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Marine biology

Ecological consequences of body size decline in harvested fish species: positive feedback loops in trophic interactions amplify human impact

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Humans are changing marine ecosystems worldwide, both directly through fishing and indirectly through climate change. One of the little explored outcomes of human-induced change involves the decreasing body sizes of fishes. We use a marine ecosystem model to explore how a slow (less than 0.1% per year) decrease in the length of five harvested species could affect species interactions, biomasses and yields. We find that even small decreases in fish sizes are amplified by positive feedback loops in the ecosystem and can lead to major changes in natural mortality. For some species, a total of 4 per cent decrease in length-at-age over 50 years resulted in 50 per cent increase in predation mortality. However, the magnitude and direction in predation mortality changes differed among species and one shrinking species even experienced reduced predation pressure. Nevertheless, 50 years of gradual decrease in body size resulted in 1–35% decrease in biomasses and catches of all shrinking species. Therefore, fisheries management practices that ignore contemporary life-history changes are likely to overestimate long-term yields and can lead to overfishing.

1. Introduction

There is a growing realization that humans are drastically changing the nature of trophic interactions in marine ecosystems, both directly through selective harvesting and indirectly through environmental changes [1–3]. One of the ways that marine food-webs are being modified by humans is through decreasing sizes of marine fishes [1,2]. This decrease is caused by: (i) direct removals of oldest and largest individuals through size-selective harvesting, (ii) contemporary evolution towards smaller size-at-age owing to selective harvesting of fast growing individuals or climate change, (iii) contemporary evolution towards increased/earlier energy allocation to reproduction, and consequently smaller realized size-at-age owing to high fishing mortality, and (iv) physiological declines in growth rates owing to increasing temperatures and decreasing oxygen concentration in warmer oceans [1–8]. All of these factors are likely to affect different species to a different extent, leading to differential changes in body sizes across the ecosystem, and subsequently modifying food-webs. However, to date there is little knowledge as to how the potential size decrease in harvested species will affect their biomasses and long-term yields and how this should be taken into account in marine ecosystem management [2–4]. Assessing human impacts on the food-web dynamics in complex marine environments poses a tremendous challenge, but conditional predictions can be made through the use of ecosystem models.

The South East (SE) Australian marine ecosystem has been modelled using the whole-of-system modelling framework *Atlantis*. This implementation makes extensive use of data specific to the region and has been applied to evaluate alternative strategies for fisheries management [9–12]. The model includes size-based feeding interactions and is therefore well suited to explore ecosystem-level impacts of declining fish body sizes. We modified the model to simulate body size decrease in five demersal SE Australian trawl fisheries species. The ecosystem responses were explored in a full-factorial manner, where four different levels of fishing were combined with three levels of decrease in body size.

2. Material and methods

The *Atlantis* modelling framework is based on a 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. Nitrogen is used as the currency of the model and its flow is tracked through the biological groups in the system. The model parameterized for SE Australian ecosystem has 70 geographical cells ranging in size from 573.5 to 390 000 km² and up to seven water column layers per cell (see the electronic supplementary material, figure S1) matched to system bioregions and geomorphology. Fifty-seven ecological groups are modelled (see the electronic supplementary material, table S1), the majority of them aggregate species with similar size, habitat and diets, 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. All vertebrate groups have 10 age bins, each corresponding to 1–10 calendar years, depending on the longevity of the group. The main ecological processes modelled are consumption, growth, waste production, movement, recruitment, habitat-dependency and other mortality (e.g. disease; see further details in 9–12, electronic supplementary material and at <http://atlantis.cmar.csiro.au/>). The model was parameterized using data from 36 separate 20–90 year catch time-series and available scientific surveys over the last 50 years [11]. Pattern-oriented modelling, which simultaneously fits all model parameters to the available data [13], was used to obtain the parameter values. In order to explore the sensitivity of our findings to the chosen set of biological parameter values, we ran identical simulations using a conservative set of parameters that assumed weaker species interactions, thus leading to less pronounced trophic cascade and predator–prey responses (see the electronic supplementary material, table S6).

For the purpose of this study, we simulated fishing and body size change in five SE Australian demersal fish species that constitute the main catch of the SE Australian shelf and offshore trawl fisheries. The species are jackass morwong (*Nemadactylus macropterus*), tiger flathead (*Platycephalus richardsoni*), silver warehou (*Seriolella punctata*), blue grenadier (*Macrurus novaezelandiae*) and pink ling (*Genypterus blacodes*) (figure 1, see the electronic supplementary material, tables S5 and S6 for the main predators and diet items of the five species). A simple spatially uniformly distributed exploitation rate strategy was used. The same fishing rate was applied to all five species throughout the entire simulation period, based on logistic selectivity curves that represent average selectivity for each species as imposed by the fisheries (mostly trawling, details in the electronic supplementary material). Bycatch associated with the take of the target species was applied using empirically estimated bycatch ratios [14]. No other incidental effects of fishing were included.

In order to simulate the decrease in body size of harvested species, we forced *a priori* chosen rates of phenotypic change. Represented in this way, our model does not simulate contemporary evolution dynamically and does not account for the potential evolution in species interactions. Here, we are interested only in the trophic changes owing to the changes in fish body size, such as shown to occur in many fisheries stocks [5,8] or as is expected through climate change [1]. Our rates of phenotypic change are conservative, corresponding to approximately 2 and 4 per cent decrease in the body length over 50 years (i.e. 0.04% and 0.08% per year) [8].

The decrease in size-at-age was achieved by modifying the maximum growth rate values in the feeding functional response equation and consequently decreasing the realized size-at-age (see the electronic supplementary material). The decrease was set to be continuous and constant over the entire simulation period. In line with the empirical observations and modelling studies [7] the length-at-age of older age bins was set to decrease faster than in the younger age bins (see the electronic supplementary material, table S2). The change in body size was set to occur at approximately equal rates in all five harvested species, but owing to multiple ecological processes the realized change varied slightly among species.

We ran 12 deterministic scenarios in a full factorial design to explore the effects of changes in body size under different fishing pressure conditions. We simulated four instantaneous fishing mortality rates of $F = 0, 0.2, 0.4$ and 0.6 per year and combined each of them with three phenotypic rates ($R = 0\%, 2\%$ and 4% decrease in length-at-age over 50 years) for all five focal species simultaneously. In reality, changes in body size will be faster for higher F values and different across species. However, the change will depend on life history, species range, its physiology and genetic diversity, generation time, gear selectivity and cannot be predicted *a priori*. Simulations were run for 90 years, and the body size of fished species was decreasing over the entire simulation period. Biomasses of most species fluctuated strongly during the first 40 years and then settled into some equilibrium; these first 40 years were therefore discarded from the final analyses.

3. Results and discussion

Our ecosystem modelling showed that even small decreases in the body size of fish species can have large effects on their natural mortality. Regardless of the fishing intensity, 50 years of directional phenotypic change in body size induced shifts in species interactions and resulted in biomasses of all harvested species except grenadier decreasing by 5–35% compared with the levels reached in simulations without directional change in body size (figure 1*a*). Similarly, catches declined by up to 35 per cent (figure 1*b*). Notably, the effects of changing body size on a particular species varied and could not be predicted *a priori*. The largest negative effect was seen in flathead and warehou, while the biomass of grenadier decreased by less than 5 per cent and numbers actually increased by up to 10 per cent. These differences in the species response to decreasing size-at-age were largely explained by the changes in their natural mortality brought about through a range of ecosystem feedback loops. At the end of the 50-year simulation, the predation mortality of flathead and warehou was 5–48% higher in scenarios with decreasing body size compared with those without directional change, while the predation mortality of grenadier decreased by 3–28% (see figure 1*c*, electronic supplementary material, table S4). The more conservative set of parameter

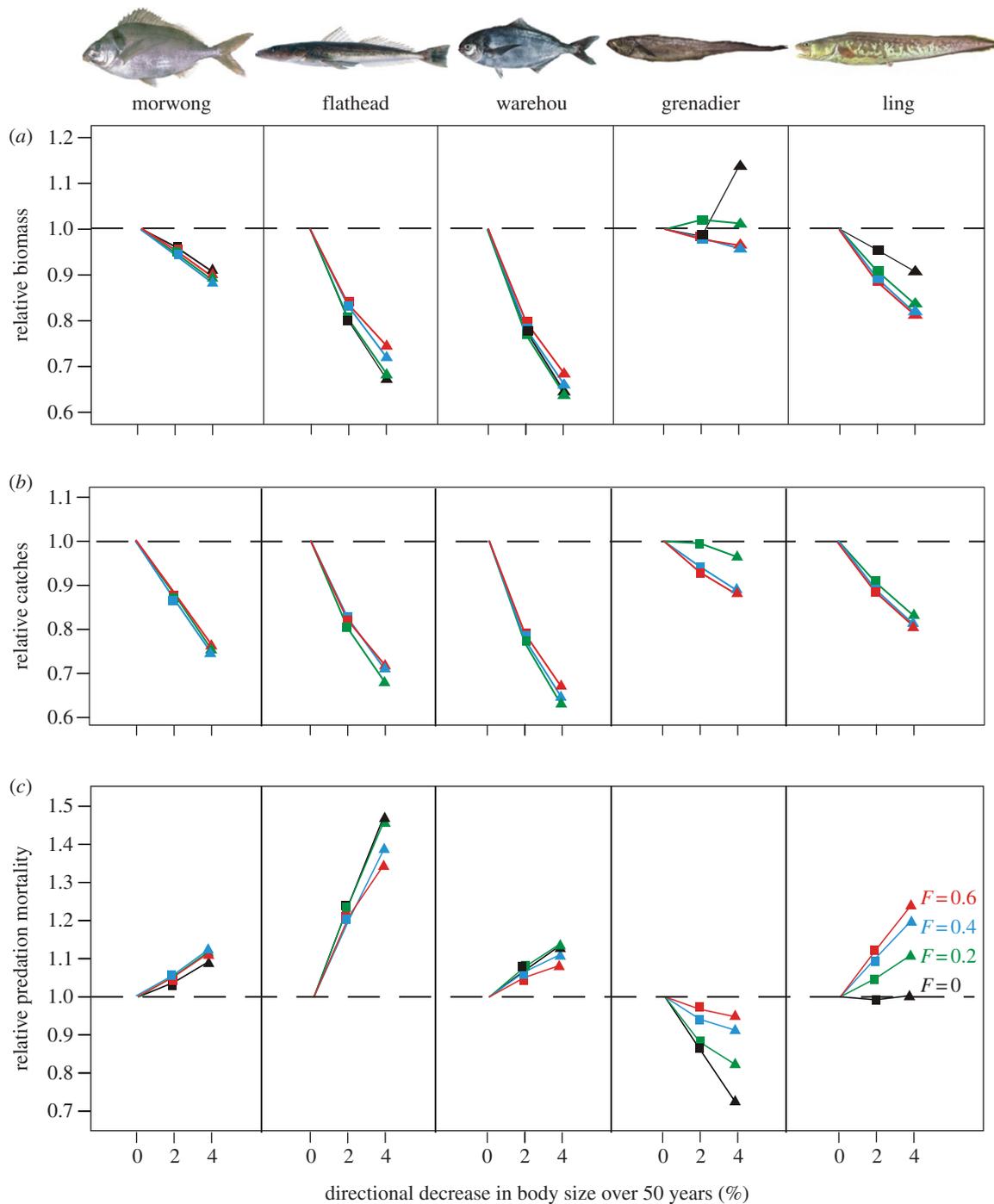


Figure 1. Final (average of years 46–50) (a) biomasses, (b) yields and (c) predation mortality of five harvested species in 12 simulation scenarios combining four fishing levels ($F = 0, 0.2, 0.4$ and 0.6) and three rates of body size decrease ($R = 0\%, 0.04\%$ and 0.08% per year). For each species, values are scaled by the baseline scenario ($F = 0, R = 0$). Fishing levels are shown in different colours and rates of size decrease are marked with different symbols.

values gave qualitatively similar changes in biomasses, numbers and natural mortality of fished/shrinking species (see the electronic supplementary material, tables S3 and S4).

The changes in natural mortality of harvested species observed in simulations with declining body size were seen even without major changes in the biomasses of their predators and were caused by other mechanisms (figure 2). Three examples of such mechanisms include: (i) increased numbers of oldest age classes of predators (barracouta in figure 2*a* and school whiting in figure 2*b*) caused by lowered predation intensity on their youngest ages by harvested/shrinking species (flathead), (ii) prey switching (by cephalopods in figure 2*b*) triggered by decreasing length, vulnerability and

biomasses of shrinking species (flathead) and (iii) changes in the distributions of functional groups (grenadier) caused by changes in their food sources (figure 2*c*). The first two factors tended to amplify the effects of body size decline through positive feedback loops, leading to the large biomass decreases in flathead and warehou. Interestingly, although grenadier also was getting smaller, its predation mortality decreased (see figure 1*b*, electronic supplementary material, tables S4 and S5). In scenarios with body size decrease, grenadier juveniles moved to more coastal areas, following the improved supply of invertebrate prey (see the electronic supplementary material, figure S2). This move increased their spatial overlap with flathead and ling juveniles and made them less vulnerable to predation from gelatinous

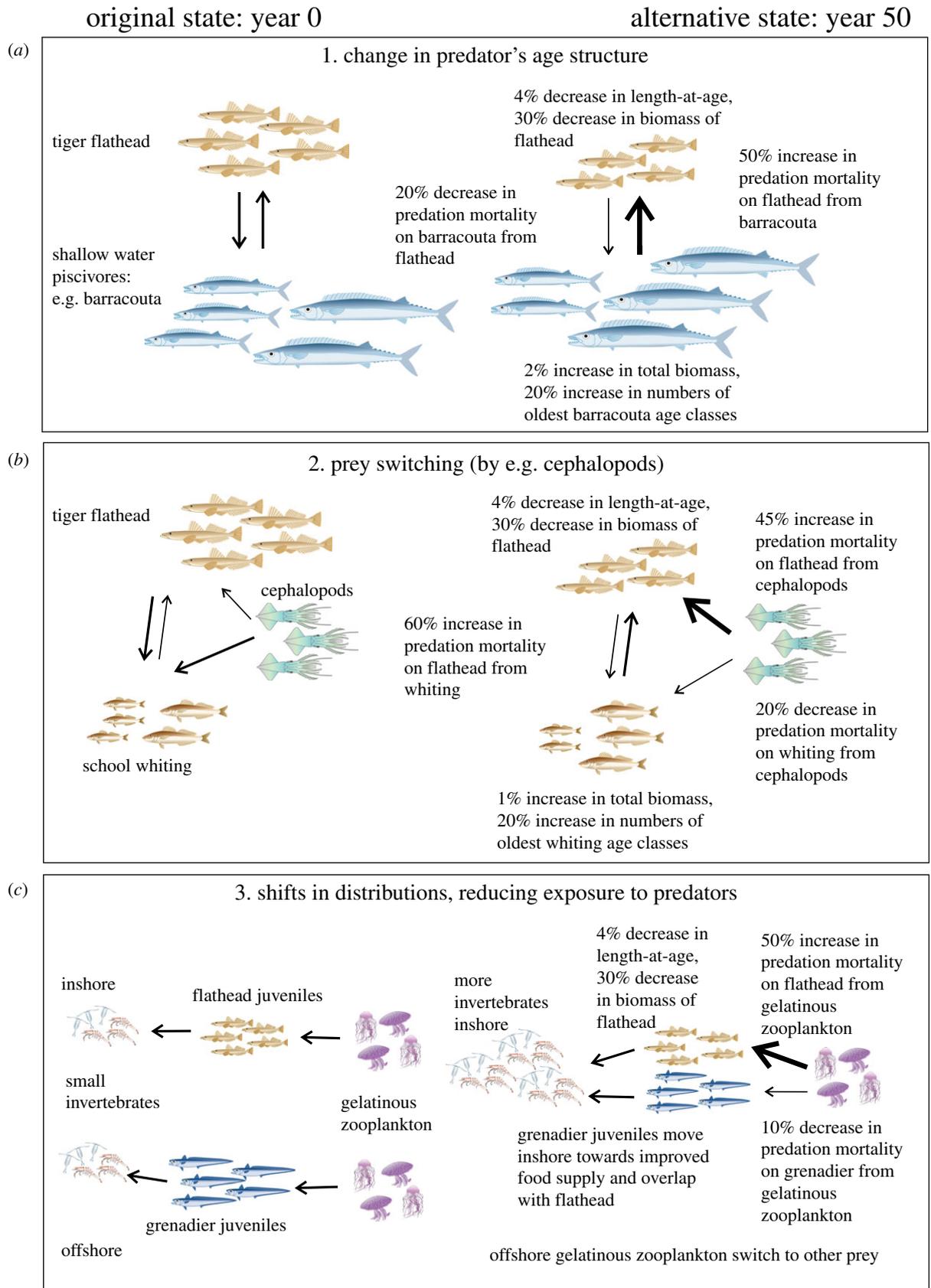


Figure 2. Three example mechanisms of ecosystem responses to body size decrease that had strong effects on biomasses of harvested species but involved only small changes in biomasses of other species. Numbers on the right side reflect the comparison between scenarios with 0% and 4% decrease in body size over 50 years and same fishing intensity ($F = 0.2$). Note that (c) includes both change in time (year 0 to year 50) and change in the spatial distribution of grenadier (offshore to inshore) (see the electronic supplementary material, Figure S2). The width of the arrows among functional groups represents the strength of predation intensity.

zooplankton and cannibalism (figure 2c). Although the exact distributions and movements of species will depend on the assumptions made in the model, and it is hard to identify a

single cause determining them, our analyses demonstrate some mechanisms (e.g. distribution shifts) that can lessen the negative effects of decreasing body size.

4. Conclusions

Predictions from complex ecosystem models are bound to be sensitive to the assumptions made and are most useful for comparing alternative scenarios. One limitation of our model is that we only simulated body size changes in five species. Therefore, we do not account for the full complexity of species interactions, e.g. selective pressures on body size of shrinking species caused by the changes in their natural mortality. Further, oxygen limitation owing to climate change is likely to lead to some, even if uneven, body size reduction in most species, and the magnitude of trophic changes will differ from those in our simulations. Nevertheless, this study identifies three main points that deserve further attention. (i) The complex mechanisms in which ecosystem can

respond to changes in fish body size mean that the effect of fishing or climate change on a particular species can range from very strong (e.g. flathead) to almost negligible (e.g. grenadier) and should be explored in an ecosystem context [15]. (ii) Predictions from ecosystem-based approaches are likely to overestimate the future biomass and catches of harvested species if contemporary changes in life-history are ignored. (iii) Predictions of biomass and yields from single-species stock assessments, as used in most fisheries management today, should routinely explore the consequences of changing body size and natural mortality of harvested species.

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