Original Article

Effectiveness of lobster fisheries management in New Zealand and Nova Scotia from multi-species and ecosystem perspectives

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In New Zealand and Nova Scotia, lobster (*Jasus edwardsii* and *Homarus americanus*, respectively) is the most valuable export fishery. Although stock assessments and indicators assist in evaluating lobster fisheries, ecosystem effects are largely unknown, hindering ecosystem-based fisheries management (EBFM). We employed ecosystem models for the Cook Strait, New Zealand and western Scotian Shelf, Nova Scotia, Canada, to evaluate trade-offs between catches and ecosystem impacts in lobster fisheries from single- and multi-species perspectives. We ran simulations to independently determine exploitation rates that produced maximum sustainable yield (MSY) for lobster, and for all fished groups. We then ran simulations using these MSY exploitation rates simultaneously, and simulations to maximize multi-species MSY (MMSY). Our results indicate that current lobster exploitation rates in both regions are greater than those producing MSY, and have significant ecosystem impacts. Simulating multi-species fisheries, in both systems the sum of single-species MSY for all fished groups was less than the sum of catches where exploitation rates were run simultaneously. Runs maximizing MMSY across the entire ecosystem increased exploitation rates on many fished groups, and produced even greater total catch—yet with much greater ecological costs—and in Nova Scotia, collapses of sharks, large predators, and lobster themselves. As fisheries management moves towards multi-species and ecosystem-based approaches, we suggest that MMSY targets should be treated similarly to MSY—not as a target, but a limit. Even then, careful evaluation is required before implementation to ensure that there are no undesirable economic or ecological consequences.

Keywords: Ecopath with Ecosim (EwE), ecosystem approach to fisheries, ecosystem-based fisheries management, *Homarus americanus*, *Jasus edwardsii*, multi-species maximum sustainable yield (MMSY).

Introduction

Globally, fisheries catches have declined since the mid-1990s (Pauly and Zeller, 2016) due to the depletion of many traditional target species, which has been accompanied by the emergence of new or intensified fisheries for non-traditional species, such as many invertebrates (Anderson *et al.*, 2011a; Eddy *et al.*, 2016). However the knowledge base with which to evaluate the impacts of these expanding invertebrate fisheries is limited (Anderson *et al.*, 2008, 2011b). Many invertebrate species fetch high market prices (Swartz *et al.*, 2013) and demand is increasing, yet for

many stocks there are no formal stock assessments nor management plans in place (Anderson *et al.*, 2008, 2011b; Eddy *et al.*, 2016). The RAM legacy stock assessment database includes only 36 invertebrate stocks of a total of 331 stocks from 21 national and international agencies (Ricard *et al.*, 2011). Lobster fisheries are one of the few invertebrate fisheries that are assessed or have indicators, and in places like New Zealand, Australia, Nova Scotia, and all of Canada, lobster is currently the highest value export fishery (DFO, 2013; MPI, 2014a). Studies investigating the ecosystem impacts of fishing finfish (Bundy *et al.*, 2009; Worm

et al., 2009) and low-trophic levels (e.g. forage fish; Smith *et al.*, 2011) have indicated strong impacts on other species in the ecosystem, and recently, studies also indicate that some invertebrates, including lobster, can play strong ecosystem roles as both predators and prey (Coll *et al.*, 2013; Eddy *et al.* 2016).

Classically, fisheries have been managed as discrete units of individual stocks or species, with the aim of fishing at a level to maximize the sustainable catch of a particular stock or species over time, referred to as the maximum sustainable yield (MSY; Hilborn and Walters, 1992). More recently, it has been recognized that this reductionist approach can result in unintended consequences, including strong impacts on the structure and functioning of the associated ecosystem via species interactions (e.g. Pikitch *et al.*, 2004; Collie *et al.*, 2016). As a result, the traditional single-species approach to fisheries has moved from MSY as a target to an upper limit (Worm *et al.*, 2009), and fisheries management considerations have broadened beyond just the management of the species being harvested to consider other species in the ecosystem (Browman *et al.*, 2004; Pikitch *et al.*, 2004; Link, 2010). This ecosystem-based fisheries management (EBFM) approach sets the management priority for the ecosystem as a whole, rather than the target fishery, with the overall objective to sustain healthy ecosystems and provide ecosystem services for humans, including fisheries (Pikitch *et al.*, 2004; Essington and Punt, 2011; Fogarty and McCarthy, 2014; Long *et al.*, 2015). This new form of management still has the same needs around acceptable impacts and associated operational management criteria, such as management targets and reference points. One such reference point is multi-species MSY (MMSY). This is analogous to single-species MSY, but at an ecosystem scale—being the maximum sustainable yield across all exploited species in an ecosystem (Walters *et al.*, 2005; Worm *et al.*, 2009). Ecosystem models are one tool that can be used to explore what MMSY might look like, but also how fishing at this level may affect associated ecosystems (e.g. Worm *et al.*, 2009; Smith *et al.*, 2011; Garcia *et al.*, 2012).

As with many other countries around the world, New Zealand has seen strong increases in the number and total catch of commercially fished invertebrate groups over the past 40 years (Anderson *et al.*, 2011a; Eddy *et al.*, 2015). New Zealand is often used as an example of a well-managed fishing nation (Pitcher *et al.*, 2009; Worm *et al.*, 2009; Costello *et al.*, 2012), especially since the introduction of the quota management system in 1986. This system gives quota holders the right to fish their share of the total allowable catch (TAC). The TAC is determined on an annual basis by the government department, the Ministry for Primary Industries, and its value is dependent on the health of the stock. Additionally, fishers and their representatives also influence quotas, and may elect to voluntarily reduce their quota in a given year based on scientific information (i.e. lobster; Breen *et al.*, 2009). Economic efficiency is not an explicit goal of this system, but has been an intended result (Annala, 1996; Newell *et al.*, 2005; cited in Miller and Breen, 2010). Presently red rock lobster (*Jasus edwardsii*) is the country's most valuable export fishery, worth $250 million for 2 683 tonnes of lobster landed in 2013 (MPI, 2014a). Prior to the shift to the quota management system, the lobster fishery was managed by input controls, such as minimum legal size regulations, no take of egg-bearing females and soft-shelled lobsters, and some local area closures. Most of these input controls remain, however the limited entry provisions were replaced by output controls of individual transferrable quota (ITQ) to the previous license holders based on catch history

(MPI, 2014b). Presently, the legislated management goal is to maintain stocks at or above the biomass that produces MSY (B_{MSY}). New Zealand has also committed to EBFM with the goal of preserving the structure and function of marine ecosystems (MPI, 2014b). However, although the New Zealand lobster fishery may be sustainable and well managed from a single-species perspective (Miller and Breen, 2010) and the potential ecosystem effects of lobster exploitation through direct and indirect food-web links have been studied (Eddy *et al.*, 2014, 2015), less understood is how the lobster fishery interacts with other fisheries in a multi-fishery and ecosystem context.

In Nova Scotia, fisheries for invertebrates have also increased in recent years, and at present, the top earning export fisheries are for lobster, crab, and scallops (DFO, 2013). In 2012, American lobster (*Homarus americanus*) was the highest valued export fishery in Nova Scotia, worth $373.5 million for 25 924 tonnes (DFO, 2013) and was also the most valuable export fishery in all of Canada, worth $1.06 billion for 58 370 tonnes (DFO, 2013). The high Nova Scotian lobster catches in recent years have been attributed to a reduction in the abundance of other predators in the food web following the collapse of Atlantic cod (*Gadus morhua*), leading to reduced ecological and economical resilience of the ecosystem (Steneck *et al.*, 2011). Like New Zealand, Nova Scotia also employs input controls such as limited entry, fishing seasons, and trap limits, as well as technical measures including a minimum legal size and prohibition on landing berried females. There are no output controls such as quotas (Tremblay *et al.*, 2013). Lobster are managed under an Integrated Fishery Management Plan in Nova Scotia (DFO, 2011), which requires a precautionary approach, with science advice to establish reference points, consideration of species at risk, other by-catch issues, and habitat impacts (DFO, 2011; Tremblay *et al.*, 2013). The Integrated Fishery Management Plan has conservation and socio-economic goals: the main conservation goal is to limit negative impacts on the ecosystem, and the main social and economic goal is to help create the circumstances for economically prosperous fisheries wherein fishing enterprises are more self-reliant, self-adjusting, and internationally competitive, including supporting "healthy and prosperous Aboriginal communities" (IFMP, 2011). Currently, the industry is applying for Marine Stewardship Certification (MSC) to enable it to be more internationally competitive.

Here, we evaluate the ecosystem effects of two long established lobster fisheries in New Zealand and Nova Scotia, how they influence other species of commercial importance or conservation interest, quantify the differences in ecosystem effects for MSY and MMSY targets, and explore the ecological and catch trade-offs between exploitation levels and broader ecosystem consequences. We employ two case studies with expanding invertebrate fisheries and published ecosystem models; in Nova Scotia, Canada (western Scotian Shelf) and New Zealand (Wellington south coast, Cook Strait). We then evaluate the impacts of the lobster and multi-species fisheries from an ecosystem perspective.

Methods
Study areas and ecosystem models
Selection of study areas

We chose these two systems because they have both been examined and compared for their single-species fisheries management (Miller and Breen, 2010), however not from multi-species and

ecosystem perspectives. We were interested to investigate invertebrate fisheries, as invertebrates have been shown to have life history traits that produce different ecosystem effects and MSY results than for finfish species ((Perry *et al.*, 1999; Eddy *et al.*, 2016). Lobster fisheries are the most valuable export in both New Zealand and Nova Scotia (DFO, 2013; MPI, 2014a), have fisheries management plans (MPI, 2014b; DFO, 2011), and are well studied with accompanying Ecopath with Ecosim (EwE) ecosystem models (Araújo and Bundy, 2011; Eddy *et al.*, 2014) that permitted assessments from multi-species and ecosystem perspectives. EwE uses a mass-balance approach to follow biomass as it flows through, and is removed from, an ecosystem (Pauly *et al.*, 2000; Christensen and Walters, 2004a).

It has been shown that ecosystem model structure can affect simulation results, with number of trophic groups, connectance of the ecosystem, connectance of trophic groups, and relative biomass of trophic groups as important factors (Collie *et al.*, 2016). To test that our results would not be driven by these factors alone, we used a database of simulations of the ecosystem effects of invertebrate fisheries of 73 different exploited invertebrate groups from 12 different EwE models (including the two models employed here; Eddy *et al.*, 2016). The number of trophic groups per model only explained 0.1% of observed variation in average ecosystem impact, while ecosystem connectance explained 12.6% of observed variation in average ecosystem impact, and relative biomass of trophic group explained 0.04% of observed variation in average ecosystem impact (Eddy *et al.*, 2016). These results gave us confidence that the simulation results presented here were not solely driven by differences in ecosystem model structure.

New Zealand

The temperate Cook Strait region of New Zealand (41°S, 174°E) is characterized by high wind and wave energy, and is the confluence of three currents (the East Cape, D'Urville, and Southland). The rocky reef ecosystem is comprised of macroalgae (mostly *Lessonia variegata* and *Macrocystis pyrifera*) as well as associated encrusting invertebrate communities, which provide habitat for a large number of invertebrate and vertebrate species (Eddy *et al.*, 2014). The commercial fishery in this region is dominated by the rock lobster fishery (locally referred to as crayfish), however fisheries for finfish species such as blue cod (*Parapercis colias*) and butterfish (*Odax pullus*) also exist. There are also recreational fisheries for lobster, abalone (locally referred to as "paua", *Haliotis australis* and *H. iris*), and urchin (locally referred to as "kina"; *Evechinus chloroticus*). EwE models were developed for the Wellington south coast, a well-studied and representative area of the Cook Strait, for the time periods 1945 and 2008 (Eddy *et al.*, 2014). These models were linked using time series of lobster fishery mortality (*F*), calibrated to a time series of lobster biomass, and were capable of reproducing historical trends of lobster biomass (Eddy *et al.*, 2014). A portion of the model area is now protected by the Taputeranga Marine Reserve, which was established in 2008, however the 2008 model was parameterized for the exploited ecosystem prior to protection (Eddy *et al.*, 2014). The lobster fishery associated with our New Zealand study area is for the crayfish 4 stock (CRA4), which spans a geographic range from Hawke's Bay on the east coast of the north island to the Kapiti coast on the west coast of the north island. CRA4 was heavily depleted in 1998, and resulted in fishers voluntarily agreeing to shelve (not fish) 41% of their quota in 2007 and 61% of

their quota in 2008 (Breen *et al.*, 2009). Fisheries in the model were parameterized for 5 of the 24 functional groups based on 2008 data (MPI, 2009).

Nova Scotia

Lobster landings over the entire east coast of North America have increased dramatically since 1980s, and the largest fisheries landings occur around the Gulf of St. Lawrence and Gulf of Maine. In Nova Scotia, EwE models were developed for the formerly groundfish dominated North Atlantic Fisheries Organization (NAFO) Division 4X, located in a transition zone between the Scotian Shelf Large Marine Ecosystem (LME) and the Northeast U.S. Shelf LME (Sherman and Hempel, 2008, Araújo and Bundy, 2011). North Atlantic Fisheries Organization (NAFO) Division 4X is comprised of the western Scotian Shelf and the Bay of Fundy: the western Scotian Shelf is a wide continental shelf area influenced by currents from the Labrador Current and the Gulf of St. Lawrence; the Bay of Fundy is characterized by the magnitude of its tides, which generate intense vertical mixing caused by bottom turbulence and generate high levels of marine productivity. Published NAFO Division 4X EwE models represent the average state of the ecosystem in the years 1995–2000 (Araújo and Bundy, 2011), and for 1970s, which served as starting point for the dynamic simulations of past trends and calibration of model parameters (Araújo and Bundy, 2012). For comparative purposes, the model used here was parameterized to represent the average state of the ecosystem for 2008. The model has 58 functional groups, 31 of which are fished (27 of these have been subjected to heavy fishing). Lobster are managed by Lobster Fishing Areas (LFA), four of which occur in the model area: LFA 34–38 (Araújo and Bundy, 2011). Most recent stock assessments indicate that lobster stocks in all four LFAs are healthy, based on three key indicators (landings, commercial catch rate and summer research survey catch rate; Tremblay *et al.*, 2012). The 3-year running averages of these indicators were well above the proposed upper stock reference points (DFO, 2014a,b). Exploitation rates in LFA 34 are high (average 0.71–0.77), but are not considered to put the stock at risk since environmental conditions remain favourable for lobster (Tremblay *et al.*, 2013).

Modelling strategy
Lobster fisheries
We estimated single-species MSY for lobster in each model by running simulations of varying exploitation rates (*u*) until the model stabilized. During these simulations, the exploitation rates of all other fished groups were held at their most recent levels (2008). Level of lobster depletion was then calculated as the proportion of lobster biomass at an exploitation rate i (B_i), compared with unfished biomass (B_0; $1 - B_i/B_0$). Unfished biomass was calculated from simulations with no lobster fisheries exploitation ($u = 0$). The ecosystem impact of each exploitation rate was calculated as the proportion of other functional groups in the model with biomass changes of ± 20% and ± 40%, compared with the simulation where lobster was unfished ($u = 0$).

Multi-species fisheries
The above simulations keep the fishing mortality of other species at their current rates. However, exploitation rates for these species also change through time, and in order to place lobster fisheries in an ecosystem context and to include interactions with other
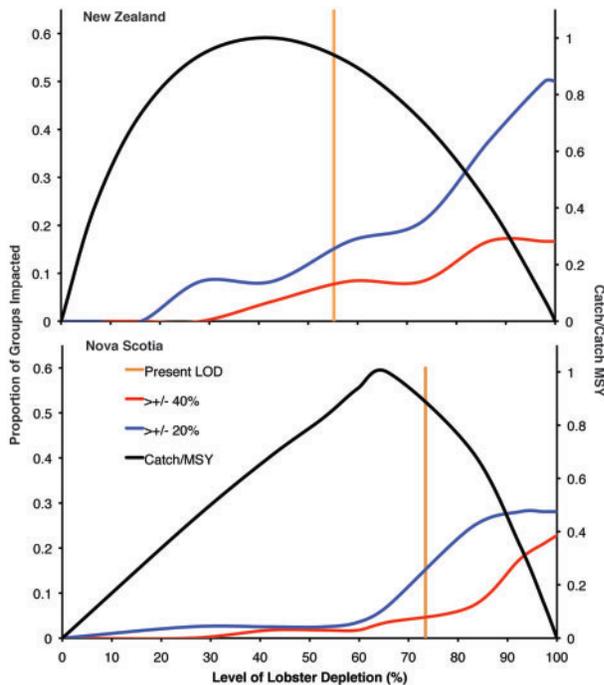
Figure 1. Lobster catches and ecosystem effects as a function of lobster level of depletion (LOD) in New Zealand and Nova Scotia. Catch is represented as the proportion of the catch compared with the single-species lobster maximum sustainable yield (MSY). Ecosystem effects are represented by the proportion of other functional groups impacted by biomass changes of $\pm$ 20% and $\pm$ 40% within the ecosystem as a function of the level of lobster biomass depletion. Present lobster LOD is indicated by the vertical line.

fisheries, we explored optimal management strategies across all exploited species using four approaches.

First, using the same method above as for lobster, we also estimated exploitation rates that produced single-species MSY (u_{MSY}) for all other fished groups. These u_{MSY} values were thus calculated independently of each other as is the case in single-species fisheries management, and did not consider interactions among fisheries. The total theoretical ecosystem catch was thus estimated as the sum of single-species MSYs.

Next, in order to understand how the fisheries interacted with each other in a multi-species context, we ran a simulation that simultaneously used all of the independently estimated single-species u_{MSY} values from above, in the same simulation. We calculated the total ecosystem catch across all fisheries and calculated the associated ecosystem impacts as the proportion of functional groups impacted by $\pm$ 40% biomass as well as the proportion of functional groups that collapsed ($<10\%$ B_0).

Thirdly, to explore a spectrum of possible ecosystem catches and to explore where the optimum catch is located, we ran a series of simulations to capture the multi-species MSY (MMSY) curve, using multiples of all u_{MSY} values from above (k; $k = 0$, 0.1, 0.2, ... 1, 2, 3, ..., 20; *sensu* Walters *et al.*, 2005; Worm *et al.*, 2009). The simulation described in the previous paragraph therefore corresponded to $k = 1$. We report the total ecosystem catches and ecosystem impacts as a function of ecosystem level of depletion, calculated as the proportion of total ecosystem biomass of exploited groups for a fishing scenario compared with total ecosystem biomass of exploited groups without fisheries exploitation ($1 - B_i/B_0$).

The previous simulations varied the value of k of all exploitation rates simultaneously. However it may be possible to achieve a greater total ecosystem catch by varying exploitation levels for individual groups independently (i.e. not by a common k multiple). In our final set of simulations, we used the fisheries policy search routine in EwE (Christensen and Walters, 2004b), to further explore this parameter space, by varying economic and ecological objectives with weightings between 0 and 1 (0, 0.1, 0.2, ..., 1.0), which effectively maximize the objective based on the weighting. For the ecological function (mandated rebuilding), the objective was to achieve a targeted rebuilding biomass, which was set to 40% of unfished biomass (or 60% depletion; *sensu* Worm *et al.*, 2009). The objective of the economic function [social value (employment)] was to maximize the total ecosystem catch. We highlight a "safe operating space", for simulations that achieve the ecological function of a mandated rebuilding target of 40% unfished biomass for all exploited species. The results from these simulations were combined with the results from the simulations that varied the value of k from above, to produce an aggregate of fisheries management scenarios with their resulting catches and ecosystem impacts.

To investigate the relationship between the ecosystem exploitation rate ($u = C_i/B_i$; where C_i is the catch of ecosystem i) and the ecosystem level of depletion ($1 - B_i/B_0$), we examined these relationships for MMSY simulations in each ecosystem to determine if any step functions in ecosystem biomass with increasing exploitation rate were observed.

Results
Lobster fisheries
Comparing current exploitation rates to the single-species MSY results indicates that lobster exploitation rates for New Zealand and Nova Scotia are presently higher than those predicted to produce MSY (12% greater level of depletion in New Zealand; 8% greater level of depletion in Nova Scotia; Figure 1). The present exploitation rates have similar effects on the broader ecosystem for Nova Scotia (15% of groups have a biomass change of $\pm$ 20% and 5% show a change of $\pm$ 40%) and New Zealand (17% of groups have a biomass change of $\pm$ 20% and 8% show a change of $\pm$ 40%; Figure 1; Tables 1 and 2). Moreover, the potential for future change, were exploitation rates to rise, is higher in New Zealand than Nova Scotia. Responses for Nova Scotia show that when the level of depletion of lobster reaches 90%, 28% of groups change by at least 20%. In contrast, were New Zealand's level of depletion to rise from 55% to 90%, 38% of functional groups would be affected by at least a 20% biomass change (Figure 1; Tables 1 and 2).

In New Zealand, trophic groups that are predicted to be the most negatively affected by lobster exploitation at MSY are the unfished groups; sea cucumbers, sessile invertebrates, and sponges, while the unfished groups birds, mobile invertebrate herbivores, and phytal/infaunal inverts were predicted to increase the most (Table 1). In Nova Scotia, increasing exploitation of lobster has a positive effect on their prey species, such as small and large crabs and echinoderms, and the larger predators, longhorn sculpin, cod, haddock and halibut, all of which increase with increasing exploitation of lobster (Table 2). In both systems, a

Table 1 New Zealand ecosystem model trophic groups with trophic level (TL), prey groups (for consumers), and relative biomasses, catches, and proportion of total catch for different fisheries management simulations.

	Trophic group	TL	Prey groups	MSY u value	MMSY u value	Relative biomass at lobster MSY	Relative biomass at $k=1$	Relative biomass at MMSY	Catch at $k=1$ (t/km^2)	Catch at MMSY (t/km^2)	% of total catch at $k=1$	% of total catch at MMSY
1	Birds	3.85	3, 4, 5, 6, 8, 11			1.35	1.95	2.52				
2	Lobster	3.06	3, 4, 6, 8, 17, 19	0.4	0.7	0.57	0.78	0.69	0.53	0.60	75.4	79.1
3	Mobile invertebrates herbivore	2.00	16, 17, 18, 19			1.16	1.19	1.26				
4	Abalone	2.09	10, 16, 17, 18, 19	0.5	0.875	1.06	0.50	0.34	0.12	0.10	16.6	13.3
5	Urchin	2.09	10, 16, 17, 18, 19	0.4	0.7	1.05	0.54	0.40	0.025	0.023	3.6	3.1
6	Mobile invertebrates carnivore	3.75	1, 2, 3, 4, 5, 6, 7, 8, 9, 10			1.08	1.26	1.42				
7	Sea cucumber	3.22	23			0.91	0.74	0.64				
8	Phytal/infaunal invertebrates	2.30	16, 17, 22, 23			1.12	1.35	1.49				
9	Sponges	2.79	21, 22, 23			0.93	0.79	0.71				
10	Sessile inverts	2.79	21, 22, 23			0.93	0.89	0.85				
11	Fish cryptic	3.57	8, 10, 20			1.14	1.64	2.03				
12	Fish invertebrate feeders	3.88	3, 4, 5, 6, 8, 9, 10			1.05	1.38	1.59				
13	Fish piscivores	4.77	11, 12, 13, 14, 15	0.3	0.525	1.07	0.56	0.43	0.0048	0.0046	0.68	0.61
14	Fish planktivores	3.89	8, 20, 23			1.02	1.23	1.31				
15	Fish herbivores	2.00	17, 18, 19	0.1	0.175	1.00	0.71	0.63	0.027	0.029	3.8	3.9
16	Microphytes	1.00				0.99	0.99	0.99				
17	Macroalgae canopy	1.00				0.99	1.00	1.00				
18	Macroalgae foliose	1.00				1.00	1.01	1.02				
19	Macroalgae crustose	1.00				1.05	1.07	1.10				
20	Meso/macrozooplankton	3.17	20, 21, 22			1.02	1.00	1.00				
21	Microzooplankton	2.42	21, 22, 23			1.02	1.07	1.09				
22	Phytoplankton	1.00				1.00	0.99	0.99				
23	Bacteria	2.22	23, 24			1.00	1.00	1.00				
24	Detritus	1.00				1.00	1.00	1.00				

The three different management simulations are: the simulation that maximized the single-species lobster MSY (only biomass response indicated), the simulation where all single-species u_{MSY} values were run simultaneously ($k=1$), and the simulation that maximized MMSY. Biomasses are relative to unfished biomass ($1-B_i/B_0$). The "prey groups" column indicates which other trophic groups (according to numbered list) are preyed upon by consumers.

decrease in current exploitation rates was projected to lead to an increase in lobster catch.

Multi-species fisheries

Total multi-species catches for New Zealand and Nova Scotia increased when moving from the sum of catches estimated from single-species u_{MSY} runs for individual groups (0.63 and 2.61 t/km^2, respectively), to the sum of catches when all u_{MSY} values were run simultaneously (0.71 and 3.27 t/km^2, respectively), to the sum of catches when MMSY was maximized (0.75 and 4.56 t/km^2, respectively; Tables 1 and 2). In New Zealand, these increases were due to increases in catches of lobster and herbivorous fishes (butterfish; *Odax pullus*), and in Nova Scotia, this was mainly due to increases in catches of herring, mackerel, other pelagics, and haddock.

For both the New Zealand and Nova Scotia models, the present ecosystem levels of depletion (28.5% in New Zealand and 19.9% in Nova Scotia) were less than those predicted to produce MMSY (39% and 48%, respectively; Figure 2). Present ecosystem levels of depletion were also lower than the levels of depletion in the simulation where all of the exploitation levels for individual fisheries that produced MSY were simultaneously run in the same simulation ($k=1$), which for New Zealand was marginally higher at 29.3% level of depletion and for Nova Scotia occurred at 24.3% level of depletion

(Figure 2). At these exploitation levels, the proportion of functional groups with a biomass change of $\pm$40% was 21% and 32% in New Zealand and Nova Scotia, respectively (Figure 2), and 21% in both locations at current ecosystem level of depletion. In contrast, at exploitation levels predicted to produce MMSY, 33% of functional groups were impacted by at least a 40% change in biomass in New Zealand, although no groups collapsed (<10% B_0), while in Nova Scotia, 52% of groups were impacted by at least a 40% change in biomass, and 17% of groups collapsed (<10% B_0; Figure 2). We have highlighted simulations that achieve a rebuilding mandate of 40% of unfished biomass (Figure 2); for New Zealand, this means fishing at levels of ecosystem depletion <29%, while for Nova Scotia, this means fishing at levels <18% ecosystem depletion.

Looking specifically at impacted groups in the MMSY scenarios, in New Zealand, the biggest biomass declines for unexploited species were for sea cucumbers, sponges, and sessile invertebrates, which were 13%, 10%, and 5% lower in biomass compared with the simultaneous MSY scenario (Table 1). Groups predicted to show the greatest increases in biomass under the MMSY scenario included birds, cryptic fishes, invertebrate feeding fishes, and mobile invertebrate carnivores, with 29%, 24%, 15%, and 12% greater biomass compared with the simultaneous MSY scenario (Table 1). For Nova Scotia, under the MMSY scenario, numerous groups were predicted to collapse, including sharks, large pelagics, pollock (<49 and >49 cm size classes), demersal

Table 2 Nova Scotia ecosystem model trophic groups with trophic level (TL), prey groups (for consumers), and relative biomasses, catches, and proportion of total catch for different fisheries management simulations.

	Trophic group	TL	Prey groups	MSY u value	MMSY u value	Relative biomass at lobster MSY	Relative biomass at $k=1$	Relative biomass at MMSY	Catch at $k=1$ (t/km²)	Catch at MMSY ($k=1.8$) (t/km²)	% of total catch at $k=1$	% of total catch at MMSY
1	Whales	4.08	52, 33, 32, 53, 34			1.00	0.92	0.91				
2	Toothed cetaceans	4.839	33, 38, 12, 32, 28			1.02	0.80	0.70				
3	Seals	4.76	33, 24, 27, 34, 17			1.01	1.50	2.14				
4	Sea birds	4.37	52, 32, 34, 35, 38			1.01	1.09	1.29				
5	Sharks	4.72	33, 27, 23, 34, 32	0.054	0.11	1.00	0.34	0	0.00080	0	0.024	0
6	Large pelagic	4.77	40, 51, 19, 30, 11	0.167	0.33	1.01	0.43	0	0.0053	0	0.16	0
7	Cod <1 year	3.66	52, 42, 46, 53, 47			1.05	0.76	0.73				
8	Cod 1–3 year	3.98	52, 42, 41, 33, 32	0.11	0.23	1.06	0.77	0.74	0.018	0.034	0.54	0.75
9	Cod 4–6 year	4.46	32, 34, 33, 24, 41	0.44	0.88	1.06	0.62	0.45	0.052	0.076	1.58	1.66
10	Cod ≥7 year	4.47	32, 34, 33, 24, 41	0.42	0.84	1.07	0.27	0.09	0.0036	0.0023	0.11	0.05
11	Silver Hake <25 cm	3.84	52, 42, 34, 46, 53	0.12	0.24	0.99	0.90	0.34	0.011	0.008	0.32	0.17
12	Silver Hake 25–31 cm	3.88	52, 42, 34, 53, 11	0.42	0.85	0.99	0.85	0.32	0.053	0.039	1.61	0.86
13	Silver Hake ≥31 cm	4.60	32, 52, 34, 33, 38	0.12	0.25	1.00	0.58	0.14	0.0037	0.0018	0.11	0.04
14	Halibut <46 cm	3.76	42, 52, 41, 32, 49	0.0020	0.0041	1.01	0.75	0.30	1.391E-05	1.10E-05	0.00043	0.00024
15	Halibut 46–81 cm	4.57	32, 12, 52, 41, 28	0.018	0.035	1.02	0.88	0.43	0.00027	0.00027	0.01	0.01
16	Halibut ≥82 cm	4.60	32, 12, 52, 41, 28	0.24	0.48	1.03	0.44	0.15	0.0043	0.0029	0.13	0.06
17	Pollock <49 cm	3.81	42, 52, 34, 53, 46	0.016	0.032	0.97	0.79	0.00	0.0022	0	0.068	0
18	Pollock ≥49 cm	4.06	52, 42, 33, 32, 35	0.21	0.43	0.97	0.58	0.00	0.092	0	2.81	0
19	Demersal piscvores	4.45	52, 32, 29, 33, 34	0.21	0.43	1.01	0.54	0.00	0.034	0	1.05	0
20	Large benthivores	3.48	43, 52, 42, 41, 47	0.13	0.25	0.95	0.42	0.00	0.011	0	0.35	0
21	Skates <49 cm	3.65	52, 42, 49, 53, 41	0.067	0.13	1.00	0.76	0.28	0.0039	0.0028	0.12	0.06
22	Skates ≥49 cm	3.89	42, 52, 24, 49, 41	0.12	0.24	1.00	0.61	0.16	0.0092	0.0047	0.28	0.10
23	Dogfish	4.31	52, 32, 51, 42, 33	0.086	0.17	0.89	0.44	0	0.13	0	4.00	0
24	Redfish	3.79	52, 42, 34, 53, 46	0.082	0.164	1.00	0.71	0.19	0.10	0.05	3.10	1.18
25	American plaice <26 cm	3.42	42, 44, 52, 43, 49			0.99	0.96	1.92				
26	American plaice ≥26 cm	3.58	52, 47, 43, 49, 44	0.20	0.41	1.02	0.73	1.14	0.0082	0.0255	0.25	0.56
27	Flounders	3.22	49, 46, 48, 53, 44	0.13	0.25	1.02	0.54	0.00	0.041	0	1.27	0
28	Haddock <3 year	3.44	52, 49, 53, 47, 42	0.013	0.0256	0.99	1.01	2.79	0.0014	0.0076	0.04	0.17
29	Haddock ≥3 year	3.49	47, 52, 49, 42, 41	0.25	0.49	1.01	0.68	1.37	0.12	0.47	3.54	10.27
30	Longhorn sculpin <25 cm	3.74	52, 42, 41, 49, 34			1.01	2.00	9.06				
31	Longhorn sculpin ≥25 cm	3.77	52, 42, 41, 34, 49	0.17	0.34	1.12	1.70	6.79	0.0045	0.0359	0.14	0.79
32	Herring <4 year	3.83	52, 42, 53, 46, 48	0.16	0.32	1.12	1.08	1.09	0.65	1.32	19.97	29.05
33	Herring ≥4 year	3.83	52, 42, 53, 46, 48	0.29	0.58	1.00	0.94	0.83	0.95	1.67	28.95	36.67
34	Other pelagic	3.60	52, 53, 42, 46, 56	0.14	0.27	1.01	0.99	1.27	0.14	0.37	4.38	8.07
35	Mackerel	3.76	52, 53, 42, 46, 49	0.12	0.24	0.99	3.58	7.40	0.055	0.227	1.68	4.99
36	Mesopelagic	3.37	53			1.02	1.31	1.71				
37	Small-medium benthivores	3.61	52, 42, 49, 46, 44			1.00	2.20	4.49				
38	Squids	3.95	52, 42, 38, 49, 32	1.27	2.5	1.00	0.85	0.60	0.13	0.18	3.99	4.03
39	Lobster	3.07	44, 47, 58, 48, 49	0.40	0.80	1.00	0.44	0.00	0.41	0	12.44	0
40	Large crabs	3.18	44, 49, 43, 45, 47			0.21	1.50	2.71				
41	Small crabs	2.63	58, 50, 49, 45, 48			1.11	1.97	3.98				
42	Shrimps	2.62	58, 53, 52, 56, 49			1.14	1.22	1.56				
43	Scallop	2.05	58, 56, 55	0.13	0.27	0.99	0.74	0.03	0.23	0.02	6.97	0.45
44	Bivalves	2.09	56, 55, 58			0.99	1.02	1.05				
45	Other molluscs	2.84	44, 58, 50, 42, 46			1.00	0.92	0.90				
46	Other arthropoda	2.04	58, 50, 46			0.99	0.98	0.94				
47	Echinoderms	2.05	58, 44, 45, 48, 49			0.99	1.30	1.84				
48	Sessile benthic groups	2.23	56, 58, 55, 52, 53			1.12	1.00	1.04				
49	Worms	2.17	58, 50, 49, 46			1.00	0.98	0.92				
50	Meiofauna	2.05	58, 50			0.99	0.98	0.94				
51	Gelatinous zooplankton	3.41	53, 52, 54, 56, 55			0.99	1.18	1.29				
52	Macrozooplankton	2.92	53, 58, 56, 54, 52			1.00	0.99	0.98				
53	Mesozooplankton	2.37	56, 54, 55, 53			1.00	0.99	0.97				
54	Microzooplankton	2.34	58, 56, 55, 54			1.00	1.00	1.00				
55	Microflora	2.00	58			1.00	0.99	0.98				
56	Phytoplankton	1.00				1.00	1.00	1.00				
57	Discards					1.00	0.34	0.01				
58	Detritus					0.91	1.00	0.99				

The three different management simulations are: the simulation that maximized the single-species lobster MSY (only biomass response indicated), the simulation where all single-species u_{MSY} values were run simultaneously ($k=1$), and the simulation that maximized MMSY. Biomasses are relative to unfished biomass ($1-B_i/B_0$).
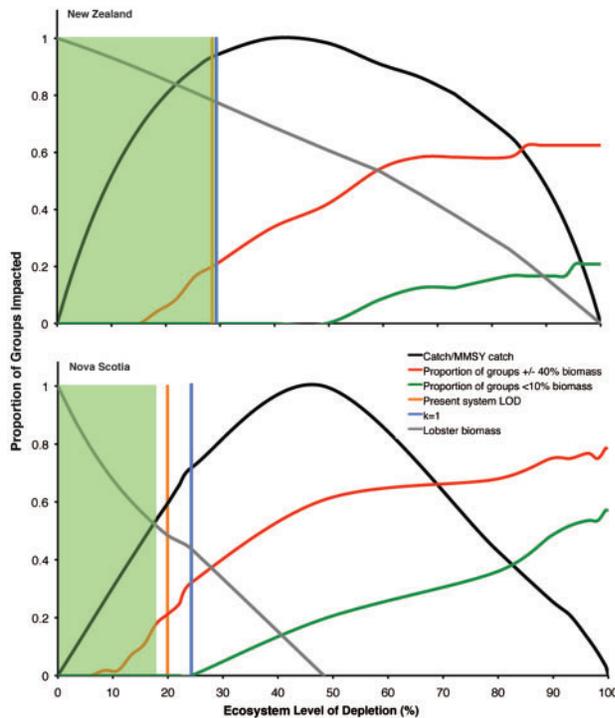
Figure 2. Ecosystem catches and ecosystem effects of multi-species fisheries exploitation in New Zealand and Nova Scotia. Catch is represented as the proportion of the predicted catch at multi-species maximum sustainable yield (MMSY). Ecosystem effects are represented by the proportion of other functional groups impacted by biomass changes of ± 40% and decreases >90% within the ecosystem as a function of the level of ecosystem depletion. The simulation where all single-species u_{MSY} values were run simultaneously ($k = 1$) as well as the present ecosystem LOD are indicated as vertical lines. The shaded regions (safe operating space) indicate the simulations that satisfied the mandated rebuilding criterion, where no individual exploited group dropped <40% of its unfished biomass.

piscivores, large benthivores, dogfish, flounders, and lobster (Table 2). Groups that showed the greatest biomass increases compared with the simultaneous MSY scenario were: longhorn sculpin (<25 & >and >25 cm), mackerel, haddock (<3 years), small-medium benthivores, small crabs, and large crabs with 706%, 509%, 392%, 278%, 229%, 201%, and 121% biomass differences, respectively (Table 2).

Consequences of MMSY targets for lobster

In New Zealand, allowing exploitation rates to reach MMSY would see lobster more heavily exploited than with MSY set as the management limit, with a relative biomass of 69% of unfished biomass in the MMSY scenario compared with 78% in the simultaneous MSY scenario. Lobster catches are predicted to be greater in the MMSY scenario at 0.60 t/km² and accounting for 79% of total ecosystem catch, compared with 0.53 t/km² (comprising 75% of catch) in the simultaneous MSY scenario (Table 1). In Nova Scotia, allowing for MMSY results in lobster collapse, while in the simultaneous MSY scenario lobster biomass is at 44% of unfished biomass, with catches of 0.41 t/km², accounting for 12% of total ecosystem catch (Table 2).

In New Zealand, the higher lobster catches under the MMSY scenario come at a fisheries cost for abalone, sea urchin, and

piscivorous fishes, which decrease to 34%, 40%, and 43% of unfished biomass, respectively, compared with biomasses of 50%, 54%, and 56% of unfished biomass under the simultaneous MSY scenario (Table 1). The reduced biomasses of these groups in the MMSY scenario also results in lower catches compared with the simultaneous MSY scenario, with decreases of 15%, 8%, and 5% for abalone, urchin, and piscivorous fishes, respectively (Table 1). Herbivorous fishes decrease in biomass by 8% in the MMSY scenario compared with simultaneous MSY, however catches increase by 10% in the MMSY scenario (Table 1). In Nova Scotia, the MMSY scenario results in the collapse of lobster, pollock (>49 cm), and dogfish, while redfish and scallop biomasses decrease by 50% and 91% compared with the simultaneous MSY scenario, respectively, leading to catch decreases of 73% and 96% (Table 2). The ecosystem is essentially predicted to become simpler under MMSY, after fishing down predators and releasing the more productive groups from predation, resulting in increased catches of lower trophic level species such as longhorn sculpin, haddock, mackerel, and herring (Table 2).
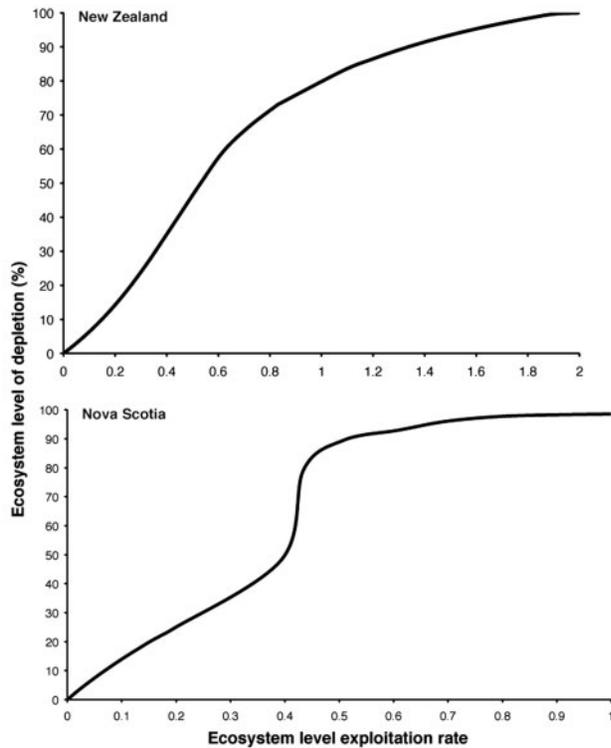
MMSY and exploitation rates

While lobsters and their ecosystem roles were the focus of this work, it is still informative to consider the shape of the overall ecosystem exploitation patterns, as this provides a context for the lobster findings. The relationship between the exploitation rate (u) of the ecosystem and level of ecosystem depletion indicated a logistic function for New Zealand, whereby at high exploitation rates, the cumulative impacts on the ecosystem level of depletion were attenuated (Figure 3). The cumulative impacts on the ecosystem level of depletion were also attenuated at higher exploitation rates in Nova Scotia, but a step change was observed between exploitation rates of 0.4–0.5, resulting in depletion increasing from 48% to 90% (Figure 3). The ecosystem consequences of this step change are substantial, as 12% of groups within the ecosystem were projected to collapse at $u = 0.4$ which included sharks and large pelagics, while at $u = 0.5$, 41% of groups are collapsed, including toothed cetaceans. The resulting ecosystem is dominated by sculpin (<25 and >25 cm) and mackerel, which are 21-, 14-, and 7-fold more abundant than when unfished, respectively (Table 2). Catches are dominated by pollock (>49 cm), mackerel, and sculpin (>25 cm), which account for 43%, 35%, and 12% of the total catch, respectively (Table 2).

In the Nova Scotia model, there are 31 groups in the model that are fished, 27 of which have been subjected to heavy fishing since 1950s (Zwanenburg *et al.*, 2002). Of these, 13 have a present exploitation rate that is estimarted to be within ± 20% of u_{MSY}, while 6 fisheries have exploitation rates greater than u_{MSY}. A few groups have very low current exploitation rates, much lower than those predicted to produce MSY, because they are barely fished (e.g. squids, other pelagics, and longhorn sculpin), they are migratory or their biomass is uncertain. The inclusion of these groups in the estimate of total ecosystem exploitation rate make it seem low (0.11). However, the average exploitation rate for the more heavily fished species is 0.3, which is closer to that predicted to produce MMSY (0.39).

Discussion

Ecosystem impacts of lobster MSY and MMSY targets

Our results indicate that lobster fisheries in New Zealand and Nova Scotia are presently fished at higher exploitation levels than predicted to achieve MSY from single-species perspectives. This is

Figure 3. Relationship between ecosystem level of depletion (LOD) and ecosystem level exploitation rate ($u = C_i/B_i$) for Cook Strait, New Zealand and western Scotian Shelf, Canada ecosystem models.

predicted to have significant effects on other species in the ecosystem through direct and indirect feeding linkages, and a reduction of exploitation rates is predicted to both increase lobster catches as well as reduce ecosystem impacts. Similar win–win situations have also been shown for the reduction of other invertebrate fisheries, such as abalone and urchin fisheries in New Zealand (Eddy et al., 2015).

Exploited groups other than lobster in both New Zealand and Nova Scotia are presently fished at levels lower than predicted to produce MMSY in our simulations. Interestingly, for both regions, total ecosystem catch was lower when exploitation rates predicted to produce MSY for individual species were run individually or simultaneously compared with simulations that maximized MMSY. In both ecosystems, the exploitation level that produced MMSY resulted in major changes in the ecosystem. In Nova Scotia, at MMSY, 12% of all groups within the ecosystem collapsed (<10% B_0 biomass), and 29% of fished stocks collapsed. The structure of the ecosystem changes with the loss of most of the higher trophic level commercial species present, which are "replaced" by lower trophic level species such as benthic invertebrates and fin-fish like pollock, sculpin, and mackerel—which also comprised the majority of catches. The predators of these low trophic level species, like marine mammals and seabirds, also increase. Similarly, in New Zealand, at MMSY, commercial species—abalone, urchin, and piscivorous fish—decrease while invertebrate feeding fishes, cryptic fishes, and mobile invertebrate carnivores increase in biomass, as do their predators, such as birds.

Importantly, these results indicate that for both the New Zealand and Nova Scotia ecosystems, fishing at MMSY could

have broader ecosystem effects than fishing at MSY simultaneously across individual stocks. This is why attempts to find new ecosystem based fishing strategies and reference points need to recognize ecosystem structure and differential productive capacity across species. It will not be sufficient to simply take single species theories and apply them at ecosystem scales. Fishing in proportion to productivity has been suggested as one means of dealing with these issues (the "balanced harvest" concept; Garcia et al., 2012), though debate continues around its true potential (Burgess et al., 2015; Froese et al., 2016) and it was not explored further here.

In both the New Zealand and Nova Scotia simulations, fishing at MMSY—which occurs at higher ecosystem exploitation rates than currently in use—leads to greater ecosystem effects, and greater depletion of lobster (which crashes in Nova Scotia) compared with the use of single-species MSY targets. In Nova Scotia, the u_{MSY} estimates are for an ecosystem that has been heavily fished for decades. At the step change observed for MMSY at $u = 0.4$, most stocks that were already heavily fished were projected to collapse, leaving species such as longhorn sculpin and American plaice to contribute to MMSY at higher exploitation levels, suggesting lower ecosystem resilience. The history of fisheries exploitation on the western Scotian Shelf has been very unbalanced with high exploitation rates, as has been shown for the eastern Scotian Shelf (Bundy et al., 2005). At present, lobster catches on the Atlantic coast of Nova Scotia are the highest that they have been historically (Miller and Breen, 2010), suggested to be related to a simplification of the food web following collapses of coastal groundfish stocks (Boudreau and Worm, 2010; Steneck et al., 2011), although this has not been shown mechanistically.

In terms of lobster fisheries management, our results agree with the analysis by Miller and Breen (2010), who concluded that management of the lobster fisheries in New Zealand and Nova Scotia could be improved. Through the use of ecosystem modeling, we have found that reducing current lobster fisheries exploitation levels could improve fisheries catches and also reduce ecosystem impacts. These findings have important implications for EBFM of these fisheries, as we have provided evidence that these fisheries are having impacts on the structure and functioning of associated ecosystems.

Fisheries interaction effects

Similarly to our findings, a study from the southern Benguela, South Africa, for an ecosystem model developed with Atlantis (Fulton, 2010; Fulton et al., 2011), also reported that the sum of catches from simulations that applied u_{MSY} levels individually was lower than total catch from a simulation that applied u_{MSY} levels to all stocks simultaneously (Smith et al., 2014). These observations were explained by a greater catch of smaller fish, and because the carrying capacity for smaller fishes increased as a result of decreased competition, and the carrying capacity of larger fishes decreased due to fewer smaller fish for prey (Smith et al., 2014). It has been found that in almost all cases examined, indirect food-web effects increase the productivity of harvested species, yields produced by simultaneously using u_{MSY} values can vary greatly from predicted u_{MSY} values, and that the direction of change in catch for individual groups is not consistently related to trophic level (Walters et al., 2005). Examining 31 ecosystems used in Worm et al. (2009), the sum of single-species MSYs was less than MMSY in 61–71% of cases and came at a significant cost

to top and medium level predators. A closer examination of productivity of different groups found that planktivores are most often the most productive exploited group and that the sum of pelagic catches is almost always greater than the sum of demersal catches (Gaichas *et al.*, 2012; Lucey *et al.*, 2012). Our results, taken in combination with these studies, further supports the need for fisheries management bodies to manage at both the level of the ecosystem as well as at the level of individual stocks.

Strategies for EBFM

Discussions about how to apply EBFM have been ongoing for more than a decade (special issue by Browman *et al.*, 2004), with no clear resolution. The combination of the existing global fishing and biodiversity conventions underline that maintaining the structure and functioning of the ecosystem is important (CBD, 2000; UN FAO, 2001), and this is reflected in national policies defining the goals of EBFM (e.g. as is the case for both New Zealand and Nova Scotia: MPI, 2014b; DFO, 2011). Finding useful reference points and generalizable strategies that achieve sustainable catches while meeting the ecosystem structure and function requirements is an ongoing exercise. One of the first steps is to see whether concepts from single-species fisheries management translate to ecosystem scales. In terms of fisheries management targets for New Zealand and Nova Scotia, we suggest that just as MSY is a limit for single-species fishing, MMSY should be considered an upper ecosystem limit. While MMSY maximized the total catches across ecosystems, it came with strong ecological costs in both systems, and the collapse of both fished and unfished groups in Nova Scotia, including lobster—the most economically valuable fishery. This may be due, in part, to the simplified search criteria used to find MMSY, as in reality, the estimation of a socially acceptable MMSY would be preceded by extensive involvement and consultation with stakeholders to establish ecosystem and societal objectives for the ecosystem, which would be incorporated into the optimization methods to estimate exploitation rates that meet these objectives. Such objectives could include a provision whereby no species should collapse, or rebuilding strategies for species with low biomass (Worm *et al.*, 2009). If we consider only the subset of simulations run here where the rebuilding criteria of 40% unfished biomass were met (the "safe operating space", Figure 2), there is much lower ecosystem impact. In these circumstances, for New Zealand, this would mean fishing at 75% of MMSY levels, while for Nova Scotia it would mean fishing at 37% of MMSY levels. Catch under these scenarios is lower than under MMSY, creating a tension with stakeholders or managers whom solely focus on maximal food security provision. In New Zealand, there is a 16% reduction from MMSY total catch to the total catch in the simulation where no exploited group decreases <40% unfished biomass, while in Nova Scotia this would require a 46% reduction in total catch. Given that there has been a long-term increase in lobster landings in most areas of Nova Scotia and that current landings are at record highs (DFO, 2015), a 46% reduction in landings would be a hard sell to the lobster fishing industry.

Perhaps reassuringly for managers, it appears that for the two ecosystems considered here, u_{MSY} targets are presently a better reference point than the apparently less ecologically conservative MMSY explored here. In New Zealand, it just so happens that the present ecosystem level of depletion is almost the same as that predicted when maximizing single-species u_{MSY} levels, which also

achieves the rebuilding mandate. However, we do point out that from a single-species perspective, lobster is presently exploited at levels higher than those predicted to produce MSY, a detail that can be masked when aggregating all stocks up to the level of total ecosystem catch. In Nova Scotia however, managing all individual stocks at their individual u_{MSY} levels would not achieve the rebuilding mandate of 40% unfished biomass, suggesting that the argument of doing good single-species fisheries management is enough (Rice, 2011), might not be sufficient in itself to achieve rebuilding mandates of all stocks, which we suggest is a central tenant of EBFM.

Alternative fisheries management strategies such as balanced harvesting have been proposed, such that fisheries exploitation is proportional to productivity in order to maintain the size structure of individual species and the size structure and relative abundances of species across ecosystems, and thus the structure and functioning of ecosystems (Garcia *et al.*, 2012). This results in fisheries catches dominated by smaller, more productive species, such as small pelagic fishes or productive invertebrates, but does maintain more of the ecosystem structure (Garcia *et al.*, 2012; Jacobsen *et al.*, 2014). At this stage, much work remains to be done to determine feasible patterns of exploitation to produce maximum sustainable catch (and thus food security) without compromising ecosystem structure and function, and there have been strong critiques of the approach (Burgess *et al.*, 2015; Froese *et al.*, 2015). Furthermore, if such drastically different fishing patterns are found to be more desirable than current approaches, work needs to be done on how to transition between the fishing patterns. For example, before balanced harvesting should even be considered, the ecosystem structure should be in the desired state, which may require the rebuilding of ecosystems, healthy fish populations, and sustainable fisheries (Bundy *et al.*, 2005; Garcia *et al.*, 2012). In terms of the ecosystems considered here, it is unclear what a balanced harvest-like exploitation strategy would mean for these systems in terms of implementation of the policy or the consequences for fisheries catches and ecosystem impacts, as that explicit pattern of fishing was not trialed.

Many of the studies that have considered the yield implications of a balanced harvest approach have identified its heavy reliance on lower trophic levels (Garcia *et al.*, 2012; Jacobsen *et al.*, 2014). Similarly, the MMSY scenarios here indicate that in New Zealand, this kind of approach would likely mean greater catches of a lot of smaller pelagic species. A reliance on lower trophic level fisheries is also observed in intensively fished ecosystems, as higher trophic levels have often been heavily depleted. This was observed here for the Nova Scotia ecosystem at exploitation rates higher than predicted to produce MMSY, where there were significant costs to higher trophic levels. Bundy *et al.* (2005) employed a related ecosystem model for the eastern Scotian Shelf, Nova Scotia, to compare high levels of exploitation for: only top-level predators and only low-trophic level groups, as well as moderate exploitation of all trophic levels—according to balanced harvest—finding that selective fishing for only the low-trophic level groups—not balanced harvest—maximized yield and minimized ecosystem disturbance. Yet increasing exploitation of low trophic level species can also have strong ecosystem effects, as recently shown for forage fish and invertebrate fisheries (Smith *et al.*, 2011, Eddy *et al.*, 2016). This further highlights why ecosystem objectives need to be considered from different lenses—food security, profit maximization, and conservation—to determine whether the selection of reference points that addresses all the

criteria are possible (e.g. see Smith *et al.*, 2011, who suggest conservative forage fish reference points to minimize ecosystem effects).

Concluding thoughts

The Ecopath with Ecosim (EwE) ecosystem modeling approach that we have employed here comes with trade-offs compared with the single-species stock assessment approach that has been historically employed. In order to consider ecosystem impacts of fisheries, inclusion of a majority of the functional groups in the food web is required, along with their associated biological parameters that describe their growth and consumption, as well as ecological parameters that describe feeding relationships among the functional groups. Including these parameters increases model complexity and introduces additional uncertainty, which often requires a more simplistic treatment of individual functional groups, such as an absence of size structure. These trade-offs in model complexity have been an ongoing consideration of ecosystem modelling since the field's inception, most recently reviewed in detail by Collie *et al.* (2016), but simply cannot be avoided if asking ecosystem-level questions.

As fisheries management agencies make the transition from single-species to ecosystem-based management, it is important to understand the impacts of different management targets and strategies. Simply applying theoretical concepts from classical fisheries science to ecosystems, without also applying hard learnt lessons around those concepts is likely to perpetuate past mistakes. As is the current thinking for MSY, we suggest that if an ecosystem is being managed under conservation as well as fisheries (e.g. yield) objectives, then MMSY should be considered a limit reference point, and not a target. MMSY can provide greater ecosystem wide catches, but associated ecosystem effects should be evaluated prior to implementation to ensure it does not compromise ecosystem and societal objectives. EBFM for species such as lobster needs to consider their ecological role, as lobsters have been shown to play important structuring roles within marine ecosystems (Boudreau and Worm, 2010, 2012; Eddy *et al.*, 2014). While we have not explicitly considered the impact of changing climatic conditions, it is clear from other studies (e.g. Cornwall and Eddy, 2015 for New Zealand) that lobster management in future oceans will also need to take into account ocean acidification and other shifts in environmental conditions. In Nova Scotia, any future recovery of the depleted groundfish stocks, such as cod, as recently reported for nearby Newfoundland and Labrador (Rose and Rowe, 2015), could see ecosystem roles now dominated by lobster reoccupied by groundfish, possibly resulting in decreased lobster abundances. This reinforces the messages of Miller and Breen (2010), Brown *et al.* (2012), and Pershing *et al.* (2015) that fisheries management is improved by quicker responses to changes in stocks or fisheries, and is imperative for a changing marine environment.

References

Anderson, S. C., Lotze, H. K., and Shackell, N. L. 2008. Evaluating the knowledge base for expanding low-trophic level fisheries in Atlantic Canada. Canadian Journal for Fisheries and Aquatic Sciences, 65: 2553–2571.

Anderson, S. C., Mills Flemming, J., Watson, R., and Lotze, H. K. 2011a. Rapid Global Expansion of Invertebrate Fisheries: Trends, Drivers, and Ecosystem Effects. Plos One, 6: e14735.

Anderson, S. C., Mills Flemming, J., and Lotze, H. K. 2011b. Serial exploitation of global sea cucumber fisheries. Fish and Fisheries, 12: 317–339.

Annala, J. H. 1996. New Zealand's ITQ system: have the first eight years been a success or a failure? Reviews in Fish Biology and Fisheries, 6: 43–62.

Araújo, J. N., and Bundy, A. 2011. Description of three Ecopath with Ecosim ecosystem models developed for the Bay of Fundy, Western Scotian Shelf and NAFO Division 4X. Canadian Technical Report of Fisheries and Aquatic Sciences 2952: xii + 189 p.

Araújo, J. N., and Bundy, A. 2012. Effects of environmental change, fisheries and trophodynamics on the ecosystem of the western Scotian Shelf, Canada. Marine Ecology Progress Series, 464: 51–67.

Boudreau, S. A., and Worm, B. 2010. Top-down control of lobster in the Gulf of Maine: insights from local ecological knowledge and research surveys. Marine Ecology Progress Series, 403: 181–191.

Boudreau, S. A., and Worm, B. 2012. Ecological role of large benthic decapods in marine ecosystems: a review. Marine Ecology Progress Series, 469: 195–213.

Breen, P. A., Sykes, D. R., Starr, P. J., Kim, S., and Haist, V. 2009. A voluntary reduction in the commercial catch of rock lobster (*Jasus edwardsii*) in a New Zealand fishery. New Zealand Journal of Marine and Freshwater Research, 43: 511–523.

Browman, H. I., Cury, P. M., Hilborn, R., *et al.* 2004. Perspectives on ecosystem-based approaches to the management of marine resources. Marine Ecology Progress Series, 274: 269–303.

Brown, C. J., Fulton, E. A., Possingham, H. P., and Richardson, A. J. 2012. How long can fisheries managers afford to delay action on climate change? Ecological Applications, 22: 298–310.

Bundy, A., Fanning, P., and Zwanenburg, K. C. T. 2005. Balancing exploitation and conservation of the eastern Scotian Shelf ecosystem: Application of a 4D Ecosystem exploitation index. ICES Journal of Marine Science, 65: 503–510.

Bundy, A., Heymans, J. J., Morissette, L., and Savenkoff, C. 2009. Seals, cod and forage fish: a comparative exploration of variations in the theme of stock collapse and ecosystem change in four northwest Atlantic ecosystems. Progress in Oceanography, 81: 188–206.

Burgess, M. G., Diekert, F. K., Jacobsen, N. S., Andersen, K. H., and Gaines, S. D. 2015. Remaining questions in the case for balanced harvesting. Fish and Fisheries DOI: 10.1111/faf.12123.

CBD (Convention on Biological Diversity). 2000. Ecosystem approach. COP 5 Decision V/6. Conference of the Parties 5. Convention on Biological Diversity. www.cbd.int/decision/cop/default.shtml?id=7148

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

Christensen, V., and Walters, C. J. 2004b. Trade-offs in ecosystem – scale optimization of fisheries management policies. Bulletin of Marine Science, 74: 549–562.

Coll, M., Navarro, J., Olson, R. J., and Christensen, V. 2013. Assessing the trophic position and ecological role of squids in marine ecosystems by means of foodweb models. Deep Sea Research II, 95: 21–36.

Collie, J. S., Botsford, L. W., Hastings, A., Kaplan, I. C., Largier, J. L., Livingston, P. A., Plagányi, É., *et al.* 2016. Ecosystem models for fisheries management: finding the sweet spot. Fish & Fisheries, 17: 101–125.

Cornwall, C. E., and Eddy, T. D. 2015. Effects of near-future ocean acidification, fishing, and marine protection on a temperate, coastal ecosystem. Conservation Biology, 29: 207–215.

Costello, C., Ovando, D., Hilborn, R., Gaines, S. D., Deschenes, O., and Lester, S. E. 2012. Status and solutions for the world's unassessed fisheries. Science, 338: 517–520.

DFO. 2011. Integrated Fisheries Management Plan (Summary), Lobster Fishing Areas 27-38, Scotia Fundy Sector, Maritimes Region, 2011. http://www.dfo-mpo.gc.ca/fm-gp/peches-fisheries/ifmp-gmp/maritimes/insholob-2011-eng.htm (last accessed 20 January 2015).

DFO. 2013. Provincial and Territorial Statistics on Canada's Fish and Seafood Exports in 2012. http://www.dfo-mpo.gc.ca/media/back-fiche/2013/hq-ac03a-eng.htm.

DFO. 2014a. Lobster (*Homarus americanus*) off Southwest Nova Scotia (Lobster Fishing Area 34): 2014 Stock Status Update. DFO Canadian Science Advisory Secretariat Scientific Research Document, 2014/036.

DFO. 2014b. 2014 Stock Status Update of Lobster (*Homarus americanus*) in the Bay of Fundy (Lobster Fishing Areas 35-38). DFO Canadian Science Advisory Secretariat Scientific Research Document. 2014/047.

DFO. 2015. 2015 Stock Status Update of Lobster (*Homarus americanus*) in the Bay of Fundy (Lobster Fishing Areas 35-38). DFO Canadian Science Advisory Secretariat Scientific Research Document. 2015/030.

Eddy, T. D., Coll, M., Fulton, E. A., and Lotze, H. K. 2015. Trade-offs between invertebrate fisheries catches and ecosystem impacts in coastal New Zealand. ICES Journal of Marine Science, 75: 1380–1388.

Eddy, T. D., Lotze, H. K., Fulton, E. A., *et al.* 2016. Ecosystem effects of invertebrate fisheries. Fish and Fisheries, DOI: 10.1111/faf.12165.

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

Essington, T. E., and Punt, A. E. 2011. Implementing Ecosystem-Based Fisheries Management: Advances, Challenges and Emerging Tools. Fish and Fisheries, 12: 123–124.

Fogarty, M. J., and McCarthy, J. J. 2014. Marine Ecosystem-Based Management. The Sea, Vol. 16. Harvard University Press, Cambridge, USA.

Froese, R., Walters, C., Pauly, D., Winker, H., Weyl, O. L. F., Demirel, N., Tsikliras, A. C., *et al.* 2016. A critique of the balanced harvesting approach to fishing. ICES Journal of Marine Science, 73: 1640–1650.

Fulton, E. A. 2010. Approaches to end-to-end ecosystem models. Journal of Marine Systems, 81: 171–183.

Fulton, E. A., Link, J. S., Kaplan, I. C., Savina-Rolland, M., Johnson, P., Ainsworth, C., Horne, P., *et al.* 2011. Lessons in modelling and management of marine ecosystems: the Atlantis experience. Fish and Fisheries, 12: 171–188.

Gaichas, S. K., Odell, G., Aydin, K. Y., and Francis, R. C. 2012. Beyond the defaults: functional response parameter space and ecosystem-level fishing thresholds in dynamic food web model simulations. Canadian Journal of Fisheries and Aquatic Science, 69: 2077–2094.

Garcia, S. M., Kolding, J., Rice, J., Rochet, M. J., Zhou, S., Arimoto, T., Beyer, J. E., *et al.* 2012. Reconsidering the consequences of selective fisheries. Science, 335: 1045–1047.

Hilborn, R., and Walters, C. 1992. Quantitative fisheries stock assessment: choice, dynamics and uncertainty. Kluwer Academic Publishers, Boston. 570 p.

Jacobsen, N. S., Gislason, H., and Andersen, K. H. 2014. The consequences of balanced harvesting of fish communities. Proceedings of the Royal Society B, 281: 20132701.

Link, J. 2010. Ecosystem-Based Fisheries Management: Confronting Tradeoffs. Cambridge University Press, New York. 207 p.

Long, R. D., Charles, A., and Stephenson, R. L. 2015. Key principles of marine ecosystem-based management. Marine Policy, 57: 53–60.

Lucey, S. M., Cook, A. M., Boldt, J. L., Link, J. S., Essington, T. E., and Miller, T. J. 2012. Comparative analyses of surplus production dynamics of functional feeding groups across 12 northern hemisphere marine ecosystems. Marine Ecology Progress Series, 459: 219–229.

Miller, R. J., and Breen, P. A. 2010. Are lobster fisheries being managed effectively? Examples from New Zealand and Nova Scotia. Fisheries Management and Ecology, 17: 394–403.

MPI (Ministry for Primary Industries). 2009. Logbook database extract, data publically available by request to the Ministry of Fisheries: rdm@fish.govt.nz.

MPI. 2014a. Fisheries and Aquaculture Production and Trade Quarterly Report: rdm@fish.govt.nz.

MPI. 2014b. Fisheries Assessment Plenary, May 2014: stock assessments and stock status. Compiled by the Fisheries Science Group, Ministry for Primary Industries, Wellington, New Zealand. 1381 p.

Newell, R. G., Sanchirico, J. N., and Kerr, S. 2005. Fishing quota markets. Journal of Environmental Economics and Management, 49: 437–462.

Pauly, D., Christensen, V., and Walters, C. J. 2000. Ecopath, Ecosim and Ecospace as tools for evaluating ecosystem impact of fisheries. ICES Journal of Marine Sciences, 57: 697–706.

Pauly, D., and Zeller, D. 2016. Catch reconstructions reveal that global marine fisheries catches are higher than reported and declining. Nature Communications, 7: 10244.

Perry, R. I., Walters, C. J., and Boutillier, J. A. 1999. Framework for providing scientific advice for the management of new and developing invertebrate fisheries. Reviews in Fish Biology and Fisheries, 9: 125–150.

Pershing, A. J., Alexander, M. A., Hernandez, C. M., Kerr, L. A., Le Bris, A., Mills, K. E., Nye, J. A., *et al.* 2015. Slow adaptation in the face of rapid warming leads to collapse of the Gulf of Maine cod fishery. Science, 350: 809–812.

Pikitch, E. K., Santora, C., Babcock, E. A., Bakun, A., Bonfil, R., Conover, D. O., Dayton, P., *et al.* 2004. Ecosystem-based fishery management. Science, 305: 346–347.

Pitcher, T. J., Kalikoski, D., Short, K., Varkey, D., and Pramod, G. 2009. An evaluation of progress in implementing ecosystem-based management of fisheries in 33 countries. Marine Policy, 33: 223–232.

Ricard, D., Minto, C., Jensen, O. P., and Baum, J. K. 2011. Examining the knowledge base and status of commercially exploited marine species with the RAM Legacy Stock Assessment Database. Fish and Fisheries, 13: 380–398.

Rice, J. 2011. Managing fisheries well: delivering the promises of an ecosystem approach. Fish and Fisheries, 12: 209–231.

Rose, G. A., and Rowe, S. 2015. Northern cod comeback. Canadian Journal of Fisheries and Aquatic Sciences, 72: 1789–1798.

Sherman, K., and Hempel, G. (Ed.). 2008. The UNEP Large Marine Ecosystem Report: A perspective on changing conditions in LMEs of the world's Regional Seas. UNEP Regional Seas Report and Studies No. 182. United Nations Environment Programme. Nairobi, Kenya.

Smith, A. D. M., Brown, C. J., Bulman, C. M., Fulton, E. A., Johnson, P., Kaplan, I. C., Lozano-Montes, H., *et al.* 2011. Impacts of fishing low–trophic level species on marine ecosystems. Science, 26: 1147–1150.

Smith, M. D., Fulton, E. A., and Day, R. W. 2014. An investigation into fisheries interaction effects using Atlantis. ICES Journal of Marine Science, 72: 275–283.

Steneck, R. S., Hughes, T. P., Cinner, J. E., Adger, W. N., Arnold, S. N., Berkes, F., Boudreau, S. A., *et al.* 2011. Creation of a gilded trap by the high economic value of the Maine lobster fishery. Conservation Biology, 25: 904–912.

Swartz, W., Sumaila, R., and Watson, R. 2013. Global ex-vessel fish price database revisited: A new approach for estimating 'missing' prices. Environmental and Resource Economics, 56: 467–480.

Tremblay, M. J., Pezzack, D., and Gaudette, J., Denton, C., Cassista Da-Ros, M., and Allard, J. 2012. Development of reference points for inshore lobster in the Maritimes Region (LFAS 27-38). Fisheries and Oceans Canada. Canadian Science Advisory Secretariat Research Document 2012/028.

Tremblay, M. J., Pezzack, D. S., Gaudette, J., *et al.* 2013. Assessment of lobster (*Homarus americanus*) off southwest Nova Scotia and in the Bay of Fundy (Lobster Fishing Areas 34-38). DFO Canadian Science Advisory Secretariat Scientific Research Document. 2013/078. Viii + 125 p.

United Nations Food and Agriculture Organization (FAO). 2001. The Reykjavik declaration on responsible fisheries in the marine ecosystem. Available from: Ftp://Ftp.Fao.Org/Fi/Document/Reykjavik/Y2198t00_Dec.Pdf.

Walters, C. J., Christensen, V., Martell, S. J., and Kitchell, J. F. 2005. Possible ecosystem impacts of applying MSY policies from single-species assessment. ICES Journal of Marine Science, 62: 558–568.

Worm, B., Hilborn, R., Baum, J. K., Branch, T. A., Collie, J. S., Costello, C., Fogarty, M. J., *et al.* 2009. Rebuilding global fisheries. Science, 325: 578–585.

Zwanenburg, K. C. T., Bowen, D., Bundy, A., Frank, K., Drinkwater, K., O'Boyle, R., Sameoto, D., *et al.* 2002. Decadal changes in the Scotian Shelf large marine ecosystem. In: Changing states of the large marine ecosystems of the North Atlantic. Edited by Blackwell Science Inc., Malden MA, USA.

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