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Ecosystem Effects of Invertebrate Fisheries

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Abstract

Since the 1950s, invertebrate fisheries catches have rapidly expanded globally to more than 10 million tonnes annually, with twice as many target species, and are now significant contributors to global seafood provision, export, trade, and local livelihoods. Invertebrates play important and diverse functional roles in marine ecosystems, yet the ecosystem effects of their exploitation are poorly understood. Using 12 ecosystem models distributed worldwide, we analyzed the trade-offs of various invertebrate fisheries and their ecosystem effects as well as ecological indicators. Although less recognized for their contributions to marine food webs, our results show that the magnitude of trophic impacts of invertebrates on other species of commercial and conservation interest are comparable with those of forage fish. Generally, cephalopods showed the strongest ecosystem effects and were characterized by a strong top-down predatory role. Lobster, and to a lesser extent, crabs, shrimp, and prawns, also showed strong ecosystem effects, but with lower trophic levels. Benthic invertebrates, including epifauna and infauna, also showed considerable ecosystem effects but with strong bottom-up characteristics. In contrast, urchins, bivalves and gastropods showed generally lower ecosystem effects in our simulations. Invertebrates also strongly contributed to benthic-pelagic coupling, with exploitation of benthic invertebrates impacting pelagic fishes, and vice versa. Finally, on average, invertebrates produced maximum sustainable yield at lower levels of depletion (~45%) than forage fish (~65%), highlighting the need for management targets that avoid negative consequences for target species and marine ecosystems as a whole.

Key words: Ecopath with Ecosim (EwE), ecological indicators, ecosystem-based fisheries management (EBFM), functional roles, invertebrate exploitation, trophic impacts

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Introduction

Increased depletion, protection or restrictive management of marine finfish over past decades has led to large expansions in fisheries for invertebrates and low trophic level (LTL) fish (Worm *et al.* 2009; Hunsicker et al. 2010; Anderson *et al.* 2011a; Smith *et al.* 2011; Costello *et al.* 2012; Pikitch et al. 2014). Many of these species, however, are essential food for higher trophic levels, including species of commercial and conservation interest (e.g. fish, mammals, and birds), and support overall ecosystem structure and functioning. Thus, these fisheries can have strong ecosystem consequences as recently demonstrated for forage fish and krill in pelagic ecosystems (Smith *et al.* 2011; Pikitch *et al.* 2014). Due to their wide taxonomic and functional diversity, invertebrates play varied roles in both pelagic and benthic ecosystems, such as predator, prey, herbivore, filter feeder, scavenger, and detritivore (Hunsicker *et al.* 2010; Anderson *et al.* 2011a), and some are considered keystone species (Eddy *et al.* 2014). Understanding the ecological roles of these species and the ecosystem effects of their exploitation is critical if we want to move towards a more sustainable and ecosystem-based fisheries management (EBFM) that aims to maintain or restore the structure and functioning of marine ecosystems (Pikitch *et al.* 2004).

Global invertebrate catches have increased 6-fold to >10 million tonnes annually (Figure 1) and the number of target species has doubled since the 1950s (Berkes *et al.* 2006; Hunsicker *et al.* 2010; Anderson *et al.* 2011a; 2011b). This includes an expansion of existing, and the emergence of new fisheries for molluscs (mussels, oysters, gastropods), crustaceans (lobster, shrimp, crabs, krill), cephalopods (squids, octopus), and echinoderms (sea urchins, sea cucumbers). Today, marine invertebrates provide substantial amounts of seafood and animal protein, important employment and income opportunities, high value in international markets and trade, and accounted for 14% of global fisheries catches by weight in 2012 (Berkes *et al.* 2006; Anderson *et al.* 2011b; FAO 2011; Smith *et al.* 2011). Globally, crustaceans have been the most highly valued fished group since the 1970s, valued at ~3000 USD/tonne in 2005 (Swartz *et al.* 2013). In Canada and New Zealand, lobster is now the most valuable export (DFO 2013; MPI 2014, respectively), whereas sea cucumber fisheries form the main source of income for many coastal communities in the Indo-Pacific (Anderson *et al.* 2011b). Despite their economic and societal importance, many invertebrates lack formal stock assessments or management plans, and the ecosystem consequences of their exploitation are largely unknown (Anderson *et al.* 2008; 2011a; 2011b).

Ecosystem models have been applied to study the ecosystem effects of fisheries (Worm *et al.* 2009; Fulton *et al.* 2011; Smith *et al.* 2011; Collie *et al.* 2016). Unfortunately, the paucity of information about invertebrate populations and their fisheries is also reflected in their often-poor representation within ecosystem models, where invertebrates are often lumped into coarsely resolved compartments. Here, we employ published ecosystem models with sufficient representation of invertebrate functional groups and their associated fisheries to analyze the ecosystem effects of their exploitation. In total, we simulate the effects of 73 invertebrate groups encompassing cephalopods, lobsters, crabs, shrimps/prawns, echinoderms, gastropods, bivalves and benthic invertebrates, epifauna, and infauna, from no fishing to local extinction, and then determine the ecosystem effects as the resulting biomass changes in other trophic groups.

Methods

Ecosystem model selection

We developed a set of selection criteria to apply to published Ecopath with Ecosim (EwE) models (Christensen and Walters 2004) to ensure that our questions about the ecosystem impacts of invertebrate fisheries could be tested. The first criterion was that the model had to be sufficiently resolved into at least three separate invertebrate trophic groups in order to perform simulations of invertebrate fisheries, and not just include one generic, catch-all invertebrate group; second, that it had active fisheries for at least three invertebrate trophic groups represented in the model; and third, that it was calibrated to observational survey, catch, fishing mortality, and/or fishing effort data (Table S1). From the EwE models listed at www.ecopath.org/models and additional published EwE models not listed on the website, there were only 12 models that met our selection criteria (Tables S1, S2), but were well distributed around the world (Figure 1). We also searched for replicate models in these 12 regions to represent alternative model structures developed in Atlantis and OSMOSE; however, at the time of performing the simulations, there were insufficient alternative models with appropriate resolution of invertebrates required to compare. Further details on data used to parameterize invertebrate groups and model calibration in each EwE model can be found in the Supporting Information.

Modelling approach

We used Ecosim (Walters *et al.* 1997; Christensen and Walters 2004) to run simulations of varying fishery exploitation rates (*F*) for each individual target invertebrate group, while F values for all other exploited trophic groups were kept constant at their most recent levels to produce levels of target group depletion from 0 to 100% (Eddy *et al.* 2015). Thereby, we followed a similar modelling approach as used by Smith *et al.* (2011) and Worm *et al.* (2009) for the ecosystem effects of forage fish and overall fisheries, respectively. The level of depletion (LOD) for exploited groups was calculated as the proportion of biomass for the target invertebrate group during exploitation simulations compared to the biomass of that group during a simulation where there was no exploitation of the target group (i.e. $1 - (B_i/B_0)$), calculated for the final year of simulations when groups had reached equilibrium. Models were run from their historical starting point until the most recent date using historical time series, and then fishing mortality (F) for the target invertebrate group was forced at a constant level. Simulation runs of 100 years were used to allow the model to reach equilibrium, and it was obvious that models had reached equilibrium.

Ecosystem effects

We determined the impacts of exploitation of each invertebrate group within each of the 12 ecosystems, totaling 73 invertebrate groups (Table S2). We calculated the proportion of all other trophic groups within the same ecosystem that were impacted by biomass changes of > 40% across different levels of target invertebrate group depletion (LOD = 0%, 25%, 60%, 80%, and 100%).

To understand the general ecosystem impacts of different invertebrate groups among models, we then categorized each of the 73 invertebrate groups into one of ten functional groups based on their life-history and feeding strategies (Table S2): cephalopods, lobsters, crabs, shrimps/prawns, echinoderms, gastropods, bivalves, benthic invertebrates, epifauna, and infauna. Large jellies from the California Current and euphausiids from southeastern Australia did not fall into one of these ten groups, and are not considered in the group analyses. Some of the invertebrate trophic groups from the models contained a combination of more than one of these 10 functional groups (e.g., scallops and gastropods in the Adriatic Sea model, Table S2). These groups were designated based on the majority of biomass contribution within the groups.

For each of the 10 aggregate invertebrate groups, we then calculated the average (+/- SE) ecosystem impact at different levels of depletion across all 12 models. Similarly, to understand the ecosystem effects of invertebrate exploitation in each ecosystem model, we averaged the ecosystem impacts of all invertebrate groups at different levels of depletion within each model area.

To get a better sense of the distribution of the magnitude of positive and negative biomass changes, we calculated the frequency distribution of biomass changes in all trophic groups as a response to the exploitation of all 73 invertebrate groups at 25% and 60% depletion. We chose these levels of depletion because they are commonly used fisheries reference points and they follow the methods from a study on forage fish (Smith *et al.* 2011) to allow for comparability with invertebrates. To specifically investigate the impacts of invertebrate exploitation on commercial species and species of conservation concern (birds and mammals), we similarly calculated the frequency distribution of their biomass changes. We summarized these patterns by comparing the frequency of conservation (birds and mammals), commercial, and all groups responding with an increase or decrease of 40% biomass. In order to evaluate if groups of conservation concern were already depleted at the time when our simulations began, we compared the estimated unfished biomass of bird and mammal groups from the last year our invertebrate exploitation simulations, where there was no exploitation of bird and mammal groups, to the historical bird and mammal biomass estimates from the beginning of the historical time series in each model. In most cases, there were no major differences observed when using the historical biomass compared to the estimated unfished biomass, with the exception of fin whales from the Catalan Sea model, which were estimated to be only 13% of the historical 1978 biomass. Sea otters in the northern BC model were also only 16% of the estimated historical biomass in 1950. Additionally, in the northern BC model, many populations of large whales had been drastically reduced in numbers by 1950 (Surma and Pitcher 2015), which were not captured in the model, suggesting that whales may be more affected by invertebrate fisheries than represented in our simulations.

We were interested in the degree of coupling between benthic and pelagic compartments of the ecosystems. Therefore, individual trophic groups were assigned to either benthic or pelagic compartments of the ecosystem (Table S2) based on their feeding ecology from diet matrices and we calculated the change in the aggregate biomass of the benthic and pelagic compartments. When trophic groups preyed on both benthic and pelagic compartments, they were assigned to a compartment based on the majority (>50%) of their diet. We then evaluated the impact of exploitation of benthic invertebrate groups on the biomass of pelagic fish groups, and vice versa. To do so, we calculated the proportion of benthic and pelagic fish groups that were affected by a >40% biomass change.

Ecological indicators

To explain the differences in ecosystem effects for invertebrate groups, we calculated a variety of ecosystem responses to interpret the ecosystem effects of invertebrate fisheries, using EwE output for biomass, catches, trophic levels (TL), as well as other ecological indicators (e.g., connectance, keystoneness, omnivory; Power *et al.* 1996; Libralato *et al.* 2006; Eddy *et al.* 2015; Table S2). The connectance of an exploited trophic group (the proportion of feeding linkages for the exploited group compared to the total number of feeding linkages in the entire ecosystem) has been shown to be useful for explaining the ecosystem effects of forage fish exploitation (Smith *et al.* 2011). The omnivory index (OI) indicates the breath of trophic levels that a predator preys upon. Relative total impact indicates overall change in the ecosystem, and is used as a basis for keystoneness index 1. Keystoneness indices (keystoneness index #1: Libralato *et al.* 2006; keystoneness index #2: Power *et al.* 1996) evaluate which groups have large ecosystem effects relative to their biomass (Table S2). We also calculated the relative abundance of the exploited trophic group (proportion of the exploited group biomass to the total ecosystem biomass). Additionally, we calculated the supportive role to fisheries index (SURF), which quantifies the role of different trophic groups as prey to higher trophic levels (Plagányi and Essington 2014). These ecological indicators have been shown to be useful for understanding the ecosystem effects of fisheries exploitation (Smith *et al.* 2011; Eddy *et al.* 2014, 2015). We also plotted these indicators against the rank of the largest ecosystem impact for the exploitation of each individual invertebrate trophic group for an individual ecosystem, with the following ranks following Smith *et al.* (2011). Rank of 1 = no change greater than 20% in any other trophic group; 2 = no change greater than 60% in any other trophic group; 3 = change greater than 60% in at least one other trophic group.

Ecosystem characteristics and global catch data

To explore whether differences in the average ecosystem impacts across the 12 ecosystem models could be explained by some ecosystem characteristics in the wider large marine ecosystem (LME), we tested a range of ecosystem properties accessed from the Sea Around US Project (SAUP) website (www.seaaroundus.org) for each corresponding LME including; net primary production (NPP), invertebrate catch per unit area, species richness, number of fisheries, years fished, mean total catch per year fished, sea surface temperature (SST), and LME area. To see if global catch data explained variation in observed ecosystem impacts, we investigated average invertebrate catches by LME from 2006-2010 from the SAUP for corresponding LMEs (Figure 1). To determine the temporal change in global invertebrate catch, we obtained invertebrate catches by functional group from 1950–2012 from FAO FishStatJ software, using filters for the appropriate functional groups (Figure 1). We used linear regression analysis to evaluate links between LME properties and average ecosystem impacts of invertebrate exploitation at 60% depletion.

Next, we evaluated if ecosystem model characteristics explained variation in observed ecosystem impacts. To do so, we compared the ecosystem model indicators, model area, number of trophic groups (Table S1), total ecosystem biomass, ecosystem connectance (proportion of feeding links compared to all possible links), and predatory biomass (TL >4) with the average ecosystem impact of invertebrate exploitation at 60% depletion for each ecosystem using linear regression analysis.

Trade-offs between catch and ecosystem effects

To explore the trade-off between invertebrate catch and ecosystem effects, we calculated MSY from catch data, defined as the equilibrium catch level of the simulation producing the greatest catches (following Worm *et al.* 2009, Smith *et al.* 2011). We then compared the average ecosystem effects of each of the 73 invertebrate groups for each level of depletion (LOD = 0%, 25%, 60%, 80%, 100%) to the maximum sustainable yield (MSY) for each invertebrate fishery. To do so, we created an aggregate plot of MSY and ecosystem impact by averaging the simulation results for each of the 73 trophic groups at varying levels of depletion, and calculated 95% confidence intervals.

Results

Ecosystem effects

We found considerable differences in the magnitude of ecosystem effects across exploited invertebrate groups and ecosystem models (Figures 2-3). On average, exploitation of cephalopods (mostly squids) had the greatest impacts across the 12 studied ecosystems, with >20% of other groups affected by a 40% biomass change at medium to high exploitation levels (Figure 3A). Average impacts of lobsters, crabs, and shrimp/prawns were lower, yet they had strong impacts in some ecosystems (Figure 3A, grey dots). Composite groups of benthic invertebrates, epifauna and infauna also had considerable impacts on 10-20% of other groups within the ecosystem (Figure 3A). In contrast, exploitation of urchins, bivalves and gastropods generally had lower ecosystem effects in our simulations (Figure 3A). Individually, targeted exploitation of cephalopods and shrimps in the Gulf of Thailand, cephalopods in the Catalan Sea, and euphausiids in southeastern Australia showed the greatest effects (Figure 2).

Comparing all ecosystem models, southeastern (SE) Australia showed the greatest impacts at 60 and 80% depletion, and the Gulf of Thailand at 100% depletion, while the North Sea showed the lowest impacts across all exploitation levels (Figures 2, 3B). However, the variance of our results is on a similar scale across models, indicating that average results are not driven by a few, highly sensitive models (Figure 3B).

Impacted groups

We found 85% of other trophic groups were affected by <20% biomass change at medium invertebrate exploitation (60% depletion), while 5% of groups showed a >60% biomass change (Figures 3C, S1). About half the groups showed a decline in biomass, while others increased (Figure 3C, D, S1), including birds, mammals, and commercial groups, constituting substantial changes in populations and overall ecosystem structure. The most severe decline was observed in the Adriatic Sea model, where only a 25% depletion of benthic invertebrates was predicted to cause a 99% decline in marine turtle biomass, and local extinction at higher exploitation rates (Table S3). Higher (but still plausible) exploitation rates were required to observe impacts on other groups of conservation concern. For example, dolphins in the Catalan Sea were predicted to decline by 61% biomass at 60% depletion of bentho-pelagic cephalopods, while 60% depletion of squid in Northern British Columbia resulted in a 74% decline in seal and sea lion biomass, and diving ducks declined by 81% biomass in Chesapeake Bay with 60% depletion of benthic filter feeders (Table S3).

Invertebrate exploitation can also have strong impacts on commercial species, as demonstrated by the exploitation of shrimp in the Northern Adriatic, where 25% depletion resulted in a decline in mantis shrimp biomass by 96% (Figure 3D, Table S3). Our results indicate a high coupling between benthic and pelagic ecosystem compartments, as the exploitation of either benthic or pelagic invertebrates resulted in similar average impacts on benthic fishes (such as cod), whereas pelagic fishes (such as tuna) were more strongly affected by the exploitation of benthic than pelagic invertebrates due to indirect trophic links (Figure 3E).

Trade-offs between catch and ecosystem effects

Both invertebrates and forage fish show similarly increasing ecosystem impacts with increasing exploitation, however forage fish show slightly stronger impacts (Figure 4). At 60% depletion, invertebrates impact on average 11% of other trophic groups by at least 40% biomass change, compared to 15% for forage fish (Figure 4). Analyzing target catches and ecosystem impacts across a range of exploitation levels, we found that average MSY for invertebrates is predicted to occur at lower levels of depletion (~45%) than for forage fish (~65%; Figure 4). Currently, actual levels of depletion of invertebrate groups represented in our models range from <1% to 90% depletion, with several target species, such as lobsters, cephalopods, prawns, abalone, urchins, and shellfish fished to >45% depletion (Table S2).

Ecological indicators

Our results indicate that invertebrates can play both top-down and bottom-up roles within ecosystems, with some groups scoring high keystoneness values (indicating a top-down role), while others have high SURF index values (Figure 5). Cephalopods generally had high connectance, high TL, low relative abundance, and a high keystone index 1, indicating a strong predatory role (Figure 5). In comparison, lobster, and to a lesser extent crabs and shrimps/prawns were characterized by low relative abundance, medium connectance, medium TL and high omnivory (especially for lobster), suggesting they are also predatory, but with a more generalist role than cephalopods (Figure 5). Benthic invertebrates (and to a lesser extent epifauna and infauna) were characterized by high relative abundance, low TL, high SURF index, and medium connectance, indicating a strong bottom-up role within ecosystems (Figure 5). Finally, gastropods, bivalves, and urchins had smaller ecosystem effects, suggesting that their roles as prey and herbivore grazers or filter feeders are less strong, at least in the ecosystems considered here (Figure 5).

Overall, relative abundance, connectance, keystone index 1, and the SURF index were good predictors of ecosystem impacts, whereby trophic groups with higher values had a greater rank of largest effect (Figure 6). However, some invertebrates showed large ecosystem impacts at low connectance (e.g. bivalves in the western Scotian Shelf) or low relative abundance (e.g. sergestid shrimp in the Gulf of Thailand), while other trophic groups with intermediate keystone and SURF index values showed large ecosystem impacts (e.g. nephrops in the Irish Sea and abalone in New Zealand, respectively). Other indicators such as trophic level (TL), keystone index 2, and omnivory index explained less variation in observed ecosystem impact (Table S2).

Ecosystem characteristics

Exploring underlying ecosystem model characteristics as a possible explanation for differences in average ecosystem impacts, we found that total ecosystem biomass per unit area and ecosystem connectance were negatively correlated with ecosystem impact, with each property explaining 13% of observed variation (Figure 6E, F). Other ecosystem characteristics such as number of trophic groups, model area, and predatory biomass (TL >4) did not explain much variation (<5%) in ecosystem impact. We did not find strong relationships between average ecosystem impact and the associated large marine ecosystem (LME) properties: net primary production, invertebrate catch per unit area, species richness, number of fisheries, years fished, mean catch per year fished, sea surface temperature, and LME area.

Discussion

Our results demonstrate that invertebrates play important roles in marine ecosystems and that their exploitation can have similarly strong ecosystem impacts as that of forage fish (Smith *et al.* 2011). On average, at the same level of depletion (60%), the exploitation of invertebrates affects 11% and that of forage fish 15% of other trophic groups by at least 40% biomass change. Yet the magnitude of ecosystem effects strongly varied among different invertebrate groups. Overall, relative abundance and connectance of exploited invertebrate groups were good predictors of ecosystem impacts, also observed for forage fish (Smith *et al.* 2011). However, some invertebrates showed large ecosystem impacts at low connectance or low relative abundance, a key difference to forage fish, where this was only observed at higher values (Smith *et al.* 2011).

We found that both cephalopods and lobster can play strong top-down roles, although lobster are more omnivorous and have lower trophic levels than cephalopods. As important predators in both pelagic (e.g. squid; Hunsicker *et al.* 2010; Coll *et al.* 2013) and benthic systems (e.g. lobster; Eddy *et al.* 2014), some invertebrates have organizing or keystone roles, through direct and indirect trophic relationships. The removal of these species through fishing can lead to domino effects through marine ecosystems, known as trophic cascades (Ling *et al.* 2015). In comparison, benthic invertebrates, as well as epifauna and infauna play strong bottom-up roles in marine food webs, more similar to those observed for forage fish (Smith *et al.* 2011; Pikitch *et al.* 2014). Although not directly targeted by fisheries, these invertebrate groups can be affected by bottom trawling and seafloor disturbance (Collie *et al.* 2000a; 2000b; Kaiser *et al.* 2006), with strong impacts on other trophic groups including pelagic fishes. The only groups that showed relatively weak ecosystem effects in our study were echinoderms, gastropods and bivalves, at least when considering only trophic relationships. Although not examined in this study, urchins and bivalves are known to also play important non-trophic relationships, such as transforming habitats and providing habitat, refugia, and improved water quality for other species (Day and Branch 2002; Anderson *et al.* 2011a; Ling *et al.* 2015). These more varied ecological roles played by invertebrates than forage fish need to be considered in the management of fisheries and marine ecosystems.

For fisheries management and ecosystem conservation, it is important to understand the trade-offs between target species catches, their biomass depletion, and resulting ecosystem effects (Worm *et al.* 2009; Smith *et al.* 2011). Our finding that average MSY for invertebrates is predicted to occur at lower levels of depletion than for forage fish is likely due to different life history characteristics (Perry *et al.* 1999). This highlights the potential need for more restrictive management targets. Reducing target exploitation levels to below MSY levels would secure high target catches while significantly reducing the corresponding ecosystem effects. A reduction in forage fish exploitation rate by more than half (from 60% to 25% depletion) has been suggested in order to minimize negative ecosystem consequences while maintaining 80% of catch (Smith *et al.* 2011). Our results indicate that a similar reduction of invertebrate exploitation to 25% depletion would result in an even better win-win situation, providing 90% of MSY catches.

Observed differences in the magnitude of impacts across ecosystems that we observed could be the result of ecosystem characteristics or model structure (Heymans *et al.* 2014; Collie *et al.* 2016). For ecosystem characteristics, we could not find any good relationships between average ecosystem impact and different abiotic or biotic characteristics of the associated LME. However, more highly connected ecosystems and those with higher biomass showed lower ecosystem impacts, indicating that these were better buffered against the effects of exploitation (Figure 6E-F). Unfortunately, we were unable to integrate other regional ecosystem models, such as Atlantis (Fulton *et al.* 2011) and OSMOSE (Shin and Cury 2004) into our study due to a lack of replicate models with sufficient invertebrate resolution. A similar study on the ecosystem impacts of forage fisheries, however, found their results to be robust to model structure (Smith *et al.* 2011), and we used two models also involved in their comparison (California Current EwE, SE Australia EwE). As more Atlantis, OSMOSE or other ecosystem models become available, it will be possible to also compare our results for invertebrate fisheries. However, more ecosystem models with better resolution for invertebrates are required instead of using bulk groups, as well as broader geographical coverage, particularly important for Africa and South America, where we did not have any models. We have selected those available models that were sufficiently resolved for some invertebrate groups and their fisheries, and parameterized with local data (Supporting Information). Yet there is an urgent need for better knowledge about invertebrate abundance, ecology, and fisheries through stock assessments and research surveys that can be used to complement ecosystem studies (Perry *et al.* 1999; Anderson *et al.* 2008; 2011a; 2011b; Hunsicker *et al.* 2010). Additionally, incorporating non-feeding roles of invertebrates, such as water filtration, habitat provision, and habitat transformation into ecosystem studies will provide a broader understanding of the ecological roles of marine invertebrates and the ecosystem effects of their exploitation.

Importantly, there is great disparity between the lack of assessment and management of invertebrates compared to forage or other fishes (Ricard *et al.* 2012). Many invertebrates are not assessed for biomass reference points, although some use catch per unit effort (CPUE) as input for harvest control rules (Anderson *et al.* 2008; 2011a; 2011b). For example, in the United States, only 3% of the 186 invertebrate stocks are assessed, compared to 29% of the 1188 finfish stocks (NMFS 2015). Clearly, greater attention is needed for invertebrates within fisheries management agencies. Yet there are challenges in assessing invertebrate populations due to difficulty in developing age and growth data (Punt *et al.* 2013) and serial depletion across space (Berkes *et al.* 2006; Anderson *et al.* 2011a; 2011b), which violates the assumption of most assessment models of spatial homogeneity in fishing mortality rates. Interestingly, our results suggest that on average, MSY targets for invertebrates occur at lower levels of depletion than forage fish. Although some invertebrate groups have high production rates in certain ecosystems, resulting in MSY at higher levels of depletion, for others MSY occurs at much lower depletion levels requiring more restrictive management targets. Thus, fixed targets as often developed for finfish (e.g. Australia uses 60% depletion; AFMA 2014) may not be applicable. Finally, many invertebrates do not follow traditional fisheries science models developed for finfish (Hilborn and Walters 1992), whereby only highly connected or highly abundant species have high ecosystem impacts, as observed for forage fish (Smith *et al.* 2011). Accordingly, fisheries models and management targets need to take into account that invertebrate groups have a wider variety of life history strategies relative to finfish (Perry *et al.* 1999).

We show that many species of conservation and commercial interest can be strongly affected by invertebrate exploitation, such as marine turtles, dolphins, seals and sea lions, diving ducks, and mantis shrimp. Some of these species showed very strong declines (60-99%) at low to moderate levels of invertebrate depletion (25-60%), that would be considered normal exploitation levels in fisheries management plans (AMFA 2014, MPI 2014, NMFS 2015). Therefore, the conservation and management of these groups should consider the impacts of exploiting the prey of species of conservation and commercial interest, both invertebrate and forage fish (Hunsicker *et al.* 2010; Smith *et al.* 2011; Pikitch *et al.* 2014). Overall, the majority of other trophic groups (85%) were only affected by a <20% biomass change, whereas only 5% experienced biomass changes of >60%, similar as in Smith *et al.* (2011). Thereby, about half the groups showed a biomass decline, while the other half increased. Thus, the ecosystem effects can be positive or negative for different groups, but both change the structure and function of the ecosystem (Pikitch *et al.* 2004; Smith *et al.* 2011). Consequently, the ecosystem effects of invertebrate fisheries need to be incorporated into conservation and management plans. Moreover, the diverse ecological roles of invertebrates need to be considered in EBFM that aims at sustaining ecosystem structure, function, and services. The strong contribution of invertebrates to benthic-pelagic coupling provides further rationale to manage ecosystems as a whole, rather than by their individual parts (Pikitch *et al.* 2004), as the exploitation of one compartment is not isolated from the other.

Importantly, reducing exploitation rates could come with both ecological and economic benefits; we highlight that on average, 90% of invertebrate catch can be achieved at 25% depletion, requiring less fishing effort and thereby raising profits, while strongly reducing the impacts on other trophic groups in the ecosystem. As invertebrate fisheries continue to develop and emerge around the world, their ecological consequences along with societal and economic tradeoffs need urgent attention to achieve sustainable long-term EBFM of these renewable resources.

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Supporting Information

Detailed description of individual ecosystem models, their data sources, and calibration

Table S1. Ecopath with Ecosim models used for this study with major model characteristics, and information on sensitivity analyses, input data, and model calibration.

Table S2. Ecosystem models with invertebrate trophic groups and indicators used for invertebrate fisheries simulations. Indicators describe benthic or pelagic association, trophic level (*TL*), relative abundance, connectance, omnivory, keystoneness, relative total impacts, impact on other trophic groups, and rank of impact on other trophic groups.

Table S3. Trophic groups whose biomass decreased by at least 40% during 25% and 60% invertebrate exploitation scenarios, relative to the scenario where the invertebrate group was not exploited (B_i/B_0).

Figure S1. Frequency distribution of impacts of invertebrate exploitation on the biomass of all groups, commercial groups, and birds and mammals at 25% (blue) and 60% (red) target invertebrate depletion.

Figure S2. Catch histories of finfish (blue) and invertebrates (red) used to parameterize ecosystem models.

Figure Legends

Figure 1. Spatial distribution of invertebrate fisheries catches by large marine ecosystem (LME) and locations of the twelve ecosystem models used (from left to right): Northern British Columbia, California Current, Chesapeake Bay, western Scotian Shelf, Irish Sea, Catalan Sea, North Sea, Adriatic Sea, Gulf of Thailand, Great Barrier Reef, southeast Australia, and Cook Strait. Data from the Sea Around Us Project for 2006-2010 (catch units are kg/km^2). Insert shows temporal increase of global invertebrate catches in total and by group (red = bivalves & gastropods; yellow = crustaceans; blue = cephalopods; echinoderm catches are too small to show on this scale). Data from the United Nations Food and Agriculture Organization for 1950-2012.

Figure 2. Ecosystem effects of individual invertebrate groups at varying invertebrate fisheries depletion levels in each of the 12 ecosystem models. Ecosystem effects are measured as the proportion of other trophic groups impacted by >40% biomass change.

Figure 3. Ecosystem impacts of invertebrate fisheries. Shown is the average impact measured as the proportion of other trophic groups in the ecosystem impacted by >40% biomass change (A) by exploited invertebrate group across n=12 ecosystem models, and (B) by ecosystem model at four levels of invertebrate depletion (LOD; %). (C) Frequency distribution of other species groups impacted by different levels of biomass change at 60% invertebrate depletion. (D) Proportion of birds and mammals, commercial species, and all groups impacted by a 40% increase or decrease in biomass at 60% invertebrate depletion. (E) Degree of coupling between benthic and pelagic compartments in the ecosystem at 60% invertebrate depletion as represented by the average impact of benthic (n = 46) and pelagic (n = 27) invertebrate exploitation on benthic and pelagic fishes impacted by >40% biomass (mean +/- SE).

Figure 4. Comparison of the average ecosystem impact of invertebrate exploitation (dark red line; n = 73) and other low-trophic level (LTL) exploitation (dark grey line; n = 39, data from [3]) relative to the invertebrate catch (dark blue line) and other LTL catch (dark green line) as a

function of maximum sustainable yield (MSY). Lighter lines and shaded areas indicate confidence intervals.

Figure 5. Descriptors, indicators, and ecosystem impacts by common invertebrate group indicated as average +/- SE. The title of each panel provides the description of each y-axis.

Figure 6. Relationship between different ecosystem indicators: (A) relative abundance, (B) connectance, (C) keystoneness index 1, and (D) SURF index and the rank of ecosystem effects of various invertebrate exploitation. Rank of 1 = no change greater than 20% in any other trophic group; 2 = no change greater than 60% in any other trophic group; 3 = change greater than 60% in at least one other trophic group. Ecosystem effect is represented as the average ecosystem impact at 60% invertebrate depletion for each ecosystem model (*n* = 12). Relationships between average ecosystem impact and: (E) ecosystem connectance, (F) total ecosystem biomass (t km^{-2}).