

Ecosystem effects of contemporary life-history changes are comparable to those of fishing

Asta Audzijonyte^{1,2,*}, Anna Kuparinen^{2,3}, Elizabeth A. Fulton¹

¹CSIRO Wealth from Oceans Flagship, GPO Box 1538, Hobart, Tasmania 7001, Australia

²Department of Environmental Sciences, University of Helsinki, PO Box 65, Helsinki 00014, Finland

³Department of Biosciences, University of Helsinki, PO Box 65, Helsinki 00014, Finland

ABSTRACT: Recent studies suggest that fishing and climate change can lead to a decrease in body size of fishes. While the effect of fishing on marine ecosystems has been widely explored, much less is known about the ecosystem effects of fish body size decrease. Here we used a marine ecosystem model to compare how fishing and small (<0.1% yr⁻¹) but continuous (50 yr) decreases in the average body sizes of 5 Australian demersal fish species affect ecosystem indicators, biomasses and diets of different species. We found that decreasing growth rate of the 5 species had similar and comparable impact as the introduction of fishing of these 5 species at fishing mortality rate of $F = 0.2 \text{ yr}^{-1}$. The same applied when impacts of decrease in size were compared to those of increasing fishing from $F = 0.2$ to $F = 0.4$. This suggests that declines in body size alone can lead to ecosystem responses similar in magnitude to those caused by moderate fishing. On average, body size decrease alone caused more qualitative changes in diets of all species and larger changes in the predation mortality of slower growing species than the introduction or intensification of fishing. The overall ecosystem response to fishing and slower growth of fish was largely similar and additive, suggesting that decreasing sizes of harvested fishes are likely to amplify the effects of fishing.

KEY WORDS: Diets · Ecosystem indicators · Ecosystem models · Fisheries induced evolution · Growth · Predator–prey interactions

— Resale or republication not permitted without written consent of the publisher —

INTRODUCTION

Humans are drastically changing marine ecosystems through fishing, climate change, pollution, habitat alterations and aquaculture (Halpern et al. 2008). The effects of direct biomass removals due to fishing are now well recognised and broadly discussed (e.g. Jackson et al. 2001). More recently, the focus has also been drawn to the ecosystem level effects of selective fishing and consequences of uneven harvesting across trophic levels, species and their sizes (Garcia et al. 2012, Palkovacs et al. 2012). However, through fishing and climate change, humans also induce life-history changes in fishes and invertebrates and influence marine ecosystems in

subtler, but potentially less reversible ways (Laugen et al. 2013). Fishing usually targets large and fast-growing individuals and is therefore likely to lead to reduced growth and size-at-age through direct removals of the largest individuals or/and through fisheries-induced evolution towards slower growth or higher and earlier reproductive investment (Kuparinen & Merilä 2007, Law 2007). Indeed, many fished stocks show decreasing sizes-at-age or size-at-maturation and the magnitude of this decrease correlates with fishing intensity (Devine et al. 2012, Audzijonyte et al. 2013a). Likewise, reductions in fish size are also expected under some climate change scenarios. Increased ocean temperatures and decreasing oxygen concentration are likely to have strong

*Corresponding author: asta.audzijonyte@helsinki.fi

impacts on the growth of water-breathing ectotherms; some models predict that by 2050 the median expected reduction in individual fish body weight caused by decreasing oxygen concentration could be around 8 to 12% in different oceans (Cheung et al. 2013). The pattern of temperature-induced changes in body size will, of course, be different from those caused by fishing, as climate change will potentially affect all ectotherm species rather than just the harvested stocks. However, the response to temperature changes will vary among ectotherm species (Neuheimer et al. 2011), affecting different species to differing degrees. In this way, climate change-induced shifts in body sizes will somewhat resemble those caused by fisheries-induced evolution because both processes will lead to altered size spectra of fishes in an ecosystem rather than uniform shrinkage of all components. The consequences of these size changes on the predator–prey and ecosystem dynamics remain largely unexplored.

A few recent papers have addressed the ecosystem level effects of contemporary life-history changes in fish species. Bassar et al. (2010, 2012) used mesocosm experiments to explore how guppies that have evolved under high- and low-predation environments affect stream ecosystems. They found that different guppy phenotypes, i.e. those that were adapted to either high or low predation environment, differed not only in their size-at-age and reproductive investment but also in their diets and the overall role in the streams. The effect of guppy phenotype on the stream ecosystem was often as strong as the effects of doubling their density. Another study has shown that reduction in average sizes of major benthivorous fishes in the North Atlantic has led to a trophic cascade towards more abundant phytoplankton blooms (Shackell et al. 2010); this trophic cascade was observed even without major changes in the biomasses of the benthivorous fish. These studies are illuminating but inevitably limited to either small and simple ecosystems (experiments) or data on trophic interactions (real marine ecosystems). To this end, ecosystem modelling provides an alternative tool to explore complex ecosystem processes through multiple simulation scenarios. Such simulations can then be used to build hypotheses and identify indicators that could be tested and applied in real marine ecosystems (e.g. Fulton et al. 2005).

Recently, Audzijonyte et al. (2013b) used an ecosystem model to explore how a small (2 to 4%) decrease in length-at-age of 5 harvested fish species affected their biomasses and natural mortalities. They found that positive feedback loops amplified the effects of

size decreases, resulting in an up to 50% increase in natural mortality of some ‘shrinking’ species. In this study we introduce a new aspect and compare the ecological effects of a size decrease to those caused by fishing. Our aims are threefold. First, we look at the total effects that fishing, a decrease in size or both factors together have on biomasses of focal species (those that are harvested or decreasing in size) and other species in the ecosystem. Second, we explore how fishing and changes in size affect diet connections in the ecosystem. We discuss the relative importance of fishing versus life-history changes on trophic cascades in the modelled marine ecosystem. Third, we look at how fishing and/or changes in size affect some commonly used ecosystem indicators, and hence how likely the effects are to be detected in monitoring studies. We show that over a 50 yr period, even slow rates of body size decrease ($<0.1\% \text{ yr}^{-1}$) lead to ecosystem changes comparable to those caused by an introduction of a moderate intensity fishery into an un-fished ecosystem.

METHODS

In this study we used the South East (SE) Australian marine ecosystem implementation of the Atlantis ecosystem model (Fulton et al. 2004, 2007). The model has been applied to evaluate alternative strategies for fisheries management and also includes size-based feeding interactions, which makes it well suited to explore ecosystem-level impacts of fishing and declining fish body sizes. We modified the model to simulate body size decreases in 5 important demersal SE Australian trawl fishery species and explored ecosystem level effects of fishing and body size decrease in a full factorial manner. We modelled a decline in size of 5 selected rather than all fish species, because previous studies have suggested a different response of fish species to either fishing or climate-induced size changes (Andersen & Brander 2009, Cheung et al. 2013). This means that regardless of the cause for the decline in size, it will lead to a new composition in fish sizes. Ecological consequences of such shift in size spectrum are thus a focus of our study.

Atlantis ecosystem model

A detailed description of the Atlantis modelling framework and the simulation design used is given in Audzijonyte et al. (2013b). In brief, the Atlantis is

based on dynamically coupled biophysical and fisheries submodels, where processes are modelled in interconnected cells representing major features of the physical environment (e.g. seabed type, temperature, salinity, pH, oxygen) as well as oceanographic transport. The SE Australian model has 71 geographical cells matched to system bioregions and geomorphology. The cells vary in area from 573.5 to 390 000 km² and have up to 7 water column layers per cell, ranging in depth from 20 to 2000 m (see Supplement 1 at www.int-res.com/articles/suppl/m495p219_supp1.pdf for SE Australian model map, diagram and list of functional groups and fishing selectivity parameters). The biological food web is represented by 57 functional groups. The majority of the groups aggregate species with similar size, habitat and diets (i.e. functional groups), but the key target species for the fisheries are resolved at a species level. Biological groups of lower trophic levels are represented as biomass pools, whereas vertebrates and some larger invertebrates are modelled as age-structured populations (see full details in Fulton et al. 2004, 2007, at <http://atlantis.cmar.csiro.au/>, and Supplement 1). Vertebrate groups have 10 age groups, each representing 1 to 10 calendar years depending on the longevity of the group (e.g. one age class corresponding to 10 calendar years in a long-lived orange roughy species). The time-step in the simulations is 12 h.

Representation of feeding in Atlantis

Feeding interactions between functional groups depend on availability, size-based limitations and refuge use. The modelling aims to allow for dynamic realised diets through space and time as the relative sizes and biomasses of predators, prey and habitats shift. In our simulations all functional feeding responses were based on a modified form of the Holling Type II response; previous work has shown that except for extreme cases, different functional feeding responses give similar system-level outcomes (Fulton et al. 2003). The grazing term is calculated for each age class of age-structured predator and prey separately. For the predator *j* and prey *i* the grazing is given as:

$$P_{i,j} = \frac{B_j \cdot \kappa_j \cdot \alpha_{i,j} \cdot \delta_{r,i} \cdot B_i}{1 + \kappa_j \cdot \left(\frac{\sum_{fauna} \alpha_{n,j} \cdot \delta_{r,n} \cdot B_n}{\mu_j} + \frac{\sum_{flora} \alpha_{n,j} \cdot \delta_{r,n} \cdot B_n}{\mu_j} + \epsilon_{j,3} \cdot \alpha_{DL,j} \cdot \delta_{r,DL} \cdot B_{DL} + \epsilon_{j,4} \cdot \alpha_{DR,j} \cdot \delta_{r,DR} \cdot B_{DR} \right)} \quad (1)$$

where *B* is the biomass of the group (or that age class for an age structured group), κ_j is the clearance rate of the predator (equivalent to area swept for sedentary species and area searched for mobile species; set per age class for age structured groups), $\alpha_{i,j}$ is the maximum potential availability of prey *i* to predator *j*, $\delta_{r,i}$ is the refuge accessibility of the prey (see below), $\epsilon_{j,1-4}$ is the assimilation efficiency of predator *j* on food type *x* (flora, fauna, labile detritus [DL] and refractory detritus [DR]) and μ_j is the maximum potential growth rate of the predator (specific to each age class for age structured groups). The availability parameter $\alpha_{i,j}$ is similar to the 'vulnerability' parameters in ECOSIM (Walters et al. 2000) and recognises that the entire prey population is not available to the predators at any one time. The 2 parameter sets used in our simulations differed mostly in the maximum availability of prey to predators (see details in Audzijonyte et al. 2013b). This availability of the food is further modified by the refuge parameter $\delta_{r,i}$ which is defined as:

$$\delta_{r,i} = \delta_{o,i} \cdot \delta_{h,i} \cdot \delta_{s,i} \quad (2)$$

where $\delta_{o,i}$ is the spatial overlap between predator and prey (i.e. both in the same cell and able to inhabit or pass through the same pelagic or demersal habitat types), $\delta_{h,i}$ is the habitat overlap and $\delta_{s,i}$ is the size 'overlap' or gape limitation (i.e. prey is within the gape range of a predator). If non-zero, then for benthic prey the $\delta_{o,i}$ also depends on the depth of sediment that the predator can forage.

The influence of biogenic habitat is modelled through the $\delta_{h,i}$ term, which equals 1 for prey species or life history stages that are not dependent on habitat, whereas for habitat dependent species it is defined as:

$$\delta_{h,i} = \theta_{i,a} \cdot \left(\exp(-\kappa_{i,h} \cdot A_{h,i} + \theta_{i,b}) + \frac{1}{\theta_{i,b}} \right) \quad (3)$$

where $\kappa_{i,h}$ is the refuge magnitude coefficient, $A_{h,i}$ is the weighted relative cover in the cell for the prey, $\theta_{i,b}$ is the habitat steepness coefficient, $\theta_{i,a}$ is a scalar of the overall habitat refuge effect for prey *i* (which can be dependent on ocean acidity).

The size-based refuge term $\delta_{s,i}$ is zero (prey not available to the predator) or 1 (prey available), an approach typically taken in other ecosystem models (e.g. Shin & Cury 2004, Barange et al. 2011). The prey is available to the predator if its size falls within the lower and upper prey selection size limits of the predator. The upper size limit of the prey was between 15% and 90% of the predator body size for different predator groups.

In order to explore the sensitivity of our findings to the parameterisation, we ran identical simulations using a main and an alternative (secondary) parameterisation that assumed weaker predator–prey interactions, i.e. a smaller availability of some prey biomass to predators (see details on the availability parameters in the Electronic Supplement of Audzijonyte et al. 2013b).

Simulation design

For the purpose of this study we simulated fishing and body-size decrease in 5 SE Australian fish species: jackass morwong *Nemadactylus macropterus*, tiger flathead *Platycephalus richardsoni*, silver warehou *Seriolella punctata*, blue grenadier *Macruronus novaezelandiae* and pink ling *Genypterus blacodes* (see Fig. 1). Jackass morwong is a small (30 to 35 cm) benthic invertebrate feeder maturing at about 2 to 3 yr, living to a maximum of 30 yr and mostly occurring at depths of 100 to 200 m. Tiger flathead is a medium-sized (35 to 45 cm) benthopelagic zooplanktivore, living up to 20 yr and maturing at the age of 3 to 5 yr, and an important target species on the continental shelf at depths of 40 to 140 m. Silver warehou is a medium-sized (30 to 50 cm) pelagic invertebrate feeder. They form schools close to the sea bed at depths of 200 to 600 m and live for up to 20 yr. Blue grenadier is an important target species on the continental slope at depths of 400 to 600 m, maturing at the age of 4 to 5 yr and living up to 25 yr. They are largely piscivorous, grow up to 100 cm in length and show high variability in annual recruitment. Pink ling is a large (up to 100 cm) benthic zooplanktivore occurring on the continental slope at depths of 300 to 500 m and living up to 20 yr. These species are harvested through size-selective fishing and constitute the main catch of the SE Australian shelf and offshore trawl fisheries.

Throughout the entire simulation period, fishing for all 5 species was constant and spatially uniformly distributed; the same rate was applied to all 5 species and catches were taken based on an empirically derived logistic selectivity curves (details in Supplement 1). Bycatch associated with the take of the target species was applied using empirically estimated bycatch ratios (Klaer & Smith 2012). No other incidental effects of fishing were included. In the implementation of Atlantis used for these simulations, all individuals of the same age group are equal in size. Therefore, although fishing mortality is size-selective, fishing alone does not affect the size-at-age of a species. In contrast, in scenarios simulating changes

in life-history, size-at-age of harvested species was set to decrease gradually every year. The decrease in body size of harvested species was forced using *a priori* chosen rates of phenotypic change. The decrease was modelled by modifying the maximum growth rate values μ_j in the feeding functional response Eq (1) and in this way decreasing the realised size-at-age. This value each year becomes slightly smaller in each age class of the 5 ‘shrinking’ species. The decreases in body size were set to be continuous and constant over the entire simulation period. In agreement with empirical and modelling results on effects of fisheries-induced evolution (Enberg et al. 2012) and temperature effects on fish growth (Pörtner & Knust 2007), the length-at-age of older age bins was set to decrease faster than in the younger age bins (see full details in Audzijonyte et al. 2013b). Maturation was set to occur at the same age, therefore decrease in size-at-age reduced maturation size and egg production (which is proportionally dependent on size). We emphasise that our model does not attempt to resolve causes and dynamics of the body size change, but rather look at the ecological consequences. To make our predictions conservative, the 2 simulated rates of phenotypic change correspond to approximately 2% and 4% decreases in body length over 50 yr (0.04% and 0.08% yr⁻¹). Thus decreases in body sizes in our simulations are smaller than those predicted under climate change scenarios (ca 8 to 12% by 2050, Cheung et al. 2013) or the ‘slow expected rates of fisheries-induced evolution’ (0.1 to 0.6% yr⁻¹) presented in Andersen & Brander (2009). Our rates are also considerably slower than rates reported in many empirical and simulation studies (reviewed in Audzijonyte et al. 2013a).

In this study we explore results from 9 simulation scenarios where 3 fishing mortality rates of $F = 0, 0.2$ and 0.4 yr^{-1} on all 5 species are combined in a full factorial manner with $R = 0\%, 2\%$ and 4% decrease in length-at-age over 50 yr for all 5 species. Simulations were run for 90 yr. The biomasses of many species fluctuated strongly during the first 40 yr, but settled into some equilibrium afterwards. The first 40 yr were therefore discarded as a ‘burn-in’ period, with the last 50 yr being the ‘treatment’ years. Further on, we refer to the 50 treatment years as the simulation period.

Comparing effects of decrease in body size to those of fishing

We compared the ecological effects of body size decrease in 5 key species to the impacts of introduc-

ing a fishery of the same 5 species into an unfished ecosystem. To do this we analysed changes in biomasses, diets and values of 3 ecosystem indicators in scenarios with fishing alone, with decrease in body size alone, and in scenarios with both fishing and decrease in size. We focused on the end of the 50 yr simulation period; to smooth the year-by-year fluctuations we used average biomasses and diet compositions of the last 5 yr (Years 46 to 50).

Firstly, we looked at the impacts of fishing and/or body size decrease on biomasses of both the treatment species (i.e. those harvested and/or 'shrinking') as well as the other species in the ecosystem. Specifically, we assessed whether the change in biomass due to decreasing growth rates of 5 harvested species is comparable to the biomass changes caused by the introduction of fishing at $F = 0.2$ or increasing fishing level from $F = 0.2$ to $F = 0.4$.

Second, we looked more specifically to the changes in the diets and predation of the focal species. We looked at the changes in the diet caused by food preferences alone rather than the change of the prey biomass. Therefore the relative change in the diets of a species was scaled by the relative change in the biomasses of consumed items between the compared scenarios. For example the relative change of prey i in the diet of predator j in Scenario $F2R0$ ($F = 0.2$, $R = 0$) as compared to Scenario $F0R0$ ($F = 0$, $R = 0$) is $r_{i,j}^{F2R0}$ and is given by:

$$r_{i,j}^{F2R0} = \frac{P_{i,j}^{F2R0} B_i^{F0R0}}{P_{i,j}^{F0R0} B_i^{F2R0}}$$

where $p_{i,j}$ is the proportion of the prey i in the diet of predator j and B_i is the biomass of prey i . The same calculations were conducted both when assessing changes in the diets of the 5 focal species, and when assessing predation on these 5 species, i.e. relative changes in the diets of the predators of the 5 species (detailed results presented in Supplement 2 at www.int-res.com/articles/suppl/m495p219_supp2.xls and Supplement 3 at www.int-res.com/articles/suppl/m495p219_supp3.xls). In addition we also looked at the relative changes in the mortality per predator function (Supplement 4 at www.int-res.com/articles/suppl/m495p219_supp4.xls). The mortality per predator simply calculates how many individuals of a particular prey species have been consumed by a given predator per year, divided by the total number of individuals of that prey present at the beginning of the year (where the year is tracked based on annual spawning events for the species not the Gregorian calendar). The relative change in the mortality per predator gives a better indication of the predation

mortality imposed by different predators. For example, the relative proportion of tiger flathead in the diet of barracouta in Scenario $F2R4$ ($F = 0.2$, 4% reduction in length-at-age) versus Scenario $F0R0$ (no fishing, no decrease in length-at-age) was 2.4 (i.e. 2.4-fold increase, Supplement 3), whereas the relative mortality of flathead caused by predation by barracoutas increased 4-fold (Supplement 4) due to biomass, size and age structure changes of the 2 species. Third, we also explored how 3 commonly used ecosystem indicators reflect the ecosystem changes caused by fishing, changes in body size, or both. The indicators were piscivore/planktivore fish biomass ratio, benthivore/pelagic fish biomass ratio, and biomass above the trophic level 4+ (TL4+) (Fulton et al. 2005). The TL4+ indicator was recommended by Link (2005) as an indicator reflecting status of the biodiversity, because higher trophic level species have historically been most vulnerable to, or affected by, fishing.

RESULTS

Biomass changes due to fishing or reductions in body size

The 5 target, i.e. harvested and/or decreasing in size, species responded to fishing and body size declines in different ways. The biomass of some harvested species, such as morwong and ling, actually increased with the introduction of low fishing levels ($F = 0.2$) on the 5 species (Figs. 1 & 2). Morwong and ling benefited more from reduced competition with and predation from other fished species than any losses they suffered from being targeted by fishing themselves. When an alternative parameter set was used, introduction of fishing did not result in biomass increases for morwong and ling (Supplement 2). This is because weaker inter-species interactions, assumed in this parameter set, meant that competitive predation release from fishing of other species did not benefit morwong and ling as much as in the main set of parameters.

In contrast, a decrease in body sizes led to declines in the biomasses of all target species except for grenadier, in simulations with the main set of biological parameters. For flathead, a 4% decrease in the average length-at-age resulted in biomass 32% lower than in the baseline scenario of no directional change in body size. In comparison, introduction of fishing at $F = 0.2$ alone led to a 60% decline in the final biomass. Similarly, when comparing scenarios

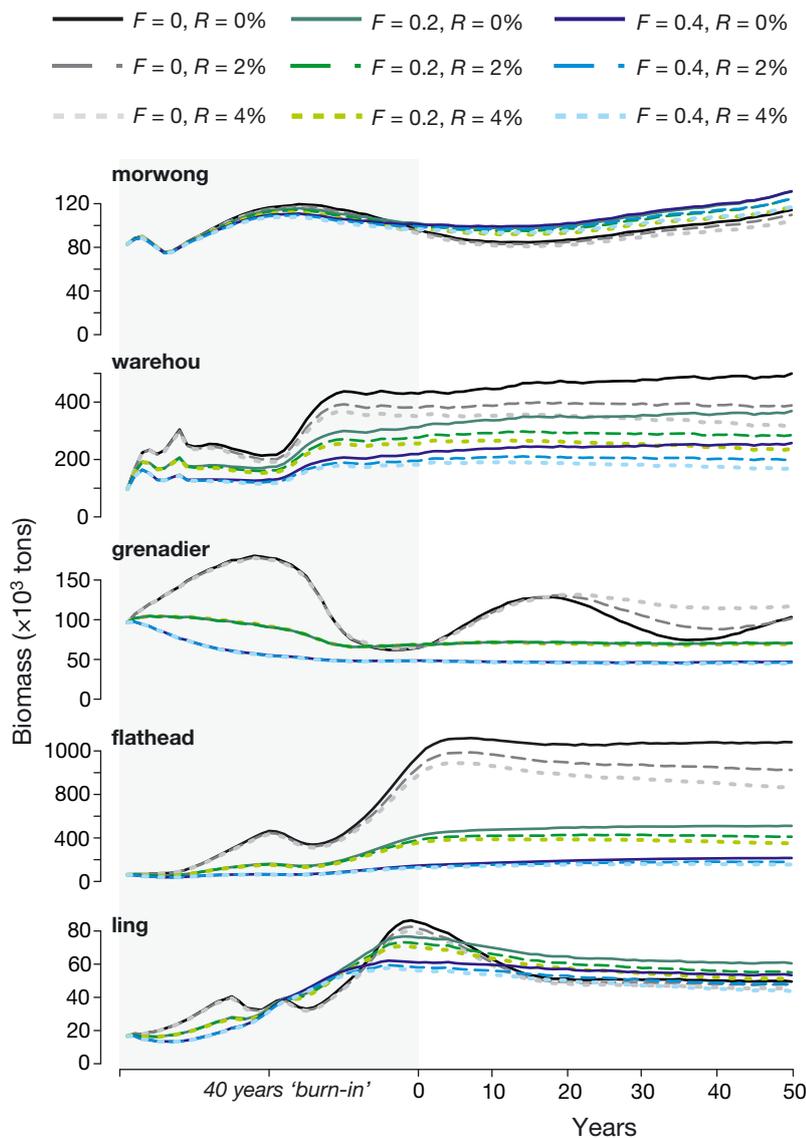


Fig. 1. Biomasses of the 5 fished/shrinking species in 9 simulation scenarios. All simulations started with the same initial biomasses, representative of the current state of the SE Australian ecosystem. The biomasses fluctuated during the first 40 yr. These 40 yr ('burn-in') were discarded from the analyses and are marked here in grey. Scenarios are marked in different colours, where F shows the fishing mortality and R shows the decrease in average body size over the 50 yr period

with low ($F = 0.2$) to moderate ($F = 0.4$) levels of fishing, the higher rate of fishing resulted in a 58% decrease in final biomass of flathead, whereas 4% decline in body size led to a 31% decrease in biomass.

The decreasing body size had even larger effects on warehou; in this species, a 4% decrease in length-at-age had a larger impact on the biomass (ca. 35% decrease) than introduction of low fishing alone (26% decrease) or an increase of fishing from $F = 0.2$

to 0.4 (30% decrease). For grenadier, decreasing body size did not affect the biomass, except in the scenarios without fishing. In these scenarios grenadier had large temporal biomass fluctuations that were dampened when their body size decreased by ca. 4% (Fig. 1). Such biomass fluctuations are indeed observed in grenadier populations and are driven by strong recruitment pulses. In reality these fluctuations occur roughly once per decade, which is also true in the model. However, the model does not see all of the pulses pass through the population, as many pulses level out quite quickly; as a consequence the period of fluctuation is much longer in the modelled system. The decrease in body size of grenadier dampens these recruitment pulses. This is because the smaller females produced less spawn resulting in weaker recruitment waves. Similarly, in scenarios with fishing the largest females were removed from the population by fishing, which also dampened recruitment waves.

Fishing of the 5 species had noticeable impacts (>1% change in biomass) on 15 other functional groups (Fig. 2). The affected groups mostly included fishes, sharks and prawns. Fishing and body size decline of the 5 targeted species affected the biomasses of most functional groups in the same direction (i.e. both led to either higher or lower biomasses); the effects were cumulative in scenarios with both fishing and decrease in size. The decrease in body size of the 5 species had roughly half as large of an effect on the biomasses of

non-targeted species as the introduction of a fishery of the same 5 species into the unfished ecosystem. The 2% decrease in the body length of the 5 targeted species resulted in 30 to 40% of the biomass changes in the non-target species as compared to the change caused by the introduction of fishing (or increasing fishing from 0.2 to 0.4). A 4% decrease in body size led to 50 to 67% of the biomass change when compared to the change caused by fishing (Fig. 2).

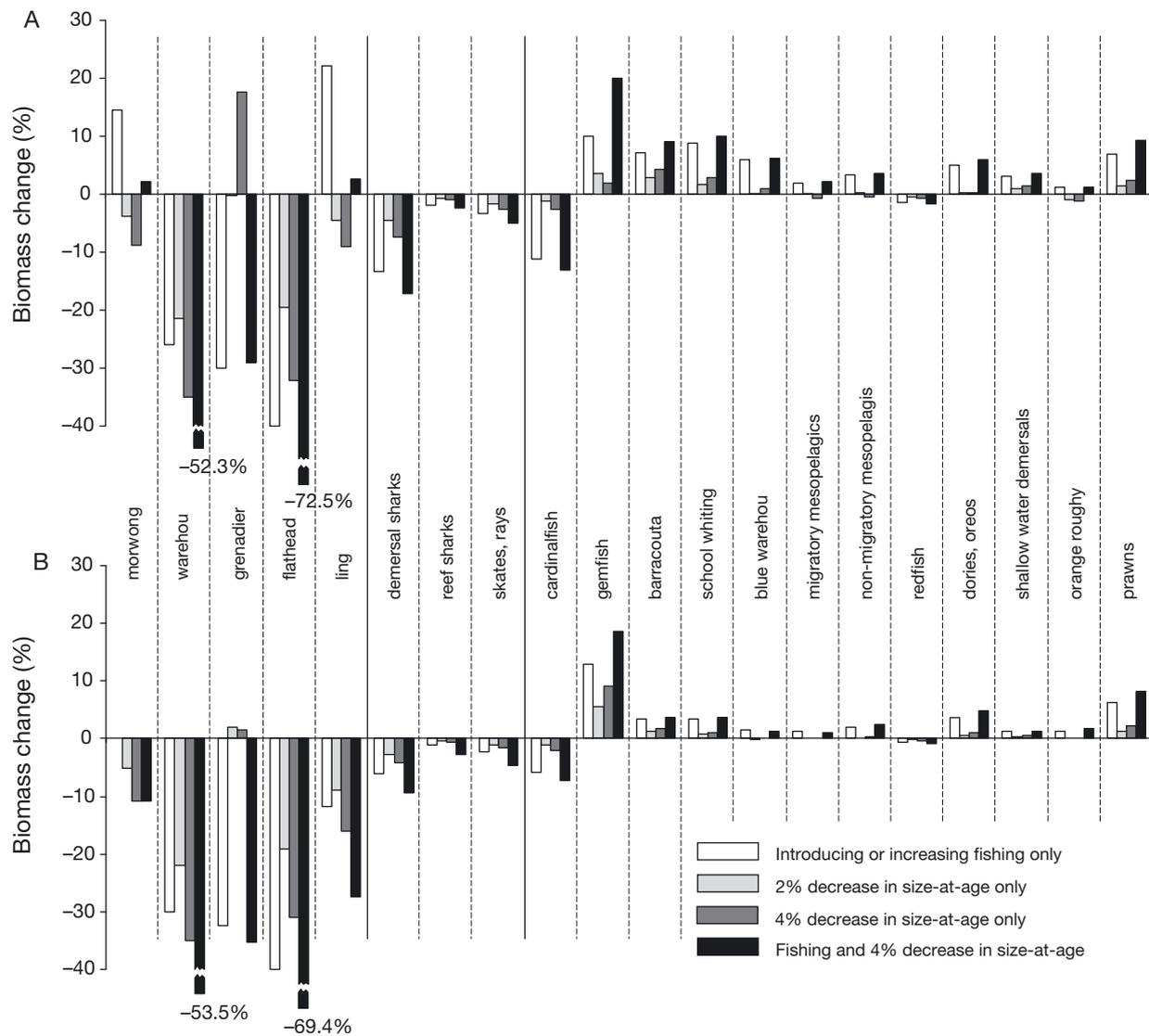


Fig. 2. Percentage difference in the final (mean of Years 46 to 50) biomasses of 20 functional groups caused by introducing or increasing fishing only (white bars), 2% and 4% decrease in length-at-age of target species only (light and dark grey), and combination of introduced fishing and 4% decrease in length-at-age of fished species (black). (A) comparison between scenarios with zero to $F = 0.2$ fishing rates, (B) comparison between scenarios of $F = 0.2$ to 0.4 fishing. Only the functional groups for which biomass changed by $> 1\%$ are shown

Changes in the diets of harvested and/or 'shrinking' species

Both fishing and a decline in size had strong impacts on the diet composition of target species. The most obvious trend caused by the decline in body size of the 5 demersal species was the increase in the consumption of invertebrate prey instead of juvenile fish (Fig. 3). The 'shrinking' of the 5 species had a large impact on the consumption of the medium size fish, such as blue mackerel, dories and oreos. These species were on the edge of the size

range that the 'shrinking' species could consume and therefore were released from predation when the 5 species got smaller. The overall change in the diets was similar in both sets of biological parameterisations (Supplement 2), although the exact quantitative change differed. The switch towards a broader invertebrate spectrum was only seen in the scenarios where decrease in body size was included; introduction of a fishery on these 5 species only increased the consumption of prawns but not other invertebrates (Fig. 3). Overall, the 4% decline in length-at-age of the 5 'shrinking' species caused more qualitative

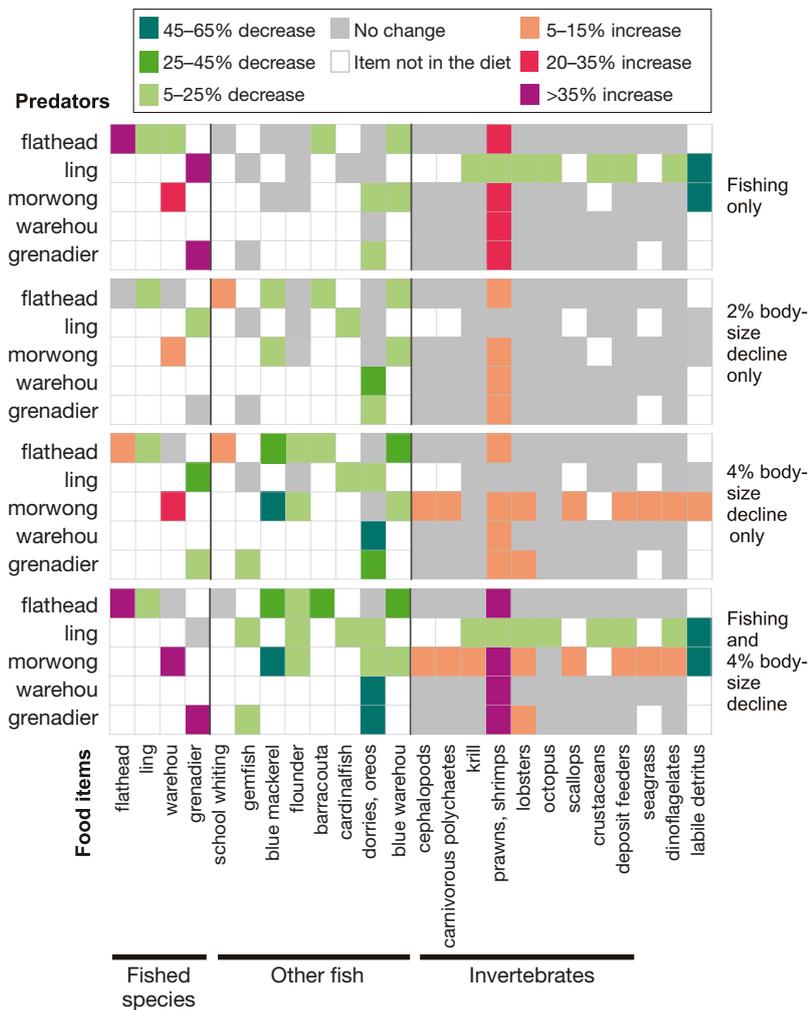


Fig. 3. Changes in the diets of the 5 harvested/shrinking species in 4 example simulation scenarios as compared to the baseline scenario of no fishing ($F = 0$) and no change in size ($R = 0\%$). Top panel: fishing at $F = 0.2$ only; middle panels: decline in length-at-age only; bottom panel: fishing at $F = 0.2$ and 4% decline in length-at-age. Green shades show a decrease in the consumption of a food item; red shades show an increase. The proportion of a food item in the diet of target fish species was scaled by the total biomass of the food item to indicate preference rather than availability

changes in their diet composition (i.e. changes in prey items) than the introduction of a fishery alone. The effects of fishing and body size decline were usually cumulative.

Changes in the predators of harvested and/or 'shrinking' species

Both fishing and body size decline had large effects on the predation pressure of the fished/'shrinking' species. Introduction of fishing alone increased predation pressure on warehou, grenadier and espe-

cially on flathead (Fig. 4, Supplements 3 & 4). The largest increase in predation was caused by piscivorous and demersal shallow water fishes, sharks, seabirds and larger pelagic invertebrates (cephalopods and gelatinous zooplankton). Introduction or intensification of fishing often led to a doubling of predation pressure on flathead, and up to a 50% increase in predation on grenadier and warehou caused by these groups (Supplement 4). For morwong and ling, introduction of fishing did not have substantial effect on the overall predation pressure, as increased predation from some species was compensated by decreased mortality from others. The main reason behind the changes in predation mortality due to fishing is the changes in the overall biomass of the fished/predated species. Species that substantially decreased in total biomass through fishing (e.g. flathead) also had the largest increase in predation pressure. While consumption by some predators decreased when the fished species biomass went down, the decrease in consumption was typically smaller than the fishing induced decrease in the biomass, and this led to stronger predation pressure. Introduction of fishing in the alternative parameter set increased predation pressure of morwong and ling, a different result from the main parameterisation where predation did not change substantially. This was because in the alternative parameterisation, the biomass of morwong and ling did not

increase with low levels of fishing, yet it did in the primary set of parameters (Supplement 2).

Decline in body size increased predation pressure on all shrinking species, except for grenadier. For ling, morwong and warehou the 4% decline in length-at-age alone resulted in a larger increase in predation pressure than the introduction of fishing. This was due to both the biomass changes of 'shrinking' species, but mostly because slower growing species remained longer in the size range available to predators. Predators that benefited from a size decrease of flathead and warehou (shallow water fishes) included other large and medium size shallow

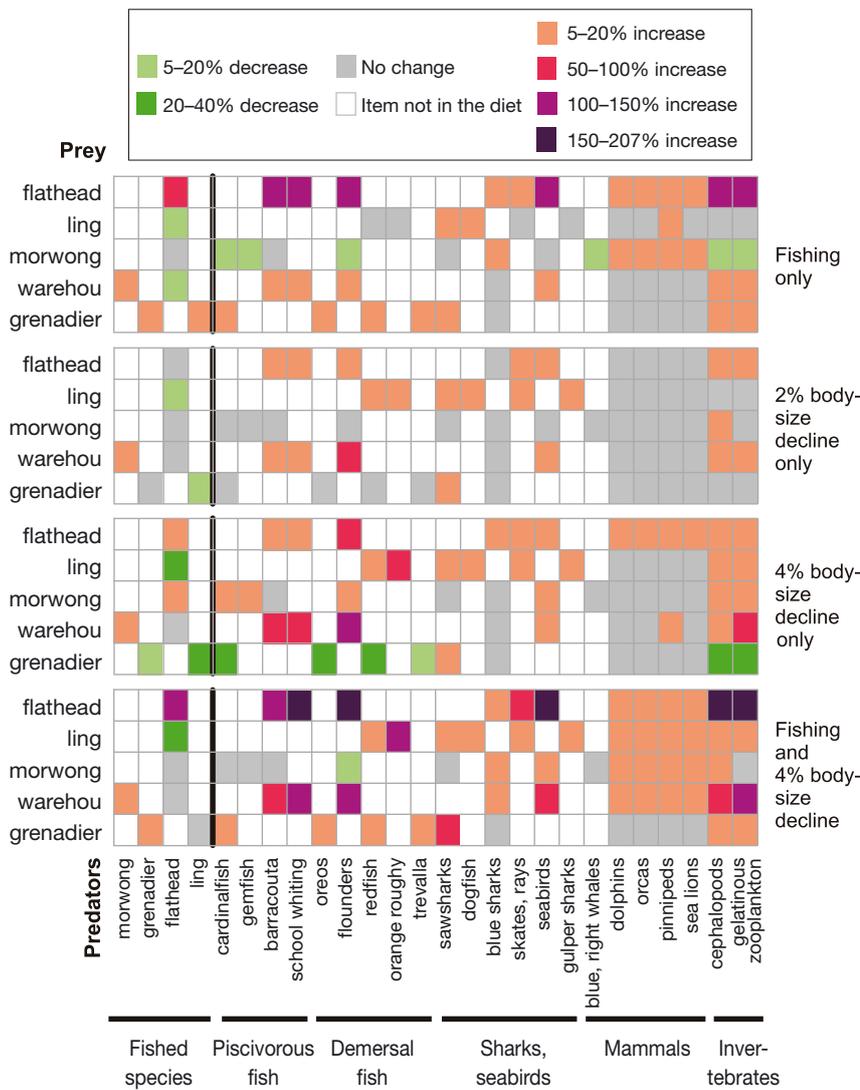


Fig. 4. Changes in the predation on the 5 harvested/shrinking species in 4 example simulation scenarios as compared to the baseline scenario of no fishing and no change in size. See Fig. 3 for details

water fish species. Predation on ling mostly intensified due to consumption by sharks and deep water orange roughy (predating on juvenile ling). The decrease in predation pressure on grenadier is explained by the shift in distribution (seen in both sets of biological parameters). In scenarios with body size decrease, grenadier juveniles moved to more coastal areas, following the improved supply of invertebrate prey. This move increased their spatial overlap with flathead and ling juveniles and made the grenadier less vulnerable to predation from gelatinous zooplankton, cannibalism and deep water fish (oreos and redfish) (see Audzijonyte et al. 2013b).

Ecosystem indicators

Both fishing and body-size decline affected all 3 assessed ecosystem indicators (Table 1). Introduction of a low fishing regime ($F = 0.2$) on the 5 demersal species led to a 6% increase in the pelagic/demersal fish ratio and 2.4% increase in the piscivore/planktivore fish ratio compared to the scenarios without fishing. The effect of the 4% decline in body size alone (without fishing) was similar — pelagic/demersal fish ratio increased by 2.9%,

Table 1. Changes in the ecosystem indicators in the simulated scenarios. The 9 scenarios include all possible combinations of 3 levels of instantaneous fishing mortality F (0.0, 0.2 and 0.4) and directional reduction in length-at-age R (0, 2% or 4% over the 50 yr simulation period). Values of 3 ecosystem indicators (see 'Methods') are given for each of the 9 scenarios in the upper row. The lower row shows the percent change in the value of an ecosystem indicator between the baseline scenario of no fishing and no decrease in length-at-age (underlined value) and each of the other 8 scenarios. TL4+ is biomass at the trophic level 4 and above (see Link 2005)

Ecosystem indicator	$F0R0$	$F0R2$	$F0R4$	$F2R0$	$F2R2$	$F2R4$	$F4R0$	$F4R2$	$F4R4$
Pelagic/demersal fish ratio	<u>0.623</u>	0.636	0.643	0.660	0.667	0.672	0.680	0.684	0.687
% change from $F0R0$		+2.2	+3.2	+6.0	+7.2	+8.0	+9.2	+9.9	+10.3
Piscivore/planktivore fish ratio	<u>0.191</u>	0.194	0.196	0.195	0.197	0.198	0.198	0.199	0.199
% change from $F0R0$		+1.8	+2.9	+2.4	+3.2	+3.6	+4.0	+4.4	+4.5
Biomass at TL4+ ($\times 10^3$ tons)	<u>5935</u>	5927	5922	5913	5909	5907	5905	5903	5902
% change from $F0R0$		-0.13	-0.21	-0.36	-0.43	-0.47	-0.50	-0.53	-0.55

and piscivore/planktivore fish ratio increased by 3%. The biomass at the trophic level 4+ changed very little, by less than 0.6%; effects of body size decline in 5 harvested species alone were about half as large as the effect of introducing fishing.

DISCUSSION

Some of the ecological consequences of a decrease in body size, modelled using the Atlantis ecosystem modelling framework, have recently been presented in Audzijonyte et al. (2013b). The authors demonstrated the importance of positive feedback loops in predator–prey interactions that can amplify the effects of life-history changes. The present study extends previous analyses and introduces a new aspect of ANOVA-like comparisons around the effects of fishing, decrease in body size, or both effects combined on biomasses of species and on the trophic interactions in the ecosystem. We show that moderate fishing and changes in body size of some fish species have similar and comparable impacts on biomasses and diets of different functional groups across the marine ecosystem. While fishing mainly affected the biomasses of harvested species through direct removal of fish, the decrease in body size more strongly altered feeding interactions and predation mortalities. When fishing was combined with decreasing body size their impacts were often synergistic, whereby decreasing length-at-age of harvested fishes amplified the effects of fishing. Palkovacs et al. (2012) reviewed effects of fishing and extirpation of top predators in a marine ecosystem, warning about trophic cascade responses caused by the modifications of food webs by fishing. In this study we show that even small but continuous decreases in sizes of some fish species can have trophic cascade responses similar or stronger to those caused by moderate fishing.

Life-history changes in fish can shape ecosystems more than fishing

There is an increasing amount of evidence that intraspecific phenotypic differences of key ecosystem species can be of equal, or even greater, importance to the ecosystem dynamics than the abundance of the species itself. For example, Bassar et al. (2010, 2012) conducted mesocosm experiments with 2 different phenotypes of guppies, evolved under high and low predation regimes and differing in their size, growth, maturation and reproduction traits. The 2 guppy phenotypes had different diets and excretion rates, and

consequently different effects on invertebrate density, algal biomass, productivity and nutrient flux in the stream ecosystem. For many ecosystem variables—such as algal stocks, invertebrate biomass and decomposition rate—the phenotype of guppies had larger effects than the doubling of their density. Bassar et al. (2012) also showed that indirect effects of guppy phenotypes, manifested through nutrient recycling or trophic cascades, had larger impacts on algal biomass and primary productivity than the direct consumption effects. In the experiment of Bassar et al. (2012) many indirect effects were of different direction and cancelled each other out, so their cumulative effect was relatively small. However, it is equally possible that indirect effects can accumulate, amplifying the ecological differences between different phenotypes.

Our modelling study predicted that changes in size-at-age will have similar or even larger impact on diets of both species decreasing in size as well as other related species in the ecosystem than the introduction or intensification of fishing itself. This means that the trophic cascade response caused by decreasing size could possibly be stronger than the response caused by moderate fishing. Changes in diets caused by fishing were mainly due to a truncated age structure of the fished species, whereby overall diets of fished species were dominated by diets of young fish. In contrast, long-term reduction in length-at-age affected diets of all age classes and cascaded through the food web. The effects of this long-term slow reduction in size (i.e. ca. 0.1% yr⁻¹ over 50 yr leading to the final change of ca. 4%), are likely to be different from the effects of large but short-term decreases in size, such as those caused by yearly fluctuations in growth rates due to changes in food supply. The long-term slow but directional change resulted in slow changes in age composition of different functional groups, triggering positive feedback loops in the trophic interactions (Audzijonyte et al. 2013b). For example, a 25% decrease in the biomass of warehou caused by fishing at $F = 0.2$ increased predation from shallow water fishes (barracouta, trevally) by 1 to 2%. In contrast, while the 4% average decrease in length-at-age had a similar effect on the biomass of warehou (35% decline), predation on warehou from shallow water fishes increased by 45 to 70% (Supplements 3 & 4). Decreased size of warehou and flathead meant that predation by warehou and flathead on juveniles of other shallow water fishes also decreased, leading to improved survival. The larger numbers of other shallow water fishes in turn predated more heavily on warehou and flathead, leading to positive feedbacks (Audzijonyte et al. 2013b).

Our study can be compared to the findings of Shackell et al. (2010) which showed a trophic cascade increase in phytoplankton blooms due to a decrease in the average size of benthivores. Trophic cascade responses reported in Shackell et al. (2010) were largely caused by fishing (and climate change) and subsequent demographic decrease in average fish size, i.e. direct removal of older and larger individuals. Based on the results of our modelling exercise, we hypothesise that a trophic cascade response from decrease in size-at-age could be even stronger. Of course, the magnitude of the response caused by either fishing or decreasing body size will depend on the intensity of fishing and the speed of phenotypic change. If decrease in size is caused by fisheries-induced evolution, then intensive fishing will lead to fast rates of phenotypic change; therefore the relative impact of fishing and 'shrinking' could be similar to those found in our study. Empirically reported rates of phenotypic change can be as fast as 2 to 4% yr⁻¹ (reviewed in Audzijonyte et al. 2013a). Although the fastest changing traits were related to maturation, many reported changes in growth were still within the range of 0.5 to 1% yr⁻¹ for *F* values of 0.2 to 1. Future modelling work should be conducted to explore the effects of very intensive fishing and fast changes in growth or other traits. To make our conclusions cautious in the controversial area of fisheries-induced evolution and sustainable fisheries management, we chose to model conservative rates of phenotypic change, and found that even these slow rates lead to fairly large impacts on the biomasses and trophic interactions. Our preliminary power analyses showed that in places with extensive field surveys, such as those in NW Atlantic, changes in diets of the magnitude reported in our study could be detectable in 5 to 10 yr (Type I and II error rates of 0.05 and 0.9); but longer periods would be required in a noisy system.

Changes in natural mortality caused by fishing

Our study suggests that introducing or increasing the intensity of fishing, even without any changes in size-at-age, can increase predation mortalities of harvested species. There are several possible reasons for that. First, the predators may tend to stick to their usual prey even if its abundance is declining. This is especially likely if harvested fish aggregate in small geographical areas where predators can catch them easily, such as appears to be the case of seal predation on NW Atlantic cod (Swain et al. 2011). Another

possible reason for increased natural mortalities of stocks depleted by fisheries is a shift in an ecosystem state. Harvested and depleted stocks may impose weaker predation pressure on other fishes, allowing them to increase in abundance and in turn predate heavily on juveniles of harvested species. Such shift in ecosystem states may have explained the delayed recovery of Baltic cod, as its fry was being heavily predated by Baltic herring (Köster & Möllmann 2000); the stock has increased in recent years. Other examples of changes in the trophic control are provided in Frank et al. (2007). Unfortunately, data needed to detect such changes in predation mortality is demanding and unavailable for most stocks. Yet, this information is essential because natural mortality is an important determinant of stock productivity, and hence its ability to sustain fishing (Vert-pre et al. 2013, Wayte 2013). We suggest that diet monitoring should be an essential part of fisheries management, the task made easier and more feasible with recent advances in DNA-based diet identification (Deagle et al. 2009).

Some cautionary remarks on ecosystem modelling

Many parameters are required in the end-to-end ecosystem models, such as the one used in our study (Fulton 2010). One of the most uncertain aspects is the diet, especially the strength of trophic connections. Moreover, parameterising the model from data collected in a system that has been fished for decades (which is currently the case with most marine ecosystems) may not reflect biological dynamics in an unfished ecosystem. It is possible, or even likely, that through a long fishing period the system has undergone strong changes and adjustments in productivity, but we have no data to assess it. The 2 parameter sets we used differed in the maximum available biomass of some prey items to predators (details in Audzijonyte et al. 2013b) and had large effects on biomasses of many species (Supplement 2), suggesting extreme caution when interpreting results in a quantitative manner. Yet, the relative importance of fishing and size decreases of fishes was similar in both sets of parameters, suggesting that our finding might be relatively robust.

Post & Palkovacs (2009) reviewed studies where ecological and evolutionary feedback loops have been shown, and where evolution of a predator and a prey affected their ecological interactions and led to further evolutionary response. In our study we did not model the evolution of the 'shrinking' species

dynamically and therefore do not account for the possible evolutionary changes in size due to the altered feeding interactions. Experiments and empirical evidence reviewed in Post & Palkovacs (2009) typically involved 2 to 3 interacting species, whereas our ecosystem model had 57 functional groups; adding dynamic evolution into it would be extremely challenging. We can hypothesise that if natural selection opposed the effects of fishing, the overall decrease in size of harvested species would be smaller. However, we have already used very conservative rates of phenotypic change; the actual decrease in size caused by fishing or climate change is likely to be larger. Moreover, if the decrease in size is caused by physiological mechanisms due to oxygen limitation in warmer waters, natural selection imposed by predators is not expected to counteract this decrease. With this in mind, we believe that actual changes in trophic interactions caused by fishing and/or climate change are likely to be larger than modelled here.

Conclusions and future directions

This study presents the ecosystem level analyses of the relative ecological importance of size decrease in fish versus fishing and raises a few hypotheses to be tested in future studies. We suggest that fish decreasing in size will switch towards larger intake of invertebrate prey, releasing predation pressure on juveniles of other fish. Some of the fish that enjoyed predation release from 'shrinking' fish were (as adults) predators or these 'shrinking' species themselves. Thus, the decrease in size of some fish species triggered feedback loops where growing numbers of predators caused still further decline in biomasses of 'shrinking' species. In contrast, the effects of fishing alone (biomass removals) were more reversible, as fishing did not cause such feedback loops. Our predictions could be tested in real ecosystems by exploring diet composition of harvested species through time, while attempting to account for environmental effects. Some preliminary and limited data on diets of tiger flathead actually showed larger proportion of invertebrate prey in samples collected in autumn of 2010 compared to autumn of 1990 (C. Bulman unpubl. data); however more data is needed to assess whether there is indeed such a trend happening.

Despite the inevitable limitations of our modelling study, 2 main conclusions can be drawn and are likely to be applicable to a range of marine ecosystems: (1) decreases in fish body sizes are likely to have similar or even stronger ecosystem level effects

than moderate fishing, and (2) the effects of fishing and changes in body size are often similar and additive, whereby 'shrinking' amplifies the effects of fishing. While the ecological effects of the reduction in size-at-age are manifested over relatively long time scales and may seem of low concern to immediate fisheries management, they will lead to changes in natural mortality and productivity of fish stocks. Such decreases in productivity may remain unnoticed for a period of time and could potentially lead to overfishing. Monitoring life-histories and diets of harvested stocks should therefore be an important part of sustainable and precautionary fisheries management.

Acknowledgements. We thank Cathy Bulman for the comments on the manuscript and preliminary diet data. This study was supported by CSIRO. The research leading to these results has also received funding from the Academy of Finland (A.K.) and from the European Union's Seventh Framework Programme (FP7/2007-2013) under grant agreement no. 244706/ECOKNOWS project (A.K.). However, the paper does not necessarily reflect European Commission's views and in no way anticipates the Commission's future policy in the area.

LITERATURE CITED

- Andersen KH, Brander K (2009) Expected rate of fisheries-induced evolution is slow. *Proc Natl Acad Sci USA* 106: 11657–11660
- Audzijonyte A, Kuparinen A, Fulton EA (2013a) How fast is fisheries-induced evolution? Quantitative analysis of modelling and empirical studies. *Evol Appl* 6:585–595
- Audzijonyte A, Kuparinen A, Fulton EA (2013b) Ecological consequences of body size decline in harvested fish species: positive feedback loops in trophic interactions amplify human impact. *Biol Lett* 9:20121103
- Barange M, Allen I, Allison E, Badjeck MC and others (2011) Predicting the impacts and socio-economic consequences of climate change on global marine ecosystems and fisheries: The QUEST_Fish framework. In Ommer RE, Perry RI, Cochrane K, Cury P (eds) *World fisheries: a social-ecological analysis*, 1st edn. Blackwell, Oxford
- Bassar RD, Marshall MC, López-Sepulcre A, Zandonà E and others (2010) Local adaptation in Trinidadian guppies alters ecosystem processes. *Proc Natl Acad Sci USA* 107: 3616–3621
- Bassar RD, Ferriere R, López-Sepulcre A, Marshall MC, Travis J, Pringle CM, Reznick DN (2012) Direct and indirect ecosystem effects of evolutionary adaptation in the Trinidadian guppy (*Poecilia reticulata*). *Am Nat* 180: 167–185
- Cheung WWL, Sarmiento JL, Dunne J, Frölicher TL and others (2013) Shrinking of fishes exacerbates impacts of global ocean changes on marine ecosystems. *Nat Clim Change* 3:254–258
- Deagle BE, Kirkwood R, Jarman SN (2009) Analysis of Australian fur seal diet by pyrosequencing prey DNA in faeces. *Mol Ecol* 18:2022–2038

- Devine JA, Wright PJ, Pardoe H, Heino MM (2012) Comparing rates of contemporary evolution in life-history traits for exploited fish stocks. *Can J Fish Aquat Sci* 69: 1105–1120
- Enberg K, Jørgensen Ch, Dunlop ES, Varpe Ø and others (2012) Fishing-induced evolution of growth: Concepts, mechanisms and the empirical evidence. *Mar Ecol* 33: 1–25
- Frank KT, Petrie B, Shackell NL (2007) The ups and downs of trophic control in continental shelf ecosystem. *Trends Ecol Evol* 22:236–242
- Fulton EA (2010) Approaches to end-to-end ecosystem models. *J Mar Syst* 81:171–183
- Fulton EA, Smith ADM, Johnson CR (2003) Mortality and predation in ecosystem models: Is it important how these are expressed? *Ecol Model* 169:157–178
- Fulton EA, Fuller M, Smith ADM, Punt A (2004) Australian Fisheries Management Authority Report R99/1546. CSIRO, Hobart
- Fulton EA, Smith ADM, Punt AE (2005) Which ecological indicators can robustly detect effects of fishing? *ICES J Mar Sci* 62:540–551
- Fulton EA, Smith ADM, Smith DC (2007) Alternative management strategies for southeast Australian Commonwealth fisheries: Stage 2: quantitative management strategy evaluation. Australian Fisheries Management Authority, Fisheries Research and Development Corporation. <http://atlantis.cmar.csiro.au>
- Garcia SM, Kolding J, Rice J, Rochet MJ and others (2012) Reconsidering the consequences of selective fisheries. *Science* 335:1045–1047
- Halpern BS, Walbridge S, Selkoe KA, Kappel CV and others (2008) A global map of human impact on marine ecosystems. *Science* 319:948–952
- Jackson JBC, Kirby MX, Berger WH, Bjørndal KA and others (2001) Historical overfishing and the recent collapse of coastal ecosystems. *Science* 293:629–637
- Klaer NL, Smith DC (2012) Determining primary and companion species in a multi-species fishery: implications for TAC setting. *Mar Policy* 36:606–612
- Köster FW, Möllmann C (2000) Trophodynamic control by clupeid predators on recruitment success in Baltic cod? *ICES J Mar Sci* 57:310–323
- Kuparinen A, Merilä J (2007) Detecting and managing fisheries-induced evolution. *Trends Ecol Evol* 22:652–659
- Laugen AT, Engelhard GH, Whitlock R, Arlinghaus R and others (2014) Evolutionary impact assessment: accounting for evolutionary consequences of fishing in an ecosystem approach to fisheries management. *Fish Fish* 15: 65–96
- Law R (2007) Fisheries-induced evolution: present status and future directions. *Mar Ecol Prog Ser* 335:271–277
- Link JS (2005) Translating ecosystem indicators into decision criteria. *ICES J Mar Sci* 62:569–576
- Neuheimer AB, Thresher RE, Lyle JM, Semmens JM (2011) Tolerance limits of fish growth exceeded by warming waters. *Nat Clim Change* 1:110–113
- Palkovacs EP, Kinnison MT, Correa C, Dalton CM, Hendry AP (2012) Fates beyond traits: ecological consequences of human-induced trait change. *Evol Appl* 5:183–191
- Pörtner HO, Knust R (2007) Climate change affects marine fishes through the oxygen limitation of thermal tolerance. *Science* 315:95–97
- Post DM, Palkovacs EP (2009) Eco-evolutionary feedbacks in community and ecosystem ecology: interactions between the ecological theatre and the evolutionary play. *Philos Trans R Soc Lond B Biol Sci* 364:1629–1640
- Shackell NL, Frank KT, Fisher JAD, Petrie B, Leggett WC (2010) Decline in top predator body size and changing climate alter trophic structure in an oceanic ecosystem. *Proc R Soc Lond B Biol Sci* 277:1353–1360
- Shin YJ, Cury P (2004) Using an individual-based model of fish assemblages to study the response of size spectra to changes in fishing. *Can J Fish Aquat Sci* 61:414–431
- Swain DP, Benoit HP, Hammill MO, McClelland G, Aubry É (2011) Alternative hypotheses for causes of the elevated natural mortality of cod (*Gadus morhua*) in the southern Gulf of St. Lawrence: the weight of evidence. *DFO Can Sci Advis Sec Res Doc* 2011/036
- Vert-pre KA, Amoroso RO, Jensen OP, Hilborn R (2013) Frequency and intensity of productivity regime shifts in marine fish stocks. *Proc Natl Acad Sci USA* 110:1779–1784
- Walters C, Pauly D, Christensen V, Kitchell JF (2000) Representing density dependent consequences of life history strategies in aquatic ecosystems: EcoSim II. *Ecosystems* 3:70–83
- Wayte SE (2013) Management implications of including a climate-induced recruitment shift in the stock assessment for jackass morwong (*Nemadactylus macropterus*) in south-eastern Australia. *Fish Res* 142:47–55

Editorial responsibility: Katherine Richardson, Copenhagen, Denmark

Submitted: April 3, 2013; Accepted: October 3, 2013
Proofs received from author(s): December 12, 2013