Contributed Paper

Effects of near-future ocean acidification, fishing, and marine protection on a temperate coastal ecosystem

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Abstract: *Understanding ecosystem responses to global and local anthropogenic impacts is paramount to predicting future ecosystem states. We used an ecosystem modeling approach to investigate the independent and cumulative effects of fishing, marine protection, and ocean acidification on a coastal ecosystem. To quantify the effects of ocean acidification at the ecosystem level, we used information from the peer-reviewed literature on the effects of ocean acidification. Using an Ecopath with Ecosim ecosystem model for the Wellington south coast, including the Taputeranga Marine Reserve (MR), New Zealand, we predicted ecosystem responses under 4 scenarios: ocean acidification + fishing; ocean acidification + MR (no fishing); no ocean acidification + fishing; no ocean acidification + MR for the year 2050. Fishing had a larger effect on trophic group biomasses and trophic structure than ocean acidification, whereas the effects of ocean acidification were only large in the absence of fishing. Mortality by fishing had large, negative effects on trophic group biomasses. These effects were similar regardless of the presence of ocean acidification. Ocean acidification was predicted to indirectly benefit certain species in the MR scenario. This was because lobster (Jasus edwardsii) only recovered to 58% of the MR biomass in the ocean acidification + MR scenario, a situation that benefited the trophic groups lobsters prey on. Most trophic groups responded antagonistically to the interactive effects of ocean acidification and marine protection (46%; reduced response); however, many groups responded synergistically (33%; amplified response). Conservation and fisheries management strategies need to account for the reduced recovery potential of some exploited species under ocean acidification, nonadditive interactions of multiple factors, and indirect responses of species to ocean acidification caused by declines in calcareous predators.*

Keywords: Ecopath with Ecosim, ecosystem modeling, EwE, fisheries exploitation, indirect effects, *Jasus edwardsii*, lobster

Efectos Futuros de la Acidificación Oceánica, la Pesca y la Protección Marina sobre un Ecosistema Costero Templado

Resumen: *Entender las respuestas ambientales a los impactos antropogénicos globales y locales es primordial para predecir los estados futuros de los ecosistemas. Usamos una estrategia de modelado de ecosistemas para investigar los efectos independientes y acumulativos de la pesca, la protección marina y la acidificación oceánica sobre un ecosistema costero. Para cuantificar los efectos de la acidificación oceánica en el nivel de ecosistema, usamos información de la literatura revisada por colegas sobre los efectos de la acidificación oceánica. Al usar un modelo de ecosistema Ecopath con Ecosim para la costa sur de Wellington, incluyendo la Reserva Marina Taputeranga (RM), Nueva Zelanda, pronosticamos las respuestas ambientales bajo cuatro escenarios: acidificación oceánica + pesca; acidificación oceánica + reservas marinas (RM) (sin pesca); ninguna acidificación oceánica + pesca; ninguna acidificación oceánica + RM para el año 2050. La pesca tuvo un mayor efecto sobre la biomasa de los grupos tróficos y sobre la estructura trófica que la acidificación oceánica, mientras que los efectos de la acidificación oceánica sólo fueron mayores en la ausencia de la*

*pesca. La mortandad por pesca tuvo efectos negativos mayores sobre la biomasa de los grupos tróficos. Estos efectos fueron similares sin importar la presencia de la acidificación oceánica. Se pronosticó que la acidificación oceánica beneficiaría indirectamente a ciertas especies en el escenario RM. Esto se debió a que la langosta (*Jasus edwardsii*) sólo recuperaba hasta el 58% de la biomasa de la RM en el escenario de acidificación oceánica + RM, una situación que benefició a los grupos tróficos de los cuales se alimenta la langosta. La mayoría de los grupos tróficos respondieron de manera antagónica a los efectos interactivos de la acidificación oceánica y las reservas marinas (46% redujo su respuesta); sin embargo, muchos grupos respondieron de manera sinérgica (33% amplió su respuesta). Las estrategias de conservación y manejo de pesquerías necesitan responder por el potencial de recuperación reducido de algunas especies explotadas bajo la acidificación oceánica, las interacciones no aditivas de múltiples factores y las respuestas indirectas de las especies a la acidificación oceánica causada por la declinación de depredadores calcáreos.*

Palabras Clave: Ecopath con Ecosim, efectos indirectos, EwE, explotación pesquera, *Jasus edwardsii*, langosta, modelado de ecosistemas

Introduction

To accurately predict the ecosystem effects of anthropogenic disturbances, one needs to consider multiple impacts that occur on a variety of geographical scales. These range from global-scale impacts such as temperature rises and ocean acidification (OA) to local-scale impacts such as pollution or the exploitation of species (Russell & Connell 2012). Anthropogenic perturbations to ecosystems do not usually occur in isolation, and combining 2 or more impacts can result in different outcomes that cannot be determined by simply adding their cumulative effects together (Crain et al. 2008).

The effects of anthropogenically related disturbances on individual species can result in large-scale changes in the interaction directions and strengths within ecosystems, thereby altering overall ecosystem function (Estes & Palmisano 1974; Shears & Babcock 2002; Ling et al. 2009). The study of ecosystem dynamics quantifies interactions among species or trophic groups by tracking the flow of energy through food webs and quantifies the effects of changes in environmental conditions. Models can be used to determine the impacts of fisheries exploitation on target and nontarget species (direct and indirect effects respectively) in an entire ecosystem connected by feeding relationships, an alternative to a single species focus, as is done in traditional stock assessment approaches (Browman & Stergiou 2004; Pikitch et al. 2004). Using modeling programs such as Ecopath with Ecosim (EwE: Christensen & Walters 2004), it is possible to quantify how ecosystems respond over time to climate change and fishing, and to predict outcomes for conservation and management scenarios.

Ocean acidification, could act in concert with many other anthropogenic disturbances to affect future marine ecosystems (Boyd 2011). As anthropogenic CO_2 emissions are increasingly absorbed by the oceans, the pH of surface seawater and the concentration of carbonate ions decrease, whereas the concentrations of bicarbonate and dissolved inorganic carbon increase (Raven et al. 2005).

This shift in seawater carbonate chemistry is predicted to have a wide range of effects on marine species, including interfering with calcareous species' ability to maintain net calcification (Rodolfo-Metalpa et al. 2011), altering the acid–base balance within organisms (Pörtner 2008), and changing the behavioral traits of fishes and invertebrates (Munday et al. 2009). It is difficult to predict the interactive effect of OA and many local ecosystem stressors, such as fishing, on marine ecosystems based on currently used laboratory and field methods.

Use of ecosystem models to scale up single species responses to OA, and to incorporate these responses across multiple trophic groups, can enhance the predictions of the ecosystem effects of OA. The results of multiple perturbation experiments can be used as model input to predict how an ecosystem may respond when the growth, mortality, and consumption rates of specific species are all simultaneously affected by OA (Kaplan et al. 2010; Griffith et al. 2011; Griffith et al. 2012). The ecosystem modeling approach can utilize known responses of species to OA and integrate species interactions on the basis of food-web feeding relationships to predict how individual groups will respond. The next step forward in modeling the effects of OA—incorporating its effects on mortality, productivity, and consumption rates of taxonomic groups—is yet to be implemented in published models.

We tested if a local anthropogenic disturbance (fishing) is predicted to have a greater influence than a global anthropogenic stressor (OA) on the structure and function of a temperate coastal ecosystem. We used an existing ecosystem model for the Wellington south coast, New Zealand, to predict the impacts of near-future OA, fishing exploitation, and marine protection at the Taputeranga Marine Reserve (MR) established in 2008, for the year 2050. The 4 scenarios we tested were a fully factorial combination with or without OA, and with or without fishing (absence of fishing indicates an MR scenario): OA + fishing (OA); OA + no fishing (OA + MR); no OA + fishing (base); and no OA + no fishing (MR). To predict the effects of OA, we used a novel approach, where effect
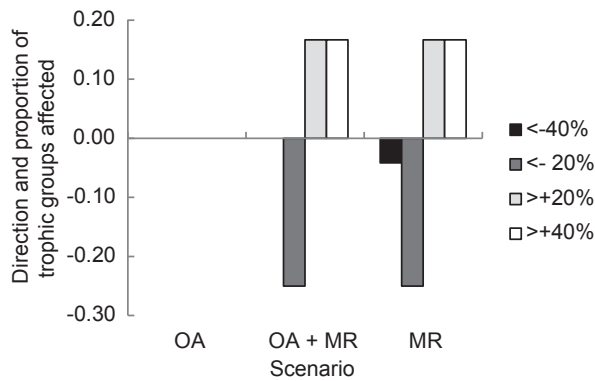
Figure 1. Proportion of trophic groups affected by at least −20% and −40% (i.e., greater than a −20% or 40% decrease), and > +20% and > +40% (i.e., greater than a 20% or 40% increase) for each modeled ecosystem scenario (OA, ocean acidification; OA + MR, OA + marine reserve; MR, marine reserve) relative to the base scenario (no OA + fishing).

sizes were determined by standardizing the effects of OA on the basis of published research.

Methods

Study Area

The Wellington south coast is characterized by intertidal and subtidal nearshore environments of soft and mobile substrates and rocky reef, representative of the Cook Strait region of New Zealand (Fig. S5; see Eddy et al. 2014 for a full description). Space in the rocky reef ecosystem is dominated by macroalgae (mostly *Macrocystis pyrifera* and *Lessonia variegata*). Lobster (*Jasus edwardsii*), a keystone species when sufficiently abundant, have been reduced to 20% of their unfished biomass by fishing (Breen & Kim 2006). This has caused an increase in lobster prey biomasses (Eddy et al. 2014). There are also commercial and recreational fisheries for abalone (locally referred to as *pāua* [*Haliotis australis* and *Haliotis iris*]) and finfish species such as blue cod (*Parapercis colias*) and butterfish (*Odax pullus*) (Eddy et al. 2014).

Calculating the Effects of OA

We modified the model of Eddy et al. (2014) by using measurements from published OA studies (see Table 1 for means and standard errors). Responses were calculated similarly to effect sizes in meta-analyses (see Gurevitch et al. 1992), except they were standardized by the control and treatment carbonate chemistry used in particular studies. This is because OA research has been conducted over a range of carbonate chemistry conditions due to

local variability and differing research goals (Riebesell et al. 2010).

All studies were analyzed to determine predicted species' responses for the year 2050 (550 μatm pCO$_2$) in the Taputeranga MR. We calculated the concentrations of dissolved inorganic carbon and total alkalinity, pH on the total scale, and the partial pressure of CO$_2$ (pCO$_2$) based on measurements made in a study. We then calculated a response curve by plotting the response of organisms against all tested conditions in a given study. Responses were calculated for both 380 (present) and 550 (2050) μatm pCO$_2$ scenarios. Overall trophic group responses were weighted by species biomass in the modelled system versus the responses of similar species taken from the literature. Trophic groups present and parameters of the model for the base scenario (Supporting Information) and the OA and OA + MR scenarios for each trophic group are in Supporting Information. Detailed descriptions of these calculations are also available in Supporting Information.

Ecosystem Modeling

We used the ecosystem model developed for the Wellington south coast, New Zealand, which includes the Taputeranga MR (Eddy et al. 2014), and EwE 6 software (Christensen & Walters 2004). EwE is based on a food-web approach and is used to quantify the flow of energy through feeding relationships within an ecosystem. It was developed for the exploited ecosystem, prior to MR implementation, and was calibrated to a historical time series of biomass and fishing mortality to tune vulnerability (v) parameters (a parameter which indicates how vulnerable a prey groups is to a predator group). We developed simulations for base and OA scenarios in the presence and absence of fishing (to simulate the effects of the MR) based on derived model modifiers (details below). The base scenario had the same parameters that were originally developed for the Wellington south coast model, which included fishery exploitation. The MR simulations were undertaken by removing fishing, and the MR scenario in the absence of OA is analogous to the scenario used in Eddy et al. (2014).

To model the effects of OA, we used the calculated impacts of OA on trophic groups to alter production (P/B_i) and consumption (Q/B_i) values in the model (see Calculating the Effects of OA for details). Due to a scarcity of studies examining Q/Bi this was applied to only 2 groups. In addition, we ran a time series of mortality until the model reached equilibrium for trophic groups that had altered mortality values (M_i) under the OA scenario. We used the Ecosim routine to run simulations to balance biomass flows in the model. We report parameterizations for the OA and no OA models in Supporting Information.

We ran simulations from 2008–2050 for the no OA scenarios and report predicted values for 2050. For MR

Table 1. Wellington south coast ecosystem model parameters and parameter modifiers used in the modeled scenarios of ocean acidification.[a]

| Trophic group (prey group code) | Ocean acidification modifier[b] | | | Fishing mortality[c] (F) | Prey groups[d] |
	Mortality (M)	Production: biomass (P/B)	Consumption: biomass (Q/B)		
Birds (1)					3, 4, 5, 6, 8, 11
Lobster (2)	1.09 (0.03)	1.04 (0.03)		0.2	3, 4, 6, 8, 17, 19
Mob invertebrate herbivores (3)	1.18 (0.04)	0.78 (0.24)			16, 17, 18, 19
Abalone (4)	1.22 (0.24)	0.78 (0.04)		0.15	10, 16, 17, 18, 19
Sea urchin (5)	1.04 (0.04)	0.94 (0.03)			10, 16, 17, 18, 19
Mobile invertebrate carnivores (6)	1.04 (0.05)	0.85 (0.12)	0.99		1, 2, 3, 4, 5, 6, 7, 8, 9, 10
Sea cucumbers (7)					23
Phytal- and infaunal invertebrates (8)	1.18	0.99			16, 17, 22, 23
Sponges (9)					21, 22, 23
Sessile invertebrates (10)	1.09 (0.04)	0.96 (0.05)	0.99		21, 22, 23
Fish, cryptic (11)	1	0.98			8, 10, 20
Fish, invertebrate feeders (12)	1	0.98			3, 4, 5, 6, 8, 9, 10
Fish, piscivores (15)	1	0.98		0.0025	11, 12, 13, 14, 15
Fish, planktivores (14)	1	0.98			8, 20, 23
Fish, herbivores (15)	1	0.98		0.018	17, 18, 19
Microphytes (16)	0.73	0.87 (0.13)			
Macroalgae, canopy (17)	1.04	1.15 (0.19)			
Macroalgae, foliose (18)	1.04	1.38 (0.19)			
Macroalgae, crustose (19)	1.10 (0.12)	0.98 (0.06)			
Meso- and macrozooplankton (20)	0.99 (0.01)	0.96 (0.07)			20, 21, 22
Microzooplankton (21)	0.99 (0.01)	0.96 (0.07)			21, 22, 23
Phytoplankton (22)	1.06 (0.06)	1.03 (0.03)			
Bacteria (23)	0.99 (0.11)	1			23, 24
Detritus (24)					

[a]*Modeled scenarios include a fully factorial combination of ocean acidification (with and without) and marine reserve (with and without).*
[b]*Proportional modifiers to the model parameters during OA scenarios (SE in parentheses if available). Trophic groups without OA modifiers were not modified directly, due to a lack of information, or were assumed not to have changed due to OA.*
[c]*Fishing mortality for trophic groups in the absence of a marine reserve. Groups without values are unfished in the model.*
[d]*Trophic groups that are preyed upon by the noted trophic group.*

scenarios, we set fishing mortality (F) to 0. For scenarios that included fishing, we used fishing mortality in 2008 as a constant value for the duration of the scenario (Table 1). Fishing and no OA (i.e., the state of the ecosystem in 2008 before the implementation of the MR; the base scenario) were used as a baseline. The responses of other scenarios (OA, MR, and OA + MR) were standardized to the base scenario to examine the effects of each scenario relative to present ecosystem state. This was calculated by dividing the response under a particular scenario by the base values. We also analyzed the interaction between OA and the impacts of fishing by each trophic group.

Ecosystem Indicators and Interaction Effects

We calculated a number of indicators to understand ecosystem responses to perturbations, including the proportion of benthic biomass affected, proportion of pelagic biomass affected, impact by trophic level (TL), and the mean trophic level of the community (mTLco;). We calculated mTLco as a weighted mean of biomass of trophic groups at TL >1; groups with a greater biomass contributed more. The mTLCo is an indicator of fishing down a food web. Trophic group level 1 are primary producers, levels above 1 indicate the group's prey source moving up the food web (see Eddy et al. 2014).

We calculated the interaction of the 2 effects, OA and MR, on trophic groups biomasses for the OA + MR scenario to determine if, when combined, the individual factors interacted in an additive (no additional stress), antagonistic (reduced stress), or synergistic (amplified stress) manner (sensu Griffith et al. 2012). Effects were calculated based on relative change in biomass compared with the base scenario (no OA + fishing). Effects were considered additive if their combined effect (sum of OA and the MR scenarios) was <5% different from their interaction effect (from the OA + MR scenario).

Sensitivity Analyses

We performed a sensitivity analysis for the OA + MR scenario, which showed the greatest ecosystem effects. We ran 6 different scenarios, including upper and lower limits of *P/B*, *Q/B*, and *M* parameter estimates, with the upper and lower bounds of 1 SE (hereafter referred to as +1 and −1 SE) when available (Table 1). Additionally, we ran scenarios on 2 key trophic groups that responded the most to the OA scenarios (lobster and abalone) in isolation to determine the direct effects of OA. In these 2 scenarios, all other trophic groups retained their parameters from the base scenario. We also ran a scenario to determine the effects of OA if only these 2 key groups were affected; parameters of all other trophic groups at their base values were held constant. Finally, to compare results of our approach with those from other approaches in which the same mortality modifier on all calcareous groups was applied, we ran a scenario where mortality was modified by 1.09 for calcareous groups (the average effect for all calcareous groups that we have calculated). This scenario is referred to as blanket modifiers.

Results

Trophic groups for which OA had the greatest direct negative effects on mortality (M_i), based on responses calculated from the literature, included microphytes, abalone, mobile invertebrate herbivores, and phytal invertebrates and infauna (>18% change). The direct effects of OA on productivity (P/B_i) were greatest (>15% change) on canopy macroalgae (positive), foliose macroalgae (positive), mobile invertebrate herbivores (negative), abalone (negative), and mobile invertebrate carnivores (negative). Groups for which responses were <6% for both values included all fishes, all zooplankton, and bacteria. There were no changes in birds, sea cucumbers, and detritus.

Removal of fishing had a much greater predicted impact on the Taputeranga MR ecosystem than disturbance caused by OA in our modeled scenarios. OA alone did not cause more than a 20% shift in the biomass of any of the trophic groups. Under both MR and OA + MR scenarios, 10 of the trophic groups had ≥20% change in biomass (Fig. 1). Trophic groups that benefited directly from reduced fishing mortality were lobster, abalone, piscivorous fishes, and herbivorous fishes (Table 2). Groups that were negatively affected by marine protection included groups that experienced increased lobster predation: mobile invertebrate herbivores, sea urchin, and phytal and infaunal invertebrates (Table 2). The only case where OA scenarios had a large effect on the biomass of trophic groups was OA + MR. The biomass of lobster was 42% less in the OA + MR scenario compared with the MR scenario, whereas the biomasses of abalone, piscivorous fishes, and herbivorous fishes were 52%, 11%, and 13% higher respectively in the OA + MR scenario than in the MR scenario. Phytoplankton biomass was predicted to increase in all 3 scenarios, indicating that the increased production to biomass ratio predicted to occur may be able to offset OA-induced mortality when integrated at an ecosystem level (Table 2). The greatest number of trophic groups responded antagonistically to the interaction of the OA and MR effects (11/24), whereas 8 groups showed synergistic interactions, and 5 groups showed additive interactions (Table 2).

The mTLco increased 4% under the MR scenario; however, it did not change by >1% in the OA and OA + MR scenarios (Supporting Information). The increase in mTLco in the MR scenario was explained by increased biomasses of presently exploited predators such as lobster and piscivorous fish such as blue cod. The increase in mTLco could also have been due to a decrease in the biomass of mobile invertebrate herbivores such as *Cookia sulcata*, a prey of lobster. The smaller mean TL under the OA + MR relative to the MR scenario was due to lower increases in lobster biomass and larger increases in abalone and herbivorous fishes (butterfish [*O. pullus*] predominately).

Although OA imposed direct mortality on some trophic groups, particularly those composed largely of calcareous species (Supporting Information), there was also indirect mortality that was caused by shifts in the abundances of top predators and their prey in this ecosystem (Supporting Information). Larger effects of OA were observed for higher TLs (Fig. 2). Biomass increases in TL 2 were mostly due to increased abundances of herbivorous fishes for the MR and OA + MR scenarios. Increases in the biomass of TL 3–4 for the MR and OA + MR scenarios were due to increases in lobster biomass; the 48% lower biomass of trophic groups TL 3–4 within the OA + MR scenario relative to the MR scenario was directly due to 42% less lobster biomass. Increases in trophic group >4 were solely due to increases in piscivorous fishes.

The sensitivity analysis indicated that the +1 SE and −1 SE scenarios had the greatest effects on the ecosystem relative to the other scenarios. Trophic groups whose responses were ≥200% different in the +1 SE relative to the −1 SE scenarios included birds, lobster, abalone, mobile invertebrate carnivores, and fish invertebrates (Table 3). The 2 scenarios where the direct effects of OA were only imposed on one trophic group had strong effects on the prey of lobster. When only lobsters were directly affected by OA, mobile invertebrate herbivores increased in biomass relative to the OA + MR scenario (Table 3). When only abalone was affected by OA, lobster biomass increased and sea urchin biomass decreased (Table 3). When only these key trophic groups were subjected to the effects of OA together, there was a lower impact (Table 3).

Table 2. Results from ocean acidification (OA), marine reserve (MR), and OA + MR scenarios indicating direction of trophic group biomass change proportional to the base scenario (no OA + fishing) with type of interaction effect.

Trophic group	Trophic level	Benthic (B) or pelagic (P)	Direction of biomass change by scenario			Interaction effect
			OA	MR	OA + MR	
Birds	3.85	P	−	−	−	antagonistic
Lobster	2.39	B	−	+	+	antagonistic
Mob invertebrate herbivores	2.00	B	−	−	−	synergistic
Abalone	2.09	B	−	+	+	synergistic
Sea urchin	2.10	B	+	−	−	additive
Mobile invertebrate carnivores	3.75	B	−	−	−	antagonistic
Sea cucumbers	3.22	B	−	+	+	additive
Phytal- and infaunal invertebrates	2.30	B	−	−	−	antagonistic
Sponges	2.79	B	−	+	+	antagonistic
Sessile invertebrates	2.79	B	−	+	+	antagonistic
Fish, cryptic	3.57	B	−	−	−	additive
Fish, invertebrate feeders	3.88	B	−	−	−	antagonistic
Fish, piscivores	4.77	P	−	+	+	synergistic
Fish, planktivores	3.89	P	−	−	−	additive
Fish, herbivores	2.00	B	−	+	+	synergistic
Microphytes	1.00	B	+	+	+	synergistic
Macroalgae, canopy	1.00	B	+	+	+	synergistic
Macroalgae, foliose	1.00	B	+	−	−	antagonistic
Macroalgae, crustose	1.00	B	+	−	−	synergistic
Meso- and macrozooplankton	3.17	P	−	−	+	antagonistic
Microzooplankton	2.42	P	−	−	−	antagonistic
Phytoplankton	1.00	P	+	+	+	additive
Bacteria	2.22	B	−	+	+	synergistic
Detritus	1.00	B	−	−	−	antagonistic
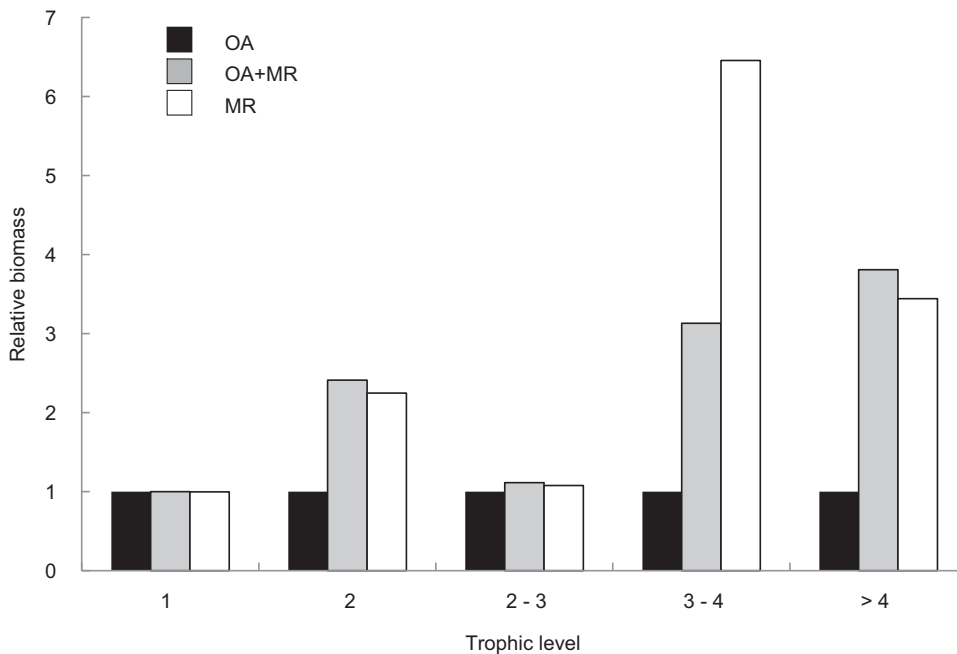
Figure 2. Biomass of trophic groups in 3 ecosystem scenarios (OA, ocean acidification; OA + MR, OA + marine reserve; MR, marine reserve) by trophic level relative to biomass in the base ecosystem scenario (no OA + fishing).

Table 3. Results of sensitivity analysis indicating changes in trophic group biomasses relative to the biomasses in the ocean acidification (OA) + marine reserve (MR) scenario.

Trophic group	+1 SE	−1 SE	OA on lobster only	OA on abalone only	OA on abalone and lobster only	Blanket OA[a]
Birds	1.03	3.58[b]	0.93	1.02	1.00	0.91
Lobster	0.54[b]	1.23[b]	1.02	1.82[b]	1.02	1.78[b]
Mobile invertebrate herbivores	1.05	0.15[b]	1.12	1.08	0.99	1.11
Abalone	0.96	7.33[b]	0.66[b]	0.97	0.99	0.66[b]
Sea urchin	1.02	0.65[b]	1.02	0.98	1.01	1.01
Mobile invertebrate carnivores	1.00	2.22[b]	0.97	1.02	1.01	0.97
Sea cucumbers	0.99	0.74[b]	1.00	0.98	0.99	1.01
Phytal- and infaunal invertebrates	1.02	0.99	1.00	0.99	1.00	0.99
Sponges	0.99	0.76[b]	1.00	0.99	0.99	1.01
Sessile invertebrates	1.00	0.74[b]	1.01	0.99	0.99	1.02
Fish, cryptic	1.02	0.71[b]	1.02	0.97	0.99	1.00
Fish, invertebrate feeders	1.00	2.37[b]	1.00	1.03	1.00	0.98
Fish, piscivores	1.05	1.52[b]	0.97	0.97	0.89	0.89
Fish, planktivores	0.99	1.15	0.97	0.98	1.02	1.00
Fish, herbivores	1.06	1.45[b]	0.83	0.83	0.87	0.87
Microphytes	1.00	1.03	1.00	1.00	1.00	1.00
Macroalgae, canopy	1.00	1.02	1.00	1.00	1.00	1.00
Macroalgae, foliose	1.00	1.00	1.00	1.00	1.00	1.00
Macroalgae, crustose	1.00	1.03	1.01	1.00	1.00	1.01
Meso- and macrozooplankton	1.00	1.11	0.99	1.01	1.00	0.99
Microzooplankton	1.00	1.08	1.00	1.02	1.01	1.00
Phytoplankton	1.00	1.00	1.00	1.00	1.00	1.00
Bacteria	1.00	1.03	1.00	1.00	1.00	1.00
Detritus	1.00	1.00	1.00	1.00	1.00	1.00

[a]*Mortality of 1.09 applied to all groups.*
[b]*Greater than 20% change.*

The scenario where an equal mortality value (1.09) was applied to all calcareous trophic groups resulted in the strongest effects on lobster and abalone. This suggests these groups are the most sensitive to mortality imposed by the direct effects of OA in the absence of changing production and consumption values (Table 3).

Discussion

Our modeling results suggest that the effects of local exploitation (fishing) outweigh the effects of a global perturbation (OA) on ecosystem functioning and trophic group biomasses in the Taputeranga MR on the Wellington south coast, New Zealand. Many single-species experimental studies suggest that OA will reduce the abundance of calcareous species (Kroeker et al. 2013). We did not find this was the case at the ecosystem level, because the modeled effects of near-future OA were subtle, species specific, and context dependent. Presently, the biomasses of exploited species (lobster, blue cod, and abalone) are being maintained at a fraction of their unfished biomass. On the basis of our results,

further disturbances by OA to the ecosystem would have a comparatively small ecosystem effect. Only under the no fishing scenarios (MR and OA + MR) were there significant shifts in ecosystem structure, where lobster biomass greatly increased regardless of the presence of OA (as has occured in other MRs; [Ling et al. 2009; Freeman et al. 2012]). Lobsters are omnivorous and significantly reduce the biomass of species they consume (Ling et al. 2009; Eddy et al. 2014). We predict that lobster will be directly and negatively affected by OA. In the OA + MR scenario, the recovery of lobster biomass was reduced by 42% due to the direct negative effects of OA, and subsequently there was lower mortality on the prey of lobsters (herbivores and macroalgae) within the Taputeranga MR. This reduced lobster recovery still represented a 10-fold increase in the biomass of lobster from 2008. Large shifts in ecosystem dynamics still occurred, although to a lesser degree.

Our results indicate that MR protection can mitigate some predicted effects of OA. Many trophic groups responded synergistically to the combined effects of OA and marine protection (greater biomass in the OA + MR compared with the MR scenario), particularly groups that

experienced a reduction in predation from lobsters, such as abalone and mobile invertebrate herbivores. The group that benefited the most from reduced lobster predation in the OA + MR scenario was abalone, which increased by 52% in the OA + MR scenario relative to the MR scenario. However, many groups responded antagonistically to the effects OA and marine protection (particularly lobster). Sensitivity analyses, where the direct effects of OA were applied only to one trophic group at a time, revealed that strong indirect effects were occurring. This was likely because declines in lobster biomass negatively affected prey species' biomasses and vice versa. Therefore, the ecosystem-level impacts of OA are likely to be different when indirect effects are also considered alongside direct effects.

The indirect effects of OA we found have important implications for the strategies of local and regional coastal management groups in other ecosystems where dynamics are driven by commercially exploited calcareous predators (e.g., Shears & Babcock 2002; Ling et al. 2009). Even within MRs, rocky reef ecosystems could experience shifts in structure and function due to the direct effects of OA on key calcareous predators. In contrast, changes in ecosystem structure and function due to the indirect effects of OA will not likely occur in ecosystems where there is no strong top–down control by exploited calcareous predators (e.g., Estes & Palmisano 1974; Pinnegar et al. 2000; Schiel 2011). A common goal of MRs is to rebuild the biomasses of fished species (e.g., Pauly et al. 2002). Global stressors such as OA may reduce the recovery potential of some fished species. Management should account for these slower recoveries when monitoring the recovery of calcareous species under marine protection in the future.

Management of marine ecosystems under climate change requires input from the scientific community, but the ability to provide robust quantitative predictions for the marine environment is hampered by differences in the methods used in quantitative research (Wernberg et al. 2012), sparse knowledge of changes in species' interactions under climate change (Russell et al. 2012), and a lack of agreement among scientists about how ecosystems will be altered (or not) due to climate change (Gattuso et al. 2012). Ecosystem models can provide insights. However, caution must be used when extrapolating the results of ecosystem models across large areas when predicting the effects of OA. This is due to spatial heterogeneity in pH conditions encountered by marine species (Hurd et al. 2011; Cornwall et al. 2013) and variability in other environmental factors (e.g., light, nutrients) that can influence the response of organisms to OA (Boyd 2011; Pandolfi et al. 2011; Ghedini et al. 2013). More research is also needed to determine how the behavior of key calcareous predators changes due to OA. The effect of OA on biomass of trophic groups differed when we implemented specific effects of OA

on trophic groups relative to when we used blanket modifiers (i.e., 78% difference in lobster biomass) and when we used +1 or –1 SE of modifiers. This highlights the need to use accurate, species-specific responses to stressors in modeled scenarios. The effects of OA will likely be context and scale dependent (Russell & Connell 2012). Other localities with different assemblages of species or that are governed by other environmental or ecological processes will display divergent responses to OA. Ecosystem management that focuses on alleviating local anthropogenic stressors (Brown et al. 2013), such as fishing, could reduce the effects of OA on some species in ecosystems where synergistic effects are predicted. Predicting accurate interactive effects of OA and local stressors on ecosystems will only be possible if the role of indirect effects such as food web feeding relationships are included in future research.

Acknowledgments

Supporting Information

Additional methods (Appendix S1), tables of base and OA scenario modifiers and total mortality under the modeled scenarios (Appendix S2), calculations of the effects of OA (Appendix S3), the species list (Appendix S4), map of the model area (Appendix S5), and mean trophic shift of the modeled scenarios relative to the base (Appendix S6) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than the absence of material) should be directed to the corresponding author.

Literature Cited

Boyd, P. W. 2011. Beyond ocean acidification. Nature Geoscience **4:**273-274.

Breen, P. A., and S. W. Kim. 2006. Development on an operational management procedure (decision rule) for CRA 4. Page 46. New Zealand fisheries assessment report. Available from http://fs.fish.govt.nz/Doc/10606/2006%20FARs/06_53_FAR.pdf.ashx (accessed December 1, 2013).

Browman, H. I., and K. I. Stergiou. 2004. Perspectives on ecosystem-based approaches to the management of marine resources. Marine Ecology Progress Series **274:**269-303.

Brown, C. J., M. I. Saunders, H. P. Possingham, and A. J. Richardson. 2013. Managing for interactions between local and global stressors of ecosystems. Plos One **8**. DOI: 10.1371/journal.pone.0065765.

Christensen, V., and C. J. Walters. 2004. Ecopath with Ecosim: methods, capabilities and limitations. Ecological Modelling **172**:109–139.

Cornwall, C. E., C. D. Hepburn, C. M. McGraw, K. I. Currie, C. A. Pilditch, K. A. Hunter, P. W. Boyd, and C. L. Hurd. 2013. Diurnal fluctuations in seawater pH influence the response of a calcifying macroalga to ocean acidification. Proceedings of the Royal Society B **280**. DOI: 10.1098/rspb.2013.2201.

Crain, C. M., K. J. Kroeker, and S. Halpern. 2008. Interactive and cumulative effects of multiple human stressors in marine systems. Ecology Letters **11**:1304–1315.

Eddy, T. D., T. J. Pitcher, A. B. MacDiarmid, T. T. Byfield, J. C. Tam, T. T. Jones, J. J. Bell, and J. P. A. Gardner. 2014. Lobsters as keystone: Only in unfished ecosystems? Ecological Modelling **275**:48–72.

Estes, J. A., and J. F. Palmisano. 1974. Sea Otters: their role in structuring nearshore communities. Science **185**:1058–1060.

Freeman, D. J., A. B. MacDiarmid, R. B. Taylor, R. J. Davidson, R. V. Grace, T. R. Haggitt, S. Kelly, and N. T. Shears. 2012. Tracjectories of spiny lobster *Jasus edwardsii* recovery in New Zealand marine reserves: Is settlement a driver? Environmental Conservation **39**:295–304.

Gattuso, J. P., K. J. Mach, and G. Morgan. 2012. Ocean acidification and its impacts: an expert survey. Climate Change **117**:725–738.

Ghedini, G., B. D. Russell, and S. D. Connell. 2013. Managing local coastal stressors to reduce the ecological effects of ocean acidification and warming. Water **5**:1653–1661.

Griffith, G. P., E. A. Fulton, R. Gorton, and A. J. Richardson. 2012. Predicting interactions among fishing, ocean warming, and ocean acidification in a marine system with whole-ecosystem models. Conservation Biology **26**:1145–1152.

Griffith, G. P., E. A. Fulton, and A. J. Richardson. 2011. Effects of fishing and acidification-related benthic mortality on the southeast Australian marine ecosystem. Global Change Biology **17**:3058–3074.

Gurevitch, J., L. L. Morrow, A. Wallace, and J. S. Walsh. 1992. A meta-analysis of competition in field experiments. Ammerican Naturalist **140**:539–572.

Hurd, C. L., C. E. Cornwall, K. I. Currie, C. D. Hepburn, C. M. McGraw, K. A. Hunter, and P. Boyd. 2011. Metabolically-induced pH fluctuations by some coastal calcifiers exceed projected 22nd century ocean acidification: A mechanism for differential susceptibility? Global Change Biology **17**:3254–3262.

Kaplan, I. C., P. S. Levin, M. Burden, and E. A. Fulton. 2010. Fishing catch shares in the face of global change: a framework for integrating cumulative impacts and single species management. Canadian Journal of Fisheries and Aquatic Sciences **67**:1968–1982.

Kroeker, K. J., R. L. Kordas, R. N. Crim, I. E. Hendriks, L. Ramajo, G. G. Singh, C. M. Duarte, and J. P. Gattuso. 2013. Impacts of ocean acidification on marine organisms: quantifying sensitivities and interaction with warming. Global Change Biology **19**:1884–1896.

Ling, S. D., C. R. Johnson, S. D. Frusher, and K. R. Ridgway. 2009. Overfishing reduces resilience of kelp beds to climate-driven catastrophic phase shift. Proceedings of the National Academy of Sciences **106**:22341–22345.

Munday, P. L., D. L. Dixson, J. M. Donelson, G. P. Jones, M. S. Pratchett, G. V. Devitsina, and K. B. Døving. 2009. Ocean acidification impairs olfactory discrimination and homing ability of a marine fish. Proceedings of the National Academy of Sciences **106**:1848–1852.

Pandolfi, J. M., S. R. Connolly, D. J. Marshall, and A. L. Cohen. 2011. Projected coral reef futures under global warming and ocean acidification. Science **333**:418–422.

Pauly, D., V. Christensen, S. Guénette, T. J. Pitcher, U. R. Sumaila, C. J. Walters, R. Watson, and D. Zeller. 2002. Towards sustainability in world fisheries. Nature **418**:689–695.

Pikitch, E. K., et al. 2004. Ecosystem-based fishery management. Science **305**:346–347.

Pinnegar, J. K., et al. 2000. Trophic cascades in benthic marine ecosystems: lessons for fisheries and protected-area management. Environmental Conservation **27**:179–200.

Pörtner, H. O. 2008. Ecosystem effects of ocean acidification in times of ocean warming: a physiologist's view. Marine Ecology Progress Series **373**:203–217.

Raven, J., K. Caldeira, H. Elderfield, O. Hoegh-Guldberg, P. Liss, U. Riebesell, J. Shepherd, C. Turley, and A. Watson. 2005. Ocean acidification due to increasing atmospheric carbon dioxide. The Royal Society, 68 pp. ISN: 0 85403 617 2.

Riebesell, U., V. J. Fabry, L. Hansson, and J. P. Gattuso. 2010. Guide to best practices for ocean acidification research and data reporting. Publications Office of the European Union, Luxembourg.

Rodolfo-Metalpa, R., et al. 2011. Coral and mollusc resistance to ocean acidification adversely affected by warming. Nature Climate Change **1**:308–312.

Russell, B. D., C. D. G. Harley, T. Wernberg, N. Mieszkowska, S. Widdicombe, J. M. Hall-Spencer, and S. D. Connell. 2012. Predicting ecosystem shifts requires new approaches that integrate the effects of climate change across entire systems. Biology Letters **8**:164–166.

Russell, B. D., and S. D. Connell. 2012. Origins and consequences of global and local stressors: incorporating climatic and non-climatic phenomena that buffer or accelerate ecological change. Marine Biology **159**:2633–2639.

Schiel, D. R. 2011. Biogeographic patterns and long-term changes on New Zealand coastal reefs: non-trophic cascades from diffuse and local inputs. Journal of Experimental Marine Biology and Ecology **400**:33–51.

Shears, N. T., and R. C. Babcock. 2002. Marine reserves demonstrate top-down control of community structure on temperate reefs. Oecologia **132**:131–142.

Wernberg, T., D. A. Smale, and M. S. Thomsen. 2012. A decade of climate change experiments on marine organisms: procedures, patterns and problems. Global Change Biology **18**:1491–1498.