the ecosystem based on their feeding ecology (Table 1) and we calculated the biomass change (B_i/B_0) in the aggregate biomass (across groups) in each pelagic and benthic compartment. In cases where trophic groups preyed on both benthic and pelagic compartments, they were assigned to a group based on the majority of their diet (Table 1). Moreover, total ecosystem biomass, and its change with target species depletion was calculated for all trophic groups with TLs greater than one.

Finally, to understand the role of the target species in the ecosystem (and why the system responds the way it does to their depletion), several additional indices were calculated by EwE for the model parameterized at the most recent levels of exploitation (2008), including the omnivory index (OI) and two keystoneness indices (#1: Libralato *et al.*, 2006; #2: Power *et al.*, 1996). We also calculated the relative abundance of the exploited trophic group (proportion of the group's biomass to the ecosystem biomass) and the connectance of the exploited trophic group (calculated as the proportion of foodweb linkages for the exploited group compared with the total number of foodweb linkages in the entire ecosystem), which have been shown to be useful for explaining the ecosystem effects of forage fish exploitation (Smith *et al.*, 2011). Finally, we calculated a modified version of the connectance index, the SUpportive Role to Fishery (SURF) ecosystems index (Plagányi and Essington, 2014), which weighs groups by their relative contribution to a predator's diet, rather than just whether they are part of a predator's diet or not (as in the connectance index).

Results

Exploitation effects of invertebrate fishing on other trophic groups

Increasing exploitation and depletion of the target species resulted in greater ecosystem effects for all three invertebrate groups investigated, and exploitation of lobster showed the largest ecosystem effects (Figure 2; Table 1). No ecosystem effects occurred at very low levels of depletion, but first effects appeared when depletion was >15% for lobster and abalone and >10% for urchin. At ~25% depletion, exploitation of all three invertebrate groups resulted in similar ecosystem impacts, with a small proportion of trophic groups being impacted by ± 20% biomass change (Figure 2). When depletion levels exceeded 30% for lobster and abalone, and 40% for urchin, an increasing proportion of trophic groups were impacted by ± 40% biomass change (Figure 2). At higher levels of target species depletion, the proportion of trophic groups being affected further increased in the lobster fishery, whereas it remained constant in the abalone and urchin fisheries with 10 and 5% of groups affected, respectively (Figure 2).

If these simulations capture the dynamics of the fished ecosystem, at the estimated present LOD in the actual lobster fishery (55%), ~15% of the other trophic groups in the ecosystem are impacted by at least 20% of their biomass, and ~10% of other trophic groups are impacted by at least 40% of their biomass (Table 1; Figure 2). Trophic groups whose biomass strongly increased included birds, all carnivorous fish groups, and other mobile invertebrates (including abalone and urchin), whereas sea cucumber, sponges, and sessile invertebrates decreased the most (Table 1).

For abalone exploitation, at the present LOD (62%), ~17% of other trophic groups are impacted by at least 20% of their biomass, and 8% are impacted by at least 40% of their biomass (Table 1; Figure 2). The greatest increases in trophic group biomasses were observed for several fish groups, particularly herbivorous fish, as well as sessile and several mobile invertebrate groups (including lobster and urchin), while sea cucumbers, sponges, the two zooplankton groups, and planktivores fish decreased the most (Table 1). For urchin exploitation, at their present LOD (67%), 4% of other trophic groups are impacted by at least 40% of their biomass (Table 1; Figure 2). Trophic groups that increased in biomass included herbivorous fish and abalone, while birds and sponges slightly decreased (Table 1). Interestingly, all three target species increased in biomass in response to the exploitation of each other, e.g. both abalone and urchin increased when lobsters were exploited (Table 1).

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Table 1. Results for the Wellington south coast ecosystem model invertebrate fisheries scenarios showing all trophic groups, their TL and benthic (B) or pelagic (P) association, as well as their change in biomass (relative to the unfished scenario, B_i/B_0) for the exploitation of lobster, abalone, and urchin at their present LOD and at 100% depletion.

				B_i/B_0 for lobster exploitation		**B_i/B_0 for abalone exploitation**		**B_i/B_0 for urchin exploitation**	
	Trophic group	**TL**	**Benthic/Pelagic association**	**Present LOD**	**100% depletion**	**Present LOD**	**100% depletion**	**Present LOD**	**100% depletion**
1	Birds	3.85	P	1.54	2.37	1.00	1.01	0.99	0.99
2	Lobster	2.39	B	0.42	0	1.06	1.10	1.00	1.00
3	Mob inverts herb	2.00	B	1.24	1.50	1.04	1.06	1.01	1.01
4	Abalone	2.09	B	1.09	1.21	0.32	0	1.02	1.02
5	Urchin	2.10	B	1.07	1.14	1.06	1.09	0.30	0
6	Mob invert carn	3.75	B	1.13	1.38	1.07	1.12	1.01	1.01
7	Sea cucumber	3.22	B	0.86	0.71	0.98	0.97	1.00	1.00
8	Phytal/infaunal inverts	2.30	B	1.17	1.36	0.99	0.99	1.00	1.00
9	Sponges	2.79	B	0.90	0.77	0.96	0.93	0.99	0.99
10	Sessile inverts	2.79	B	0.90	0.78	1.11	1.16	1.01	1.02
11	Fish cryptic	3.57	B	1.22	1.56	1.06	1.09	1.01	1.02
12	Fish inverts	3.88	B	1.09	1.29	1.10	1.17	1.01	1.01
13	Fish piscivores	4.77	P	1.11	1.30	1.02	1.04	1.00	1.00
14	Fish planktivores	3.89	P	1.03	1.07	0.97	0.96	1.00	0.99
15	Fish herbivores	2.00	B	0.99	1.01	1.81	2.45	1.07	1.11
16	Microphytes	1.00	B	0.99	0.98	1.00	1.00	1.00	1.00
17	Macroalgae canopy	1.00	B	0.99	0.99	1.02	1.02	1.01	1.01
18	Macroalgae foliose	1.00	B	0.99	0.99	1.01	1.02	1.00	1.00
19	Macroalgae crustose	1.00	B	1.07	1.15	1.09	1.14	1.00	1.01
20	Meso/macrozooplankton	3.17	P	1.03	1.08	0.97	0.96	1.00	0.99
21	Microzooplankton	2.42	P	1.03	1.06	0.98	0.97	1.00	1.00
22	Phytoplankton	1.00	P	1.00	0.99	1.00	1.00	1.00	1.00
23	Bacteria	2.22	B	1.00	1.00	1.01	1.01	1.00	1.00
24	Detritus	1.00	B	1.00	1.00	1.01	1.01	1.00	1.00

Trade-offs between ecosystem effects and catches

Examining the MSY curves for the three exploited invertebrate groups indicates that the present LOD is greater than that predicted to produce MSY in all cases (Figure 2). For lobster, the model indicates that the present LOD produces ~90% of the catch at MSY. For both abalone and urchin, current levels of depletion produce catch of ~85% of MSY.

A similar level of lobster catch would be gained at a LOD of 27%, or half of the present LOD (Figure 2). At this lower LOD, none of the other modelled trophic groups were impacted by >40% of their biomass, while only 10% were impacted to the extent that there was a 20% (or more) biomass change. This level of impact is approximately half of that which the model predicts at the present LOD. Results are similar for abalone and urchin, with the model indicating that at approximately half of the present LOD (30 and 33%, respectively) the catch would be the same (Figure 2), but with much lower effects on other trophic groups. At this lower LOD, no trophic groups are predicted to be impacted by >40% of their biomass in either fishery. If the LOD of the three invertebrates was reduced to the level of B_{MSY}, as calculated by the model, then the model indicates that in all three cases the impacts on other trophic groups in the ecosystem could be strongly reduced (Figure 2).

Ecosystem effects by TL

The exploitation of all three invertebrate groups show similar patterns of responses by TL, although the magnitude of change for lobster was approximately one and two orders of magnitude greater than that for abalone and urchin, respectively (Figure 3). The TL 2–3, which includes all the exploited invertebrate trophic groups, was negatively affected with increasing depletion of the target species; however, biomass increases were typical for all other TLs (Figure 3). This is explained by (i) a release of lower TLs (TL 1 and 2) from predation by the target species, (ii) decrease in competition for resources with other trophic groups from the same or higher TLs (TL 2–3, 3–4, and >4), or (iii) enhanced alternative prey for higher TLs (TL 3–4 and >4) due to a re-organization of energy flow. The exception is observed for TL 1 for the depletion of lobster, which shows a slight decrease in biomass with increasing lobster depletion (Figure 3). The *mTLco* increased with increasing exploitation of lobster, abalone, and urchin (by 0.15, 0.97, and 0.25% respectively at 100% depletion, relative to when the target group was unfished; Figure 3). These results indicate that exploiting lower TL invertebrate groups such as abalone can cause the *mTLco* of the ecosystem to increase by an entire TL.

Effects on benthic, pelagic, and total biomass

Total ecosystem biomass (of TL>1) decreased with increasing exploitation of lobster and urchins, while the total ecosystem biomass first decreased, but then increased with increasing exploitation of abalone; relative to initial total biomass (Figure 4). When the change in total ecosystem biomass is scaled to the initial biomass of the target invertebrate group, this indicates relative decreases in total ecosystem biomass of 62 and 57% for lobster and urchin, respectively, and an increase by 5% for abalone at 100% depletion of the target group.

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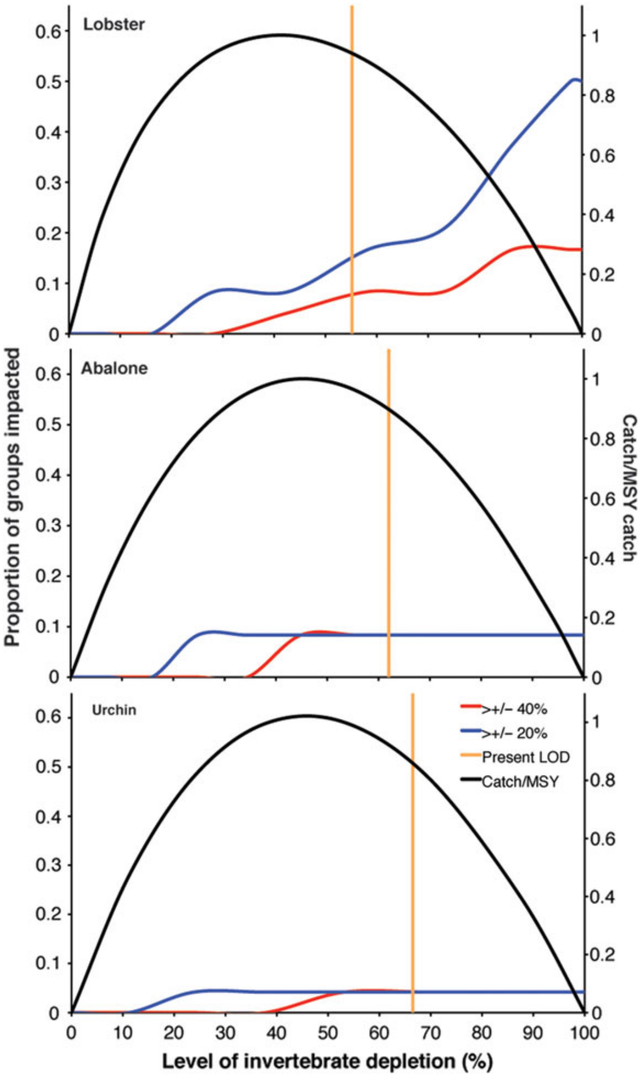

Figure 2. Invertebrate catches and ecosystem impacts as a function of LOD for the lobster, abalone, and urchin fisheries. Ecosystem impacts are measured as the proportion of other trophic groups impacted by differing levels of biomass change (B_i/B_0): an increase or decrease of 20 or 40%. LOD ranges from 0 (no exploitation) to 100% (local extinction) and the present LOD for the target fishery is indicated by the vertical line. Catch is shown as a proportion of MSY.

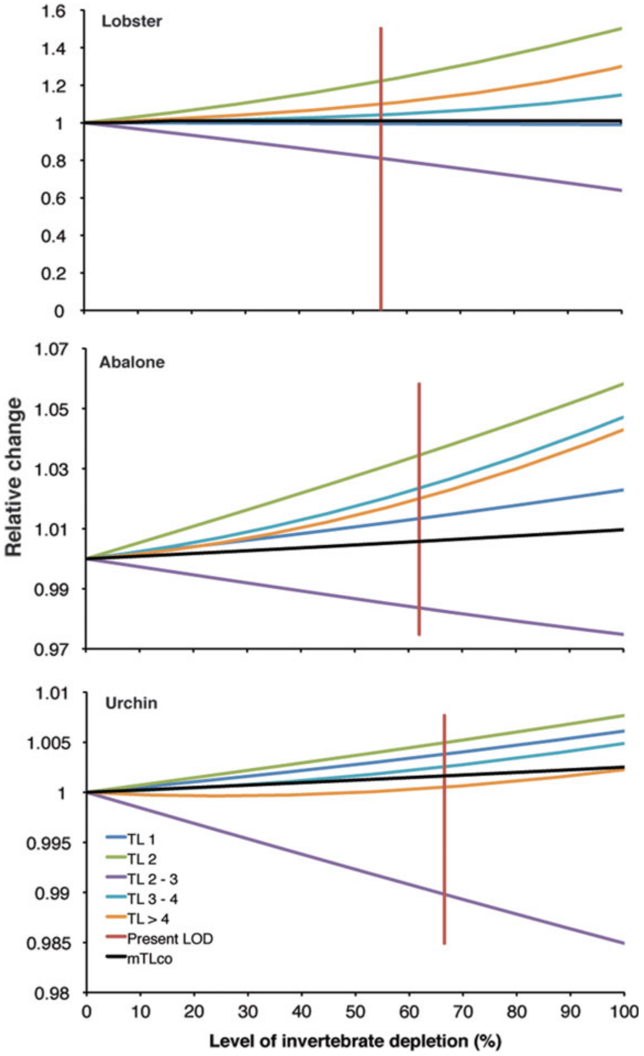

Figure 3. Ecosystem impacts of invertebrate fisheries by TL (represented as the change in biomass compared with the simulation of no exploitation, B_i/B_0) for the lobster, abalone, and urchin fisheries. The present LOD for the target fishery is indicated by the vertical line. Note that the *y*-axis scales are of different magnitudes.

Different impacts were observed for the response of benthic and pelagic compartments of the ecosystem (Figure 4). The depletion of lobster resulted in slight decreases in the benthic compartment (sea cucumber, sponges, and sessile invertebrates) and stronger increases in the pelagic compartment (birds and piscivorous fish) (Table 1; Figure 4). Depletion of abalone and urchin produced the opposite response, resulting in increases in the benthic compartment (mainly macroalgae) and decreases in the pelagic compartment (mainly meso/macrozooplankton, planktivorous fish), though about a 10-fold greater change for abalone (Figure 4; Table 1).

Ecosystem indicators

Indicators for the exploited invertebrate groups (at present exploitation rates) suggest that TL, connectance, and keystoneness index 2 (Power *et al.*, 1996; Table 2) are probably not good indicators for predicting the varying ecosystem impacts (Figures 2–4). Similarly, OI performs poorly as abalone and urchins have the same OI (Table 2), although with different magnitudes of ecosystem impacts. The SURF index (Plagányi and Essington, 2014) varied among the three exploited groups (Table 2); however, this variance did not correspond to the observed ecosystem impacts. Connectance values are likely dependent upon model structure; however, the SURF index was designed to be robust to different model structures. The keystoneness index 2 has been modified by Libralato *et al.* (2006), now referred to as keystoneness index 1, such that the biomass of the impacting group contributes to the index 1, and this indicator is a better predictor in our case. The indicators that varied most relative to the predicted ecosystem impacts were: relative abundance of trophic group and keystoneness index 1 (Table 2; Figures 2–4), with lobster having the highest values in these indicators and the highest ecosystem impacts, and urchin the lowest indicators and impacts.

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Discussion

Our results indicate that the exploitation of invertebrates on the Wellington south coast of New Zealand has considerable ecosystem effects that depend on target species and exploitation rate. The greatest changes in the biomass of other trophic groups were observed for the exploitation of lobster, followed by abalone and urchin. Interestingly, all three target groups are currently fished at levels greater than those that would produce MSY (as estimated from EwE), causing elevated ecosystem effects. Our model suggests that reducing exploitation rates would reduce these ecosystem effects, while also producing greater catches, and potentially greater economic benefit, than at present. These results are in line with other studies on the ecosystem effects of fisheries (Worm *et al.*, 2009; Smith *et al.*, 2011) and provide important information for EBFM, that aims to sustain the structure, function, and trophic linkages of ecosystems while also maintaining target species exploitation (Pikitch *et al.*, 2004).

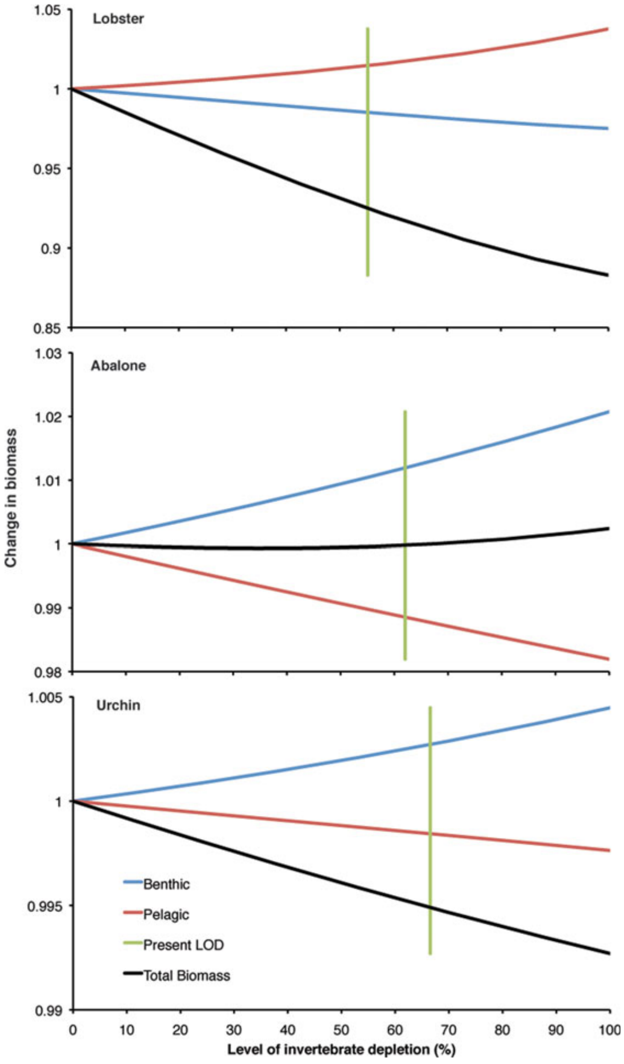

Figure 4. Change in benthic and pelagic compartments of the ecosystem and change in total ecosystem biomass (TL >1) relative to initial biomass of target group (B_i/B_0) for the exploitation of lobster, abalone, and urchin. The present LOD for the target fishery is indicated by the vertical line. Note that the *y*-axis scales are of different magnitudes.

Ecosystem effects of invertebrate exploitation

Compared with a recent study on the ecosystem effects of low-TL fisheries (Smith *et al.*, 2011), in our study, the exploitation of lobster has approximately twice the magnitude of ecosystem impacts (in terms of the proportion of other trophic groups with biomasses changes of $>40\%$) than the average low-TL group. Lobster has similarly strong effects as important forage fish groups such as anchovy, redeye, mesopelagics, sardine, and krill (Smith *et al.*, 2011). In contrast, abalone and urchin exploitation show approximately one-half and one-fifth the average ecosystems impacts of low-trophic level groups, respectively, yet at levels similar to lower impact forage fish groups such as herring, mackerel, and sprat (Smith *et al.*, 2011). One of the few studies that has investigated the ecosystem impacts of invertebrate exploitation found that the ecosystem effects of squid exploitation are similar in importance to forage fish, and that squid are an important predator and prey group in many marine ecosystems, can be a keystone group, and are sensitive to exploitation (Coll *et al.*, 2013). These results suggest that invertebrate fisheries can have considerable effects on other species in marine ecosystems and require attention in the context of EBFM. In our study, some higher TLs species (planktivorous fish, and birds) and invertebrates of potential commercial interest (sea cucumbers) or ecological importance (sponges) were negatively affected by current invertebrate fisheries. Interestingly, exploitation of one invertebrate target group generally resulted in biomass increases in the other target groups, further illustrating the need for EBFM.

Projected changes in other trophic groups range from positive to negative, both altering the underlying structure of the foodweb, thereby affecting the ecosystem functioning and integrity (Coll *et al.*, 2008; Lotze *et al.*, 2011). In our case, exploitation of lobster resulted in a decrease in the biomass of the benthic compartment, while the pelagic compartment increased, with a net decrease in total ecosystem biomass, suggesting an ecosystem under stress (Caddy and Garibaldi, 2000). Responses by TL indicate that lobster exploitation results in a decrease in primary producers (TL 1) through the release of its herbivorous prey in a trophic cascade, while exploitation of abalone and urchin produces an increase in primary producers, due to reduced direct grazing. Interestingly, the *mTLco* increased as a result of invertebrate exploitation, an observation that has also been found for forage fish and invertebrates in other systems (Shannon *et al.*, 2010, 2014).

Table 2. Indicators for exploited invertebrate groups at 2008 levels of depletion.

Trophic group	2008 LOD (%)	Relative abundance (%)	TL	Connectance (%)	SURF index	Omnivory index	Keystoneness index 1 (Libralato *et al.*, 2006)	Keystoneness index 2 (Power *et al.*, 1996)
Lobster	55	8.53	2.39	5.26	2.08E−09	0.79	−0.43	1.82
Abalone	62	2.08	2.09	5.92	4.09E−05	0.15	−0.62	1.88
Urchin	67	0.39	2.10	5.92	3.90E−06	0.15	−1.38	1.71

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Our results indicate that relative abundance and keystoneness index 1 are good ecological indicators to predict the magnitude of ecosystem effects of invertebrate exploitation. In their study of forage fish exploitation, Smith *et al.* (2011) found that abundant groups consistently have large impacts, while less abundant groups can have large or small impacts. Our results confirm this finding, where relative abundance was positively correlated to the magnitude of ecosystem impacts. Smith *et al.* (2011) also found that groups with a higher connectance of greater than ∼4% have larger ecosystem impacts. In our study, all target groups have a connectance value >4% and show variable levels of ecosystem impact; thus, this indicator may not hold true for all species in all ecosystems or may be sensitive to model structure. Smith *et al.* (2011) did not investigate keystoneness indices; however, based on our results we suggest that keystoneness index 1 (Libralato *et al.*, 2006) may be a potentially useful indicator for predicting the ecosystem effects of invertebrate fisheries. This is important, since some invertebrates, such as lobster, may have much lower relative abundance and connectance than forage fish, yet strong ecosystem effects and can thus be considered a keystone species (Eddy *et al.*, 2014). This may be a distinct difference to forage fish, which are generally highly abundant and well connected in marine ecosystems, and not considered keystone species.

Ecological role of lobster

Although having strong ecosystem effects at the present LOD, lobster plays a very different role in the marine ecosystem today compared with historical times, when its biomass was at least four times higher (Eddy *et al.*, 2014). At such high biomass levels, lobster played a much greater keystone role, with strong trophic interactions with many other groups; yet at current biomass levels, this keystone role is diminished and the trophic linkages have changed significantly (Eddy *et al.*, 2014). Importantly, when unfished, through protection by marine reserves or other management measures, the formerly strong keystone role of lobster (*Jasus* spp.) can be restored, resulting in strong structural, functional, and trophic linkage changes throughout the entire ecosystem (Shears and Babcock, 2003; Barrett *et al.*, 2009; Guest *et al.*, 2009; Jack *et al.*, 2009). Given the strong role played by *Jasus* spp. in many ecosystems, this particular invertebrate group should be closely managed to preserve its keystone role and trophic linkages.

Ecological role of urchins

Our results indicate that current levels of sea urchin exploitation do result in slight decreases in birds and sponges, as well as pelagic and overall system biomass, and slight increases in macroalgae groups. In other regions of New Zealand, particularly wave-sheltered areas, urchins have been shown to form large feeding aggregations that have transformed kelp forests into urchin barrens (Shears and Babcock, 2003), and similar urchin barrens have been reported in Tasmania (Ling *et al.*, 2009), California, Alaska (Steneck *et al.*, 2002), and elsewhere (Ling *et al.*, 2015). In our highly wave-exposed study area, urchin barrens are not generally observed (Eddy *et al.*, 2014), but do occur in areas that are heavily fished for finfish and lobster, which are important urchin predators. In contrast, areas that have been closed to fishing through marine reserve protection have reverted back to kelp forest habitats following an urchin barren (Shears and Babcock, 2003; Ling and Johnson, 2012). While increasing exploitation of urchins in areas with barrens may help to preserve kelp forests, we note that in our study urchin exploitation had negative effects on both pelagic and overall ecosystem biomass. Given the increase in sea urchin fisheries around the world (Berkes *et al.*, 2006), special management attention should be given to their variable ecological roles in different marine ecosystems.

Ecological role of abalone

Like urchins, abalone are also grazers; however, they are not known to transform macroalgal habitats to the same extent as urchins. In our study, abalone exploitation led to slight increases in macroalgae groups, but negatively affected other benthic invertebrates (sea cucumber and sponges) as well as zooplankton and planktivorous fish, with a decrease in pelagic system biomass; thus, a reduction of abalone exploitation would enhance those components. In turn, abalone biomass was positively affected by both current levels of lobster and urchin exploitation. Similarly, abalone have been positively impacted by exploitation of urchins as well as sea otters, a major predator, in California (Dayton *et al.*, 1998). In South Africa, however, abalone was sensitive to urchin exploitation, because juvenile abalone use urchins as habitat refuges as well as food sources, because urchins consume drift algae, pieces of which may then become available to juvenile abalone (Day and Branch, 2002). Management of urchin fisheries therefore needs to consider impacts on abalone populations, yet it has also been hypothesized that exploitation of top predators such as lobsters and some fish, which prey on urchins, may have exaggerated the role of urchins in sustaining abalone populations (Day and Branch, 2002). These studies highlight the complex direct and indirect relationships among species in a foodweb or ecosystem, and corroborate that an understanding of the ecosystem roles of invertebrates and the ecosystem effects of their fisheries needs more thorough investigation.

Ecosystem modelling and EBFM

Our study illustrates that ecosystem modelling is a valuable tool for exploring the ecosystem effects of invertebrate fisheries, and can thus inform EBFM. We note that ecosystem models require a lot of parameter estimates with associated uncertainty, which influences the confidence of results, and has been documented for our study area (Eddy *et al.*, 2014). The advantage of the ecosystem modelling approach compared with the traditional single-species approach is the capability to evaluate the impacts of fishing on the wider ecosystem (Collie *et al.*, in press). Present limitations for the use of ecosystem models for understanding the ecosystem effects of invertebrate fishing are largely due to a lack of knowledge about (i) invertebrate abundances, such as proper stock assessments, including information on size structure and different life-history groups (Anderson *et al.*, 2008, 2011a) and (ii) feeding relationships, both of which are required to inform ecosystem model structure and simulations; and (iii) the ability to incorporate nuanced interactions (such as the "gape limitation" of lobsters feeding on urchins; Pederson and Johnson, 2006, and change in lobster diet at different life-history stages) and non-trophic roles for invertebrates in food-web models (e.g. the urchin as refugia for juvenile abalone; Day and Branch, 2002). Although many ecosystem models are well resolved for species at higher TLs such as fish or marine mammals, lower TL groups, including invertebrates, are often lumped together without further resolution by species or biomass. Future efforts to understand non-feeding interactions and services provided by invertebrates, such as water filtration, habitat provision, and nutrient regeneration (e.g. Anderson *et al.*, 2011a), will also improve our understanding about the ecosystem roles played by

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various invertebrates and the ecosystem effects of their exploitation. Additionally, investigation into the effects of multispecies invertebrate fisheries is important to understand interactions among individual target group exploitation.

Conclusions

Our work has shown that invertebrates can play strong roles in ecosystem structure and function, and that their exploitation has considerable effects on other species and trophic groups. Future efforts to look at these effects in different ecosystems around the world will allow for a better understanding of the generality of our findings. Furthermore, comparing our results with those of other ecosystem models that have been developed with other ecological hypothesis, such as Atlantis (Fulton *et al.*, 2011), will allow further insight into the consequences of the depletion of marine invertebrates.

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