Climate-driven zooplankton shifts could cause global declines in food quality for fish

Ryan Heneghan (r.heneghan@qut.edu.au)
Queensland University of Technology https://orcid.org/0000-0001-7626-1248
Jason Everett
The University of Queensland https://orcid.org/0000-0002-6681-8054
Julia Blanchard
University of Tasmania https://orcid.org/0000-0003-0532-4824
Patrick Sykes
University of Queensland
Anthony Richardson
CSIRO https://orcid.org/0000-0002-9289-7366

Article

Keywords: zooplankton community composition, marine food webs, gelatinous zooplankton

Posted Date: November 8th, 2021

DOI: https://doi.org/10.21203/rs.3.rs-953268/v1

Title

Climate-driven zooplankton shifts could cause global declines in food quality for fish

Authors

Ryan F. Heneghan[1], Jason D. Everett[2,3,4], Julia L. Blanchard[5], Patrick Sykes[2], Anthony J. Richardson[2,3]

[1] School of Mathematical Sciences, Queensland University of Technology, Brisbane, QLD, Australia

[2] School of Mathematics and Physics, The University of Queensland, St. Lucia, Queensland, Australia

[3] Commonwealth Scientific and Industrial Research Organisation (CSIRO) Oceans and Atmosphere, Queensland Biosciences Precinct, St Lucia, Queensland, Australia

[4] Centre for Marine Science and Innovation, School of Biological, Earth and Environmental Sciences, University of New South Wales, Sydney, NSW, Australia

[5] Institute for Marine and Antarctic Studies, University of Tasmania, Hobart, TAS, Australia

Contact information

Email: ryan.heneghan@gmail.com

Abstract

Although zooplankton are the primary energy pathway from phytoplankton to fish, we understand little about how climate change will modify zooplankton communities and their role in marine ecosystems. Using a trait-based marine ecosystem model resolving key zooplankton groups, we assess climate change impacts on zooplankton community composition and implications for marine food webs globally. We find that future oceans favour food webs increasingly dominated by carnivorous (chaetognaths, jellyfish and carnivorous copepods) and gelatinous filter-feeding zooplankton (larvaceans and salps). By providing a direct energetic pathway from small phytoplankton to fish, the rise of gelatinous filter-feeders largely offsets the increase in trophic steps between primary producers and fish from declining phytoplankton production and increasing carnivorous zooplankton. However, our results indicate that future fish communities face not only reduced carrying capacity from falling primary production, but also lower quality diets as environmental conditions increasingly favour gelatinous zooplankton.

Main text

Zooplankton are a critical component of marine food webs, serving as the primary energy pathway from phytoplankton to fish[1] and a major driver of carbon sequestration to the deep oceans[2,3]. Zooplankton are extremely diverse, representing all major phyla[4], and accounting for ~40% of the world's marine biomass[5]. However, despite their abundance[5], ecological importance[6], and role in global carbon cycling[2,3], most ecosystem models resolve few zooplankton groups[6], focusing on phytoplankton or fish, particularly in climate change projections[7,8]. By not adequately resolving the zooplankton community in ecosystem models, we could miss major changes in marine food web structure and function in response to climate change[9,10,11] that have implications for ecosystem services ranging from biogeochemical cycling [2,3,12] to fisheries[1,13].

Changes in the marine zooplankton community across space and time are determined by how the vastly different functional traits of its members interact with each other and their environment[10,14]. These zooplankton functional traits – including their predator-prey mass ratios (PPMRs) and carbon content – not only govern the relative fitness of individual zooplankton[9,10,15], but also regulate their role in transferring energy from phytoplankton to fish[10,14,15]. For example, the higher the community-wide PPMR of the zooplankton community, the fewer trophic levels and less energy lost from phytoplankton to fish[16]. Communities dominated by carnivorous zooplankton (PPMR <100[17]) transfer much less biomass to higher trophic levels than filter-feeders such as larvaceans and salps[16] (PPMR >40 million[17,18]). Zooplankton community composition also alters the quality of the food available for fish, as carbon content of zooplankton varies by 1.5 orders of magnitude[19], from gelatinous zooplankton (0.5%), through crustaceans (12%), to microzooplankton (15%). Better accounting of the diversity of zooplankton functional traits will thus improve our ability to quantify carbon cycling and energy flow from plankton to fish now and under future climate change.

Here we assess impacts of climate change on the composition of zooplankton communities across the global ocean. We explore how these climate-driven changes could affect the diet quality and biomass of small pelagic (planktivorous) fish—the primary predator of zooplankton beyond zooplankton themselves—as well as the number of trophic steps from phytoplankton to fish. We use a global functional trait-based marine ecosystem model[20] (the Zooplankton Model of Size Spectra, ZooMSS) that resolves phytoplankton, two microzooplankton groups (heterotrophic flagellates and ciliates), seven meso and macrozooplankton groups (omnivorous and carnivorous copepods, larvaceans, euphausiids, salps, chaetognaths and jellyfish), and three size-based fish groups (broadly representing small pelagic fish ≤100g; medium pelagic fish ≤10kg and large pelagic fish ≤1 tonne). ZooMSS resolves the nine zooplankton groups based on the traits of size range, feeding characteristics (primarily PPMR) and carbon content (Table S1). ZooMSS captures the global distribution of zooplankton biomass and functional groups, and their growth rates reasonably well[20]. We focus our analysis on the meso and macrozooplankton (hereafter called zooplankton), organising them into three groups – carnivores (chaetognaths, jellyfish and carnivorous copepods), omnivores (euphausiids and omnivorous copepods), and filter-feeders (larvaceans and salps). ZooMSS is forced by five Coupled Model Intercomparison Project Phase 6 (CMIP6) earth system models[21] under three future (2015–2100) IPCC shared socioeconomic pathways (SSP)[22] (SSP1-2.6, SSP3-7.0 and SSP5-8.5) using historical (1980–2014) conditions as a baseline (see Methods).

Global zooplankton biomass in ZooMSS declined by between 8% (SSP1-2.6) and 18% (SSP5-8.5) from 1980-2100 (Fig. 1; Table 1). The mean decline in global zooplankton biomass was similar across the three SSPs until 2040, after which the decline under SSP1-2.6 levelled off, but continued under SSP3-7.0 and SSP5-8.5 (Fig. 1). These declines in zooplankton biomass are within the range of similar studies[23,24] and are linked to the projected decline in phytoplankton biomass (Fig. S1). Previous modelling and observational studies have also shown strong agreement between zooplankton and phytoplankton biomass changes over large spatial scales[23,24,25].

The decline in global biomass (from 1980-2100) was not uniform across zooplankton groups (Fig. 2a–c; Table 1). Omnivorous zooplankton biomass exhibited the greatest decline, by between 10% (SSP1-2.6) and 21% (SSP5-8.5). By contrast, filter-feeders experienced a more modest biomass decline of between 1% (SSP1-2.6) and 4% (SSP5-8.5). The magnitude of decline in carnivorous zooplankton biomass was similar to that in filter-feeders, decreasing between 3% (SSP1-2.6) and 6% (SSP3-7.0). Although all groups decline because of the decreasing phytoplankton biomass, the greater decline in omnivores (omnivorous copepods and euphausiids) is a consequence of the relatively greater reduction of their preferred diet of larger phytoplankton cells in comparison to smaller phytoplankton[10,14] (Fig. S2).

There was also considerable variation in the response of each zooplankton group across ocean basins (Fig. 2d–r; Table 1). This was particularly true in the Southern Ocean, where the direction of biomass change for zooplankton groups was often opposite to the global trend. From 1980-2100, omnivorous zooplankton biomass had declines of >20% under both SSP3-7.0 and SSP5-8.5 across ocean basins, excluding the Southern Ocean where omnivores increased by between 7% (SSP1-2.6) and 34% (SSP3-7.0). In contrast, filter-feeder biomass was the least affected by climate change, varying between an increase of 13% in the Arctic Ocean (SSP5-8.5) and a decrease of 11% in the Indian Ocean (SSP3-7.0). The magnitude of the change for carnivorous zooplankton was greater than filter-feeders, but less than omnivorous zooplankton, with changes in carnivore biomass varying between a decline of 16% in the Arctic under SSP5-8.5 and an increase of 4% in the Southern Ocean under SSP3-7.0.

Biomass declines across the three zooplankton groups manifest spatially as disparate shifts in the composition of the zooplankton community (Fig. 3). Under historical (1980–2000) conditions, carnivorous and filter-feeding zooplankton constitute 50–70% of the zooplankton in oligotrophic subtropical gyres (Fig. 3a,b) where phytoplankton and zooplankton biomass is lower[26,27] (Supp. Fig. S1a,b). In contrast, omnivorous zooplankton dominate in polar and upwelling regions where phytoplankton and zooplankton biomass are higher[26,27], constituting 60–90% of total zooplankton biomass (Fig. 3c). By 2100, all three SSPs show increasing dominance of carnivorous and gelatinous filter-feeding zooplankton, particularly in expanding subtropical oligotrophic gyres (Fig. 3d–l), with the magnitude of changes increasing with greater future emissions. Under SSP1-2.6, carnivorous and filter-feeding zooplankton each increased as a proportion of total zooplankton biomass by up to 10% across large areas of the ocean where oligotrophic waters are expanding, and under SSP5-8.5 by 15–30% (Fig. 3d-f). Filter-feeders such as larvaceans and salps with huge PPMRs of >10 million (Table S1) do better as oceans warm, predominantly due to the relative increase in the global biomass of small phytoplankton cells under climate change[28] (Fig. S2). The ability of filter-feeders to consume small phytoplankton and bacteria <1 µm in size[17,18,29] allows them to outcompete omnivores where small phytoplankton and bacteria are dominant[10,14,30]. Carnivores are also expected to do well as the oceans warm because of the reduced phytoplankton biomass (Fig. S1) and greater relative importance of microzooplankton[10,14,31] (Fig. S2).

Conversely, omnivorous zooplankton declined by >20% as a proportion of total zooplankton biomass under all emission scenarios, in areas where the relative prevalence of carnivores and filter-feeders increased. The greater importance of microzooplankton (Supp. Fig. S2, right column) and the decline in large phytoplankton in ocean gyres of the future (Supp. Fig. S2, centre column), decreases the total energy available for omnivorous zooplankton[10,14,31], increasing competition with carnivorous zooplankton for microzooplankton prey, and causing a decline in the dominance of omnivore relative to other zooplankton. Evidence for this projected shift from omnivores toward carnivores and gelatinous filter-feeders has already been observed in some regions[32,33], and our results suggest these shifts will intensify and expand under climate change (Fig. 2, 3). Only in the Southern Ocean and some subtropical waters where phytoplankton biomass, large phytoplankton cells, and zooplankton biomass all increased (Supp. Fig. S1, S2), did omnivorous zooplankton rise as a proportion of the total zooplankton community, with greatest increases of 10% in the Southern Ocean under the SSP3-7.0 scenario (Fig. 3h). These results represent significant potential shifts in global zooplankton community composition, given copepods—of which omnivores are dominant[34]—are the most abundant metazoans on the planet[35].

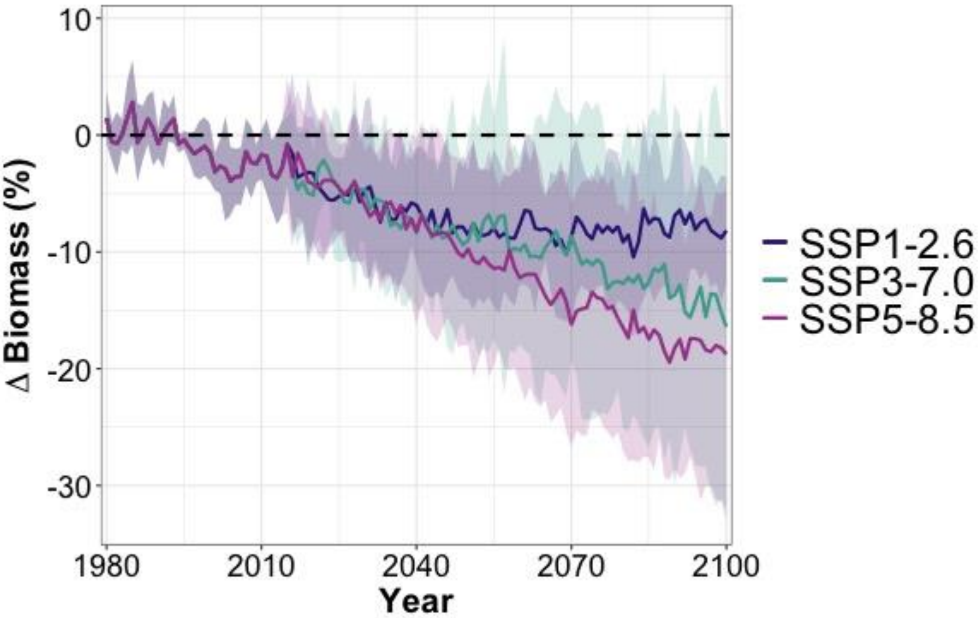

Fig. 1 | Impacts of climate change on global zooplankton biomass. Change in global zooplankton biomass (%) for three zooplankton groups from 1980–2100 under emission scenarios SSP1-2.6, SSP3-7.0 and SSP5-8.5. Solid lines give the mean change in total global zooplankton biomass, and shaded areas represent the standard deviation.

Table 1 | Mean (± standard deviation) biomass change (%) for All zooplankton, Carnivores (chaetognaths, jellyfish, carnivorous copepods), Filter-feeders (larvaceans and salps) and Omnivores (euphausiids and omnivorous copepods) across SSPs and ocean basins, from 1980 to 2100.

	Total Zooplankton			**Carnivores**			**Filter-feeders**			**Omnivores**		
	SSP1-2.6	SSP3-7.0	SSP5-8.5	SSP1-2.6	SSP3-7.0	SSP5-8.5	SSP1-2.6	SSP3-7.0	SSP5-8.5	SSP1-2.6	SSP3-7.0	SSP5-8.5
Global	−8±5	−16±15	−18±14	-3±3	−6±8	−5±9	−1±2	−3±6	−4±6	−10±6	−18±23	−21±18
Arctic Ocean	−26±30	−38±36	−32±52	−9±10	−16±14	−16±22	12±5	12±12	13±12	−25±42	−39±42	−21±80
Atlantic Ocean	−13±10	−24±8	−28±11	−7±7	−8±6	−9±9	2±5	0±10	−2±10	−16±12	−26±8	−30±11
Indian Ocean	−14±11	−29±21	−29±19	−8±9	−14±23	−12±20	−5±6	−11±15	−10±11	−19±14	−37±24	−38±22
Pacific Ocean	−9±5	−27±13	−28±14	−2±3	−7±10	−5±11	−2±2	−4±7	−4±8	−12±8	−33±17	−34±18
Southern Ocean	5±9	21±38	16±31	1±2	4±3	3±4	0±2	−3±3	−2±2	7±14	34±65	25±50%

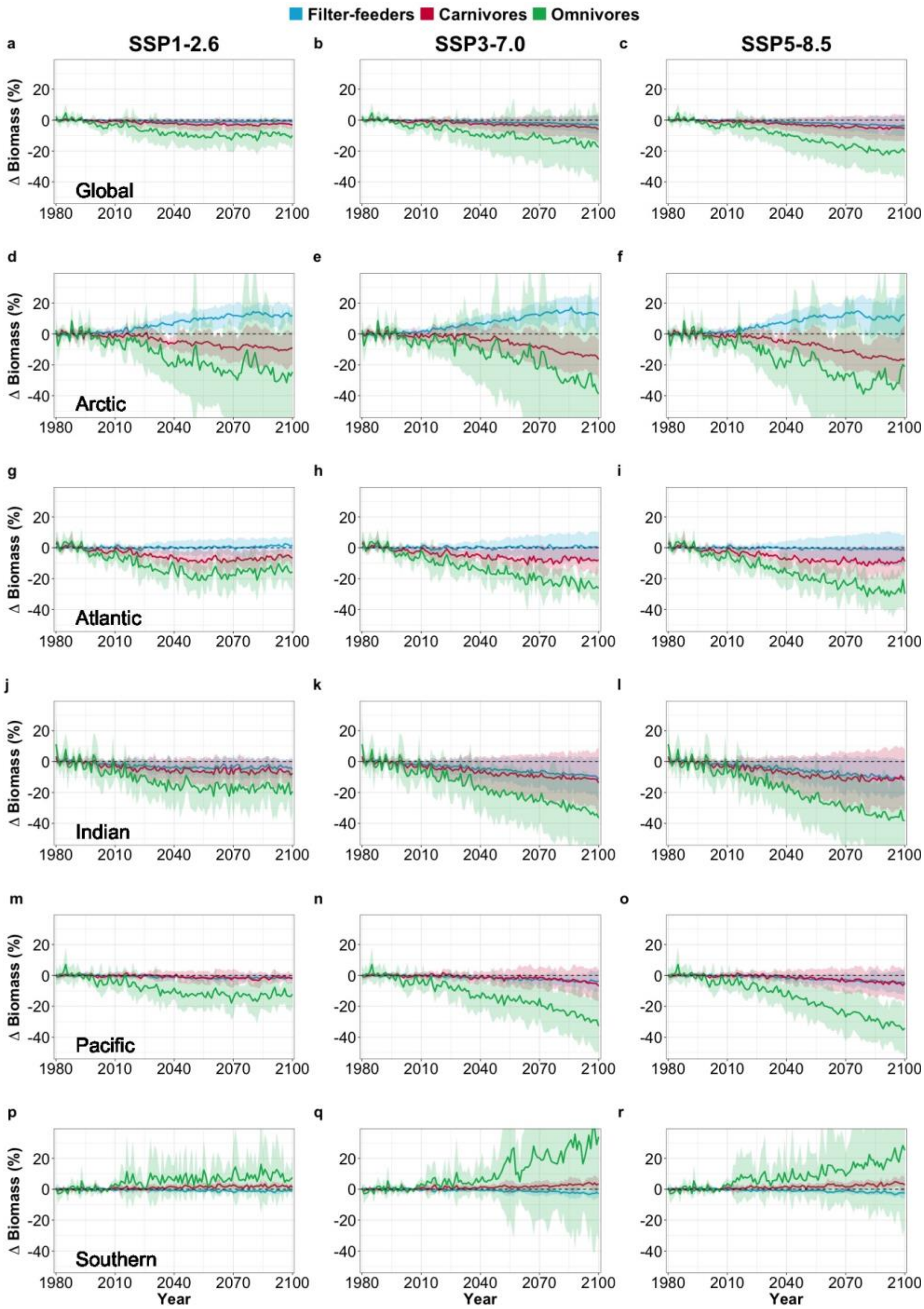

Fig. 2 | Impacts of climate change on three major zooplankton groups. Change in global biomass (%) for three zooplankton groups (Carnivores: chaetognaths, jellyfish, and carnivorous copepods; Filter-feeders: larvaceans and salps; Omnivores: euphausiids and omnivorous copepods) from 1980–2100 under emission scenarios SSP1-2.6, SSP3-7.0 and SSP5-8.5 (columns), for each Ocean (rows). Solid lines give the mean change for each zooplankton group, and shaded areas represent the standard deviation.

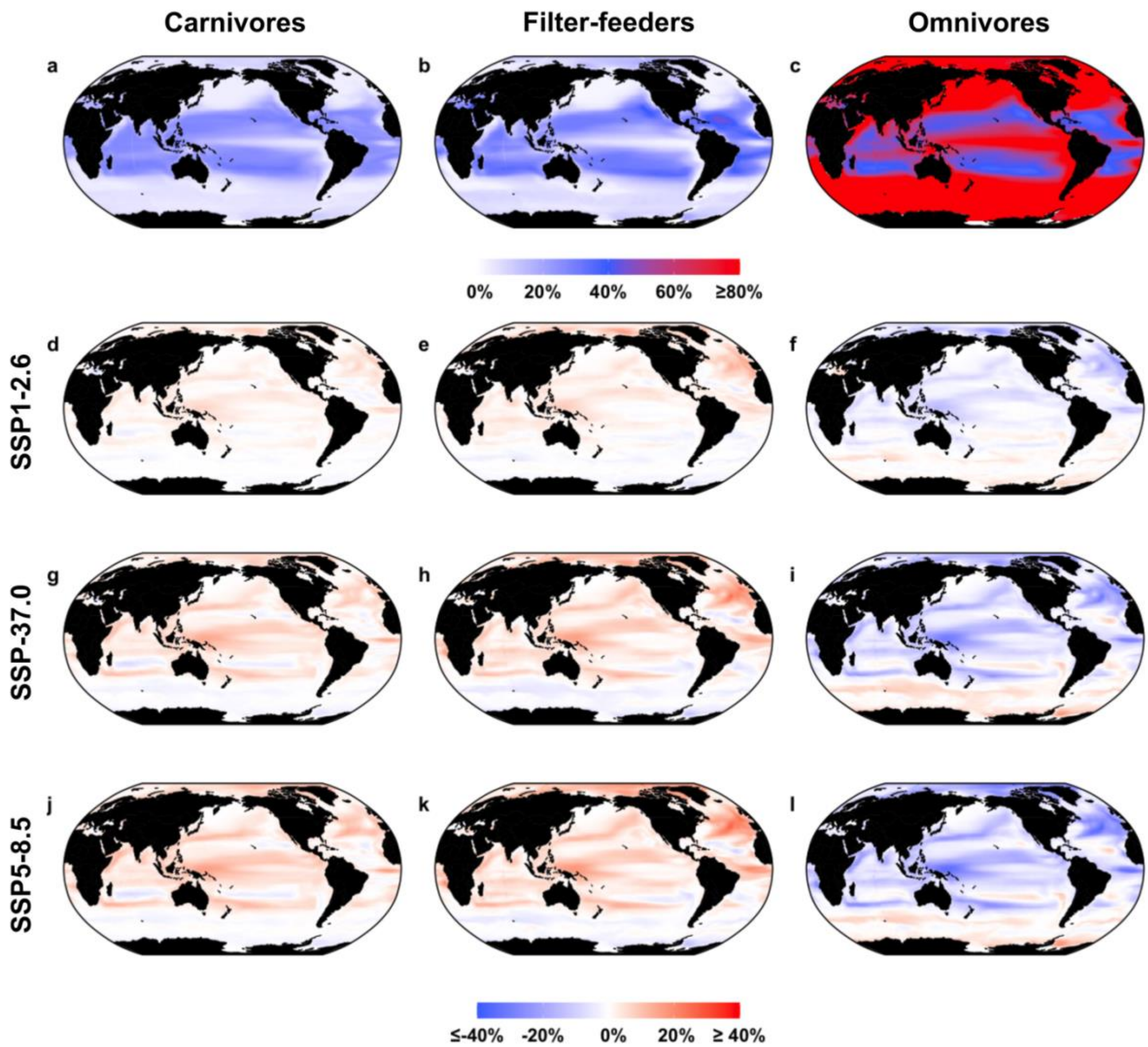

Fig. 3 | Climate-induced shifts in zooplankton community composition. a–c, The percentage of total community biomass in 1980-2000 comprising: **a**, Carnivores; **b**, Filter-feeders; and **c**, Omnivores. **d–l**, Maps of the mean change (%) of total zooplankton community biomass from: **d**, **g**, **j** Carnivores; **e**, **h**, **k**, Filter-feeders; and **f**, **i**, **l**, Omnivores in 2080–2100 compared with 1980–2000 under emission scenarios SSP1-2.6, SSP3-7.0 and SSP5-8.5 (rows).

Changes in zooplankton composition can have profound implications for the diet, trophic position and ultimately biomass of fish[1,13,16,25,31,36]. We thus used ZooMSS to explore how changes in the zooplankton community composition under SSP5-8.5 impacted small pelagic fish. Small pelagic fish play extremely important ecological roles in marine ecosystems and form some of the most economically valuable fisheries resources, contributing significantly to global food security[37]. The proportion of the diet of small pelagic fish comprising omnivorous zooplankton decreased from 74% to 66% between 1980–2100, corresponding to increases in the contribution of filter-feeders from 18% to 22%, and in carnivores from 8% to 12% (Fig. 4). These changes in small pelagic fish diet mirrored shifts in zooplankton community composition (Fig. 2,3).

However, despite future declines in omnivores (high PPMRs) and increases in carnivores (low PPMRs) that should lead to longer food chains[10,38,39], the mean trophic level of small pelagic fish increased by only 1% globally (from 3.56 to 3.59) and by at most ~1.5% in the Indian Ocean (from 3.5 in 1980 to 3.55 in 2100). Such a slight increase is a consequence of the longer food chains that would result from a rise in carnivores and decline in omnivores being largely offset by the simultaneous increase in gelatinous filter-feeders (with huge PPMRs) that lead to shorter food chains. The unique role of gelatinous filter-feeders in providing an alternative energetic pathway between primary producers and higher trophic levels has long been hypothesised based on their body sizes and large PPMRs[17,40]. However, owing to their fragile bodies, gelatinous zooplankton have been poorly studied because they rapidly disintegrate in the guts of their predators or when sampled in nets[30]. New approaches to examining diets of marine predators, such as stable isotope analysis and DNA metabarcoding, show that larvaceans and salps are often major prey items of many commercial fish species and therefore serve an important role in structuring marine ecosystems[27,41,42,43]. Our results suggest that the direct energy pathway from small phytoplankton through filter-feeders to fish will grow in importance in the future as small phytoplankton become increasingly dominant in a warming ocean[28].

The trend toward more gelatinous zooplankton drives a decrease in the quality of the diet of small pelagic fish fish under climate change (Fig. 4). Gelatinous carnivores such as jellyfish and chaetognaths, and filter-feeders such as larvaceans and salps, are 65-95% less carbon-dense than omnivorous zooplankton such as euphausiids and copepods[19]. As gelatinous zooplankton outcompete carbon-dense omnivorous groups, the quality of the diet of small pelagic fish decreases by ~5% globally, from just under 10% carbon in 1980 to 9.5% in 2100 (Fig. 4b). Although this global decline is modest, there were greater reductions in individual ocean basins of 5-13% in the Atlantic, Indian, Pacific and Arctic Oceans (1980-2100; Fig. 4). Evidence for shifts in zooplankton community composition in response to warming have already been observed during the recent marine heatwave from 2013-2016 that led to higher sea-surface temperatures and lower primary production throughout much of the North Pacific, and commonly called the "Blob"[44]. Decreases in phytoplankton production during the heatwave drove declines in the abundance of carbon-dense euphausiids and increases in gelatinous zooplankton[45], and was manifest as shifts in the diet of small pelagic fish from euphausiids to gelatinous zooplankton[46] as well as declines in their weight and energetic content[46,48]. Coupled with these empirical studies, our results indicate that future fish communities in large parts of the world's oceans face not only reduced ecosystem carrying capacity from falling primary production, but also potentially lower quality diets as environmental conditions increasingly favour gelatinous zooplankton.

Declines in phytoplankton biomass and food quality impact small pelagic fish biomass, with ZooMSS showing a 20% global decline in their biomass (from 1980-2100), and declines of 25-35% in all ocean basins except for the Southern Ocean (Fig. 4). A general expectation of climate change is that future marine ecosystems will support less fish biomass where primary production decreases[7]. At the same time, the number of trophic steps between primary producers and fish is also expected to increase in these areas, as mean phytoplankton size declines[38,39]. Our results support the first part of this expectation—less phytoplankton means lower fish biomass (Fig. 5a)—while challenging the expectation that future food webs will be longer (Fig. 4, 5b). Our results also suggest another hypothesis: less productive future phytoplankton communities will support lower-quality food webs (Fig. 5c).

To elucidate how zooplankton shapes the relationship between phytoplankton and fish, we assessed changes in the biomass, trophic level and diet quality of small pelagic fish in relation to phytoplankton biomass across all grid cells (Fig. 5). Where phytoplankton biomass declined zooplankton communities became more gelatinous, with both causing small pelagic fish biomass and diet quality to decline and their trophic level to slightly increase (Fig. 5; Supp. Fig. S1, S3). Where phytoplankton biomass increased, small pelagic fish diet quality also increased, but their trophic level did not noticeably change. Areas of phytoplankton biomass increase were isolated mostly to the Southern Ocean, where carbon-dense omnivorous zooplankton constitute >80% of the total zooplankton biomass (Fig. 3c). In these regions, contemporary small pelagic fish diet carbon content was >11% (Supp. Fig. S3a), with little scope for further increases. Similarly, small pelagic fish in these high phytoplankton biomass regions had the lowest contemporary trophic levels (<3.5), compared to other regions (Supp. Fig. S3b). Since their diet did not substantially change with warming (Fig. 4u), their trophic level also remained largely the same from 1980-2100 (Fig. 4w).

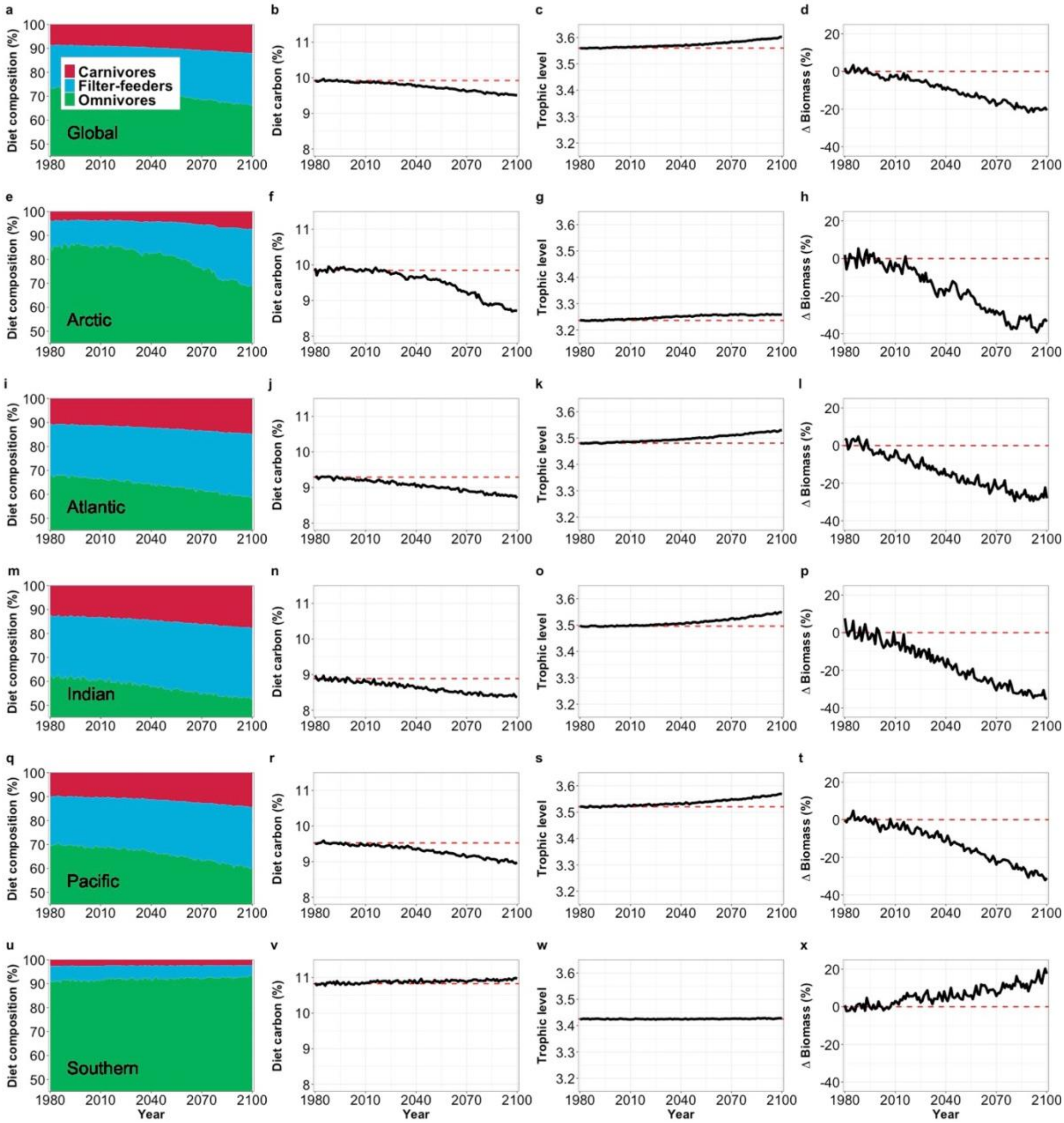

Fig. 4 | Impacts of climate change on small pelagic fish. Mean change in the diet composition (first column), diet carbon content (second column), trophic level (third column), and biomass (relative to 1980-2000; fourth column) of small pelagic fish under SSP5-8.5, for each ocean (rows), from 1980-2100. Dashed red lines represent the mean in 1980-2000.

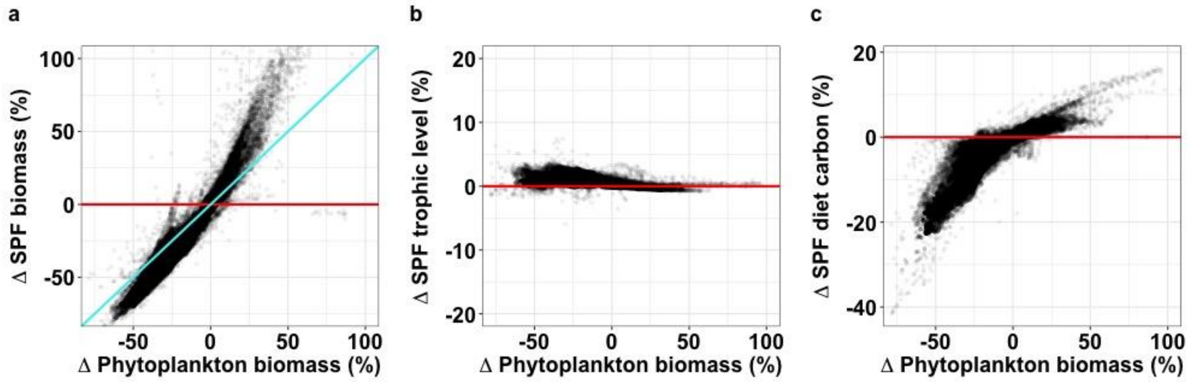

Fig. 5 | Impacts of changing phytoplankton biomass on small pelagic fish. Percentage change in the **a**, biomass, **b**, trophic level and **c**, diet carbon (%) of small pelagic fish (SPF) against the percentage change in phytoplankton biomass, for individual 1° grid squares from 1980–2000 to 2080–2100 under the SSP5-8.5 emissions scenario. Under the blue 1-1 line in **a**, where the change in phytoplankton biomass is negative, is where the decline in SPF biomass is greater than that of phytoplankton. Similarly, above the blue 1-1 line in **a**, and where the change in phytoplankton biomass is positive, is where the increase in SPF biomass is greater than that of phytoplankton. The red solid horizontal line in each figure indicates where the percentage change in each SPF attribute is zero.

In regions where phytoplankton biomass declined, small pelagic fish biomass generally declined even further (Fig. 5a), a process called trophic amplification[24]. This suggests that in regions where phytoplankton biomass decreases, climate-driven shifts towards an increase in gelatinous zooplankton groups could drive more pronounced biomass declines at higher trophic levels. At the same time, in regions such as the Southern Ocean where climate change drove an increase in phytoplankton biomass, the switch to more carbon dense zooplankton resulted in a positive amplification of small pelagic fish biomass (Supp. Fig. S1). However, it is important to note that coupling between phytoplankton and consumers in the current generation of marine ecosystem models—including ZooMSS—is incomplete, with most models not resolving predation impacts from higher trophic levels on phytoplankton[49]. This lack of coupling means that critical pathways of trophic amplification remain unresolved in these models. Nevertheless, by illuminating potential trophic amplification driven by shifts in zooplankton community composition, our results further highlight the importance of fully resolving the links between lower and higher trophic levels in marine ecosystem models.

Changes in the zooplankton community could have significant ecosystem implications beyond those described here, transforming biogeochemical cycling[12,36], carbon export[2,3] and the nutritional content of fish[32,48]. What is more, many of these implications are driven by the balance between crustaceans and gelatinous zooplankton. For instance, the concentration of bioavailable iron in the Southern Ocean is dependent upon the relative prevalence of salps versus euphausiids, with phytoplankton uptake of iron ~4.8 times greater from the breakdown of salp than krill faecal pellets[12]. At the same time, the balance of active transport of carbon via diel vertical migration of carbon-dense euphausiids and copepods versus passive transport via marine snow from gelatinous filter-feeders from surface to deeper waters is likely to shift toward passive transport in regions where filter-feeders may increase at the expense of omnivorous zooplankton[2]. Finally, increases in the prevalence of gelatinous zooplankton during the "Blob" drove down the quantity and nutritional quality of North Pacific planktivorous fish. These shifts were hypothesised to be key drivers of piscivorous seabirds and marine mammals suffering mass mortality and reproductive failure in the region during the heatwave[48].

Despite the importance of both gelatinous zooplankton and crustaceans, the majority of biogeochemical and earth system models that represent zooplankton neglect gelatinous groups, typically representing the zooplankton community with two or three groups differentiated only by body size[6]. Thus, there is a pressing need to improve zooplankton realism in models[1,6] especially under a changing climate. The trait-based modelling framework[9, 50] used here offers a powerful way to make substantial gains in our understanding of how climate change will impact zooplankton and the pivotal role they play in the world's marine ecosystems.

Data availability

Model inputs were sourced from five climate models from CMIP6 (see Methods for more information; climate model data are available here: https://esgf-node.llnl.gov/search/cmip6/). ZooMSS model outputs used in this study are available from the corresponding author on request.

Code availability

Code to run ZooMSS, analyse model outputs and generate figures are available from the corresponding author on request.

References

1. Mitra, A. *et al.* Bridging the gap between marine biogeochemical and fisheries sciences; configuring the zooplankton link. *Prog. Oceanogr.* **129**, 176–199 (2014).
2. Steinberg, D. K. & Landry, M. R. Zooplankton and the Ocean Carbon Cycle. *Ann. Rev. Mar. Sci.* **9**, 413–444 (2017).
3. Boyd, P. W., Claustre, H., Levy, M., Siegel, D. A. & Weber, T. Multi-faceted particle pumps drive carbon sequestration in the ocean. *Nature* **568**, 327–335 (2019).
4. Bucklin, A. *et al.* A Census of Zooplankton of the Global Ocean. *Life World's Ocean. Divers. Distrib. Abundance* 247–265 (2010).
5. Hatton, I. A., Heneghan, R. F., Bar-On, Y. M. & Galbraith, E. D. The global ocean size-spectrum from bacteria to whales. *Sci. Adv.* **in press** (2021).
6. Everett, J. D. *et al.* Modeling what we sample and sampling what we model: Challenges for zooplankton model assessment. *Front. Mar. Sci.* **4**, 1–19 (2017).
7. Tittensor, D. P. *et al.* Next-generation ensemble projections reveal higher climate risks for marine ecosystems. *Nat. Clim. Chang.* **in press** (2021).
8. Bopp, L. *et al.* Multiple stressors of ocean ecosystems in the 21st century: Projections with CMIP5 models. *Biogeosciences* **10**, 6225–6245 (2013).

9. Litchman, E., Ohman, M. D. & Kiørboe, T. Trait-based approaches to zooplankton communities. *J. Plankton Res.***35**, 473–484 (2013).

10. Boyce, D. G., Frank, K. T. & Leggett, W. C. From mice to elephants: Overturning the 'one size fits all' paradigm in marine plankton food chains. *Ecol. Lett.* **18**, 504–515 (2015).

11. Benedetti, F. *et al.* Major restructuring of marine plankton assemblages under global warming. *Nat. Commun.* **12**, 1–15 (2021).

12. Böckmann, S. *et al.* Salp fecal pellets release more bioavailable iron to Southern Ocean phytoplankton than krill fecal pellets. *Curr. Biol.* **31**, 2737-2746.e3 (2021).

13. Dam, H. G. & Baumann, H. *Climate Change Impacts on Fisheries and Aquaculture: A Global Analysis Vol. 1 Ch. 25* (John Wiley & Sons, West Sussex, 2017).

14. Barton, A. D. *et al.* The biogeography of marine plankton traits. *Ecol. Lett.* **16**, 522–534 (2013).

15. Hansen, B., Bjornsen, P. K. & Hansen, P. J. The size ratio between planktonic predators and their prey. *Limnol. Oceanogr.* **39**, 395–403 (1994).

16. Heneghan, R. F., Everett, J. D., Blanchard, J. L. & Richardson, A. J. Zooplankton Are Not Fish: Improving Zooplankton Realism in Size-Spectrum Models Mediates Energy Transfer in Food Webs. *Front. Mar. Sci.* **3**, 1–15 (2016).

17. Bone, Q., Carré, C. & Chang, P. Tunicate feeding filters. *J. Mar. Biol. Assoc. United Kingdom* **83**, 907–919 (2003).

18. Wirtz, K. W. Who is eating whom? Morphology and feeding type determine the size relation between planktonic predators and their ideal prey. *Mar. Ecol. Prog. Ser.* **445**, 1–12 (2012).

19. McConville, K., Atkinson, A., Fileman, E. S., Spicer, J. I. & Hirst, A. G. Disentangling the counteracting effects of water content and carbon mass on zooplankton growth. *J. Plankton Res.* **39**, 246–256 (2017).

20. Heneghan, R. F. *et al.* A functional size-spectrum model of the global marine ecosystem that resolves zooplankton composition. *Ecol. Modell.* **435**, 109265 (2020).

21. van Vuuren, D. P. *et al.* The Shared Socio-economic Pathways: Trajectories for human development and global environmental change. *Glob. Environ. Chang.* **42**, 148–152 (2017).

22. Eyring, V. *et al.* Overview of the Coupled Model Intercomparison Project Phase 6 (CMIP6) experimental design and organization. *Geosci. Model Dev.* **9**, 1937–1958 (2016).

23. Kwiatkowski, L., Aumont, O. & Bopp, L. Consistent trophic amplification of marine biomass declines under climate change. *Glob. Chang. Biol.* **25**, 218–229 (2019).

24. Stock, C. A., Dunne, J. P. & John, J. G. Drivers of trophic amplification of ocean productivity trends in a changing climate. *Biogeosciences* **11**, 7125–7135 (2014).

25. Richardson, A. J. & Schoeman, D. S. Climate impact on plankton ecosystems in the Northeast Atlantic. *Science* **305**, 1609–1612 (2004).

26. McGinty, N., Barton, A. D., Record, N. R., Finkel, Z. V. & Irwin, A. J. Traits structure copepod niches in the North Atlantic and Southern Ocean. *Mar. Ecol. Prog. Ser.* **601**, 109–126 (2018).

27. Jaspers, C., Nielsen, T. G., Carstensen, J., Hopcroft, R. R. & Møller, E. F. Metazooplankton distribution across the Southern Indian Ocean with emphasis on the role of Larvaceans. *J. Plankton Res.* **31**, 525–540 (2009).

28. Morán, X. A. G., López-Urrutia, Á., Calvo-Díaz, A. & LI, W. K. W. Increasing importance of small phytoplankton in a warmer ocean. *Glob. Chang. Biol.* **16**, 1137–1144 (2010).

29. Sutherland, K. R., Madin, L. P. & Stocker, R. Filtration of submicrometer particles by pelagic tunicates. *Proc. Natl. Acad. Sci. U. S. A.* **107**, 15129–15134 (2010).

30. Henschke, N., Everett, J. D., Richardson, A. J. & Suthers, I. M. Rethinking the Role of Salps in the Ocean. *Trends Ecol. Evol.* **31**, 720–733 (2016).

31. Jennings, S. & Warr, K. J. Smaller predator-prey body size ratios in longer food chains. *Proc. R. Soc. B Biol. Sci.* **270**, 1413–1417 (2003).

32. Atkinson, A., Siegel, V., Pakhomov, E. & Rothery, P. Long-term decline in krill stock and increase in salps within the Southern Ocean. *Nature* **432**, 100–103 (2004).

33. Schmidt, K. *et al.* Increasing picocyanobacteria success in shelf waters contributes to long-term food web degradation. *Glob. Chang. Biol.* **26**, 5574–5587 (2020).

34. Gallienne, C. P. & Robins, D. B. Is Oithona the most important copepod in the world's oceans? *J. Plankton Res.* **23**, 1421–1432 (2001).

35. Roura, Á., Strugnell, J. M., Guerra, Á., González, Á. F. & Richardson, A. J. Small copepods could channel missing carbon through metazoan predation. *Ecol. Evol.* **8**, 10868–10878 (2018).

36. Richon, C. & Tagliabue, A. Biogeochemical feedbacks associated with the response of micronutrient recycling by zooplankton to climate change. *Glob. Chang. Biol.* **27**, 4758–4770 (2021).

37. Peck, M. A. *et al.* Small pelagic fish in the new millennium: A bottom-up view of global research effort. *Prog. Oceanogr.* **191**, (2021).

38. Ryther J.H. Photosynthesis and fish production in the sea. *Science* **166**, 72-76 (1969).

39. Eddy, T. D. *et al.* Energy Flow Through Marine Ecosystems: Confronting Transfer Efficiency. *Trends Ecol. Evol.*~~**36**, 76–86 (2021).

40. Diebel, D., &Lee, S.H. Retention efficiency of submicron particles by the pharyngeal filter of the pelagic tunicate Oiopleura vanhoeffeni. *Mar. Ecol. Prog. Ser.* **81**, 25-30 (1992).

41. Llopiz, J.K., D.E. Richardson, A. Shiroza, S.L. Smith, R.K. & Cowen. Distinctions in the diets and distributions of larval tunas and the important role of appendicularians. *Limnol. Oceanogr.* **55**, 983–996 (2010).

42. Cardona, L., de Quevedo, I. Á., Borrell, A. & Aguilar, A. Massive consumption of gelatinous plankton by Mediterranean apex predators. *PLoS One* **7**, (2012).

43. Hays, G. C., Doyle, T. K. & Houghton, J. D. R. A Paradigm Shift in the Trophic Importance of Jellyfish? *Trends Ecol. Evol.* **33**, 874–884 (2018).

44. Yang, B., Emerson, S. R. & Angelica Penã, M. The effect of the 2013-2016 high temperature anomaly in the subarctic Northeast Pacific (the 'blob') on net community production. *Biogeosciences* **15**, 6747–6759 (2018).

45. Brodeur, R. D., Auth, T. D. & Phillips, A. J. Major shifts in pelagic micronekton and macrozooplankton community structure in an upwelling ecosystem related to an unprecedented marine heatwave. *Front. Mar. Sci.***6**, 1–15 (2019a).

46. Brodeur, R. D., Hunsicker, M. E., Hann, A. & Miller, T. W. Effects of warming ocean conditions on feeding ecology of small pelagic fishes in a coastal upwelling ecosystem: a shift to gelatinous food sources. *Mar. Ecol. Prog. Ser*. **617-618**, 149-163 (2019b)

47. Arimitsu, M.L. *et al.* Heatwave-induced synchrony within forage fish portfolio disrupts energy flow to top pelagic predators. *Glob. Change Biol.* **27,** 1859-1878 (2021).

48. Piatt, J. F. *et al.* Extreme mortality and reproductive failure of common murres resulting from the northeast Pacific marine heatwave of 2014-2016. *PLoS ONE* **15**, (2020).

49. Heneghan, R.F. *et al.* Disentangling diverse responses to climate change amongst global marine ecosystem models. *Prog. Oceanogr.* **in press** (2021).

50. Blanchard, J. L., Heneghan, R. F., Everett, J. D., Trebilco, R. & Richardson, A. J. From Bacteria to Whales: Using Functional Size Spectra to Model Marine Ecosystems. *Trends Ecol. Evol.* **32**, 174–186 (2017).

Methods

The model

We use the Zooplankton Model of Size Spectra (ZooMSS) v2[20], which uses the function size-spectrum framework[50] to resolve multiple zooplankton and fish groups. In brief, ZooMSS resolves a single static phytoplankton community, nine of the most prevalent zooplankton functional groups (heterotrophic flagellates and ciliates, omnivorous and carnivorous copepods, larvaceans, salps, euphausiids, chaetognaths and jellyfish) and three fish groups defined by their asymptotic sizes. The nine zooplankton groups are defined by their size ranges, feeding characteristics (e.g., PPMR) and carbon content. The three size-based fish groups are defined by their size ranges, broadly representing: small pelagic—planktivorous—fish $\leq$100g; medium pelagic fish $\leq$10kg and large pelagic fish $\leq$1 tonne. Other than their asymptotic size, the three fish groups share the same functional traits. A summary of the parameter values used to define the functional traits of the nine zooplankton and three fish communities can be found in Table S1.

ZooMSS is run on a weekly time step with sea surface temperature and chlorophyll *a* concentration averaged annually, with a 1° spatial resolution. Temperature affects the growth and mortality rates of the zooplankton and fish functional groups. Chlorophyll *a* determines the total biomass and size structure of the phytoplankton community, since phytoplankton dynamics are not explicitly represented in ZooMSS. Within each 1° cell, ZooMSS is initialised with the same zooplankton composition[20], and the community structure then emerges and changes through time, based on the relative fitness of the different groups as well as shifting environmental conditions.

To aid interpretation, in the main text we aggregated the output from the seven mesozooplankton and macrozooplankton types into three summary groups based on their feeding characteristics: omnivores (omnivorous copepods and euphausiids), carnivores (carnivorous copepods, chaetognaths and jellyfish) and filter-feeders (larvaceans and salps). Heterotrophic flagellates and ciliates were grouped together as microzooplankton and presented together with small (<5µm ESD) and large phytoplankton biomass in the Supplementary (Supp. Fig. S2).

Assessing climate impacts on global zooplankton composition and ecosystem function

We assess changes in the biomass of omnivores (euphausiids and omnivorous copepods), filter-feeders (larvaceans and salps) and carnivores (chaetognaths, jellyfish and carnivorous copepods) as well as resultant changes in zooplankton community composition and implications for small pelagic fish, under three future (2015–2100) IPCC shared socioeconomic pathway (SSP) scenarios[21] (SSP1-2.6, SSP3-7.0 and SSP5-8.5) using historical (1980–2014) conditions as a baseline. Environmental drivers required to run the model over the historical and three future SSP scenarios were sourced from five Coupled Model Intercomparison Project Phase 6[22] (CMIP6) earth system models: CESM2, GFDL-ESM4, IPSL-CM6A-LR, MPI-ESM1-2-HR, UKESM1-0-LL. We chose these five because they had been previously selected from the larger CMIP6 model cohort to provide forcings for the Fisheries and marine ecosystem Model Intercomparison Project, of which ZooMSS is a participating model (https://www.isimip.org/protocol/3/). To assess climate impacts across each of the five ocean basins, we used the regional biome mask from the Regional Carbon Cycle Assessment Process 2 (RECCAP2) working group (https://reccap2-ocean.github.io/regions/).

Calculating small pelagic fish diet and trophic level

The trophic level of small pelagic fish (TL_{SPF}) was calculated by solving:

$$TL_{SPF} = 1 + \sum_{j} TL_j \times PD_{SPF,j},$$

where TL_j is the trophic level of group j and $PD_{SPF,j}$ is the proportion of the diet of small pelagic fish, that comes from group j:

$$PD_{SPF,j} = \frac{F_{SPF,j}}{\sum_j F_{SPF,j}},$$

and F_{SPFj} is the total biomass from group j consumed by small pelagic fish. Except for phytoplankton, which have a fixed trophic level of 1, the trophic level of the different zooplankton and fish groups change with their diet, so we used the Gauss-Jacobi iteration method[51] to solve TL_{PF}.

Calculating small pelagic fish diet quality

Small pelagic fish diet quality was given by the carbon content of their diet, CC_{SPF}:

$$CC_{SPF} = \frac{C_j B_{SPF,j}}{\sum_j C_j B_{SPF,j}},$$

where B_{SPFj} is the total biomass from group j consumed by small pelagic fish, and C_j is the carbon content of group j, as a proportion of total wet biomass.

References

51. Sauer, T. *Numerical Analysis*. *2nd ed,* (Boston: Pearson Education, 2012).

Acknowledgements

PS was supported by an Australian Government Research Training Program Scholarship. JDE was funded by Australian Research Council Discovery Projects DP150102656 and DP190102293.

Author Contributions

RFH, AJR and JDE conceived the study. JDE conducted the model simulations. RFH led the writing of the manuscript. All authors contributed to analysing the results and providing feedback on the manuscript.

Competing Interests

The authors declare no competing interests.

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- ZooMSSClimChangeSupp.pdf