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Léonard Dupont[1] | **Priscilla Le Mézo[1]** | **Olivier Aumont[2]** | **Laurent Bopp[1]** | **Corentin Clerc[1]** | **Christian Ethé[3]** | **Olivier Maury[4]**

[1]Laboratoire de Météorologie Dynamique (LMD), IPSL, École Normale Supérieure, Université PSL, CNRS, Sorbonne Université, Ecole Polytechnique, Paris, France

[2]Laboratoire d'Océanographie et du Climat: Expérimentation et Approches Numériques (LOCEAN), IPSL, CNRS/ UPMC/IRD/MNHN, Paris, France

[3]PSL, Sorbonne Université/CNRS, Paris, France

[4]IRD (Institut de Recherche pour le Développement), UMR 248 MARBEC (IRD-IFREMER-CNRS-Université Montpellier), Montpellier, France

Correspondence
Priscilla Le Mézo, Laboratoire de Météorologie Dynamique (LMD), IPSL, École Normale Supérieure, Université PSL, CNRS, Sorbonne Université, Ecole Polytechnique, Paris, France.
Email: priscilla.le-mezo@lmd.ens.fr

Present address
Léonard Dupont, Station d'Écologie Théorique et Expérimentale de Moulis, CNRS, Moulis, France

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Abstract

Despite recurrent emphasis on their ecological and economic roles, the importance of high trophic levels (HTLs) on ocean carbon dynamics, through passive (fecal pellet production, carcasses) and active (vertical migration) processes, is still largely unexplored, notably under climate change scenarios. In addition, HTLs impact the ecosystem dynamics through top-down effects on lower trophic levels, which might change under anthropogenic influence. Here we compare two simulations of a global biogeochemical–ecosystem model with and without feedbacks from large marine animals. We show that these large marine animals affect the evolution of low trophic level biomasses, hence net primary production and most certainly ecosystem equilibrium, but seem to have little influence on the 21st-century anthropogenic carbon uptake under the RCP8.5 scenario. These results provide new insights regarding the expectations for trophic amplification of climate change through the marine trophic chain and regarding the necessity to explicitly represent marine animals in Earth System Models.

KEYWORDS
climate change, Earth System Model, feedbacks, high trophic levels, trophic cascades

1 | INTRODUCTION

The global ocean plays a pivotal role in controlling climate, particularly through the regulation of the partial pressure of CO_2 in the atmosphere (Sarmiento & Gruber, 2006). Indeed, the ocean absorbs a significant fraction (~25%) of anthropogenic carbon emissions, estimated at 2.5 ± 0.6 GtC year^{-1} in the 2010s (Friedlingstein et al., 2020). Even if most of the ocean carbon sink over the historical period is primarily due to physical and chemical processes (Khatiwala et al., 2013), changes in biological processes, and more specifically

Léonard Dupont and Priscilla Le Mézo—joint first authorship.

changes in the efficiency of the biological pump, have the potential to alter the ocean carbon uptake and storage in the coming centuries (Kwon et al., 2009). Therefore, careful modeling of the biological carbon pump processes is required to make realistic projections of the ocean carbon sink, especially at centennial timescales.

The biological pump processes are represented with varying levels of details in Earth System Models (ESMs). Most ESMs currently account for biology by representing only planktonic communities and using constant density-dependent mortality terms to represent the effects of high trophic levels (HTLs) on plankton biomass through grazing (Séférian et al., 2020). Phytoplankton, which are keystone elements of the oceanic carbon cycle, are primary producers that passively drift and transform inorganic carbon into organic carbon through net primary production. A portion of the carbon fixed by primary producers further flows through zooplanktonic grazers and upper trophic levels through predation. The fecal pellets produced by heterotrophic organisms, the dead bodies and cells, as well as the carbonate shells—respectively, forming the soft and hard tissue pumps—sink to the ocean interior under the action of gravity (Le Moigne, 2019). Despite intense remineralization as it sinks to the seabed, a few percent of the organic carbon is eventually sequestered away from the atmosphere for hundreds of years (Boyd et al., 2019). Processes other than gravitational settling are also important in this biologically dependent carbon pump, with diel-vertical migration (DVM) being one of the most significant ones (Boyd et al., 2019). This active pump relies on actively swimming marine mesopelagic species, including an important fraction of zooplankton and micronekton, which generally alternate between nocturnal hunting close to the surface (0–200 m) and diurnal avoidance of visual predation at deeper depth (200–1000 m) according to the predator-evasion hypothesis (Stich & Lampert, 1981). A significant part of the carbon grazed at the surface by these migratory organisms is carried and released directly in deep waters without remineralization, traveling therefore far more quickly than through the gravitational pump. The relative amount of the active transport of organic matter has been estimated to be around 15%–40% of the total production exported out of the epipelagic zone (Aumont et al., 2018; Bianchi et al., 2013). Yet, since DVM-driven export involves relatively large species that were first thought to have a minor role in carbon export, its representation remains an exception in biogeochemical models (Séférian et al., 2020). Finally, the representation of HTLs also plays an important role in stabilizing the dynamics of the ecosystem and regulating the abundance of low trophic levels (LTLs; Baum & Worm, 2009; Lynam et al., 2017).

To assess the role of HTLs in both sequestrating carbon and regulating trophic processes, we use the NEMO-PISCES-APECOSM modeling framework (hereafter called NPA), which is composed of the ocean circulation modeling platform, Nucleus for European Modeling of the Ocean (NEMO), the biogeochemical model PISCES (Aumont et al., 2015), which represents the LTLs (i.e., plankton), and the HTLs model APECOSM (Maury, 2010) (see Section 2.1). We compare two transient simulations of NPA with different coupling: one where HTLs fully interact with LTLs (hereafter called two-way [TW]) and one where the biogeochemical model evolves independently from the behavior of larger species that are simply forced one-way by LTLs

(hereafter called one-way [OW]). We run models under both coupling modes across the historical period (1850–2014) and the RCP8.5 scenario (2015–2100) using output from the IPSL-CM5A-LR ESM (Dufresne et al., 2013), and analyze the biogeochemical projections. Our goal is to assess whether climate change impacts HTLs feedback to the carbon cycle, and if so, how that may question the implicit and simple representation of HTLs currently used in most ESMs.

2 | MATERIALS AND METHODS

2.1 | Models

2.1.1 | Pelagic Interaction Scheme for Carbon and Ecosystem Studies v2

The Pelagic Interaction Scheme for Carbon and Ecosystem Studies (PISCES) is a biogeochemical model that explicitly simulates the LTLs of oceanic ecosystems (two types of phytoplankton and two types of zooplankton) along with the biogeochemical cycles of carbon and five main nutrients (NO_3, NH_4, Fe, Si, and P) (Aumont et al., 2015). Planktonic groups differ in their requirements for nutrients and in their trophic interactions. Small and large particles of organic matter are produced and lead to a passive carbon export pathway. Remineralization of organic matter, growth, uptake, and predation rates are temperature dependent. The meso-zooplankton group in PISCES does not perform vertical migrations.

2.1.2 | Apex Predators ECOSystem Model

The Apex Predators ECOSystem Model (APECOSM) represents the size-structured dynamics of HTLs communities of the ecosystem (Maury, 2010), based on individual processes such as size-based opportunistic predation. The model relies on mass conservation and uses principles from the standard Dynamic Energy Budget theory (Kooijman, 2001) to represent individual bioenergetics (food intake, growth, maintenance, development, and reproduction). The model is three-dimensional and distinguishes three distinct open-ocean pelagic communities (OOPCs) that have different habitat-based vertical distribution and movements: the epipelagic OOPC (mostly above 200 m), the mesopelagic and bathypelagic OOPC (mostly between 200 and 1000 m), and the migratory OOPC, which performs DVM, feeding in surface waters during the night and hiding from visual epipelagic predators in the mesopelagic layer during the day. These three OOPCs are not taxonomically resolved and are structured in 20 logarithmically distributed size classes, ranging from 1 to 2 m. Predation can occur both within and between communities and all physiological rates are temperature dependent.

2.1.3 | PISCES–APECOSM coupling

We used the coupled NPA framework in two different configurations. In both cases, small organisms in APECOSM (ranging from 0.1

to 2 cm) feed on the LTLs simulated in PISCES. In the OW simulation, LTLs mortality does not depend on APECOSM HTLs biomass and it is solely ruled by internal PISCES processes (e.g., with a quadratic mortality term for mesozooplankton) so that APECOSM is invisible to planktonic organisms. Besides, there is no feedback from marine animals on detritus, nutrients, and marine biogeochemistry whatsoever, similar to Lefort et al. (2014) and Le Mézo et al. (2016). In the TW simulation, the quadratic mortality term of mesozooplankton is strongly reduced (−83%) since predation from HTLs is explicitly represented and comes from the small organisms in APECOSM. Furthermore, egestion, respiration, and excretion by the upper trophic levels are routed back to the appropriate organic and inorganic compartments of PISCES so that PISCES and APECOSM exchange information bidirectionally and close nutrient and carbon cycles as detailed in Aumont et al. (2018).

2.2 | Experimental design

PISCES is part of the NEMO framework. We used the ORCA2 global configuration with the corresponding 2°×2° cos(latitude) horizontal resolution, enhanced to 0.5° at the equator, and 31 vertical levels with decreasing vertical resolution with depth (Madec, 2008). For computational reasons, NPA is forced offline using monthly fields (IPSL-CM5A-LR) over both the historical (1850–2005) and future periods (2006–2100). Future projections followed the higher emission trajectory, namely the Radiative Concentration Pathway 8.5 (RCP8.5), a scenario in which the radiative forcing steadily increases up to 8.5 W m^{-2} in 2100 due to high greenhouse gas emissions (Moss et al., 2010). We chose this most extreme scenario among the possible scenarios, as it being the strongest in terms of climate change impacts we expect the response of the ecosystem to be the largest and thus easily detectable as compared to projections with low-emission scenario. In addition, this RCP8.5 is used in almost every published study using future scenarios, which is convenient for comparing our results to previous work. We also ran a 300-year control simulation with pre-industrial climate and atmospheric CO_2 for both the OW and TW cases, to compute the anthropogenic carbon uptake and storage, and to check for any intrinsic drifts over the simulation periods. NPA was spun up for 200 years prior to launching the control period to stabilize the output fields. The historical and projection simulations are branched after 50 years of the control simulation.

2.3 | Analysis of model outputs

2.3.1 | Ocean carbon uptake and dissolved inorganic carbon (DIC) storage

The annual mean anthropogenic carbon flux from the atmosphere to the ocean is corrected for any intrinsic drift by removing the trend calculated in the control simulations from the future projection simulations. Vertical and integrated DIC anomalies (ΔDIC) are computed by taking the average value over the last 20 years of the simulations (2080–2100), and subtracting the average value of the last 20 years of the control simulation (1830–1850) used to initialize the historical simulation.

2.3.2 | Active transport

The export of carbon from the euphotic zone to the ocean interior depends on both passive (gravitational sinking of particles) and active (e.g., migration of marine animals) processes. The organic carbon particles produced by LTLs are passively sinking to depth in PISCES, while the APECOSM framework includes DVM, which contributes to the active export, and is thought to be of great importance (Aumont et al., 2018). In the TW simulation, part of the LTLs organic carbon is transferred to HTLs through predation and can thus be actively exported to depth. We assess the proportion of each of the two mechanisms (passive/active) using the egestion, excretion, respiration, and grazing terms of the OOPCs at different depths and the modeled respective sinking fluxes of large and small organic particles (see Supplementary Materials).

2.3.3 | Temperature-related biomass decrease

To study the simulated response of marine animals under RCP8.5, we use the ocean surface temperature as a proxy for the evolution of all stressors, and we compute the linear regression between the biomass anomaly and the temperature anomaly relative to the first 20 years of the historical period (1851–1870). The slopes are used to assess and compare trophic processes in Figure 3.

2.3.4 | Trophic regimes

The mesozooplankton compartment of PISCES occupies a peculiar place in our simulations because it undergoes most of the predation pressure exerted by small organisms in APECOSM, along with the large organic particles of PISCES. While the mesozooplankton-APECOSM dependency is unidirectional in the OW coupling scheme, it becomes bidirectional in the TW coupling scheme, thereby allowing biomass perturbations to fully propagate through the trophic network. To study the reciprocal dependency of LTLs and HTLs, we plotted their respective biomass anomalies (difference between the periods 2080–2100 and 1851–1870) against each other and defined three categories of trophic propagation: amplification, attenuation, and top-down control, as defined in Chust et al. (2014). Each category is divided into two subcategories: the positive (negative) amplification refers to an increase (decrease) in the biomass of LTLs and a larger increase (decrease) in the biomass of HTLs, the positive (negative) attenuation refers to an increase (decrease) in the biomass of LTLs and a smaller increase (decrease) in the biomass of HTLs; the top-down category is divided into pressure increase, which is

an increase in HTLs biomass and a decrease in LTLs biomass, and pressure release, which is a decrease in HTLs concomitant with an increase in LTLs biomass.

3 | RESULTS

3.1 | HTLs impacts on air–sea carbon fluxes and carbon storage

Our results show that the feedback from marine animals does not significantly affect the global ocean carbon sink of this century but produces differences in the distribution of ΔDIC that may have long-term consequences. The global difference in the mean air–sea carbon flux between the TW and OW simulations is low, oscillating between −0.05 and 0.06 GtC year^{-1} over the 2010s, that is, less than ±3% of the ocean anthropogenic carbon uptake (Friedlingstein et al., 2020) and of the OW global flux over that period (Figure 1a). When integrated over 1850–2100, the TW minus OW carbon uptake anomaly is 1.5 GtC, representing less than 0.3% of the OW global ocean carbon uptake over that period (494 GtC). The spatial distribution and vertical profiles of ΔDIC in response to increasing atmospheric CO_2 and climate change also show a slight difference between the OW and TW simulations by the end of the century (Figure 1b,c). Consistent with the carbon uptake anomaly, the TW coupling scheme leads to an overall higher amount of DIC (less than 2 GtC globally), mainly at the surface and below 500 m depth. In contrast, at the subsurface (200 m depth), there is relatively less DIC stored in TW than in OW (Figure 1b). The differences between the TW and OW simulations at the global scale are also spatially heterogeneous (Figure 1c), with the largest differences in carbon storage in the tropics. Upwelling regions such as the Benguela current or the eastern equatorial Pacific have lower ΔDIC concentrations in the TW simulation compared to the OW while the difference is mostly positive in the Atlantic Ocean and shows a strong east–west dipole in the tropical Pacific.

3.2 | HTLs impacts on carbon export

The full coupling between LTLs and HTLs modifies how carbon is being exported to the ocean depths, explaining the differences in ΔDIC distribution at the end of the 21st century. First, whereas year-to-year variations in carbon export are similar in the two simulations, a gradual divergence happens under the RCP8.5 forcing, leading to a larger mean decrease in carbon export of about −10% in the TW simulation compared to the OW simulation (Figure 2a). In the OW simulation, the single mechanism driving carbon export (apart from the subduction of dissolved organic carbon, not analyzed here) is the gravitational sinking of organic particles represented by small and large particles that differ by their sinking speeds. In the TW coupling scheme, around 13% of the particulate organic carbon export is replaced by active transport (Figure 2c) through DVM of organisms

represented in APECOSM (see Section 2). Under climate change, the fraction of total export that is due to active export decreases ever so slightly in the TW simulation, roughly −1.6% (Figure 2c).

Second, the changes in export and in the proportion of active transport due to full coupling between LTLs and HTLs are spatially heterogeneous, decreasing in the tropics while increasing in the Southern Ocean and the Arctic (Figures S2 and S3), in agreement with projected changes in HTLs biomass (Figures S4 and S5). These changes in the export at 200 m contribute to explaining the differences in ΔDIC storage, as both maps show similar patterns at the end of the century (Figures 1c and 2b). To get more insights into the mechanisms underlying the results regarding the carbon balance, we then investigate the evolution of the biological compartments in our two simulations.

3.3 | HTL impacts on trophic regimes

Our results show that trophic amplification is attenuated between microzooplankton and mesozooplankton, while it is apparently increased between mesozooplankton and small fish, when the top-down effects of HTLs on LTLs are taken into account in the TW simulation. In line with recent climate change projections (Kwiatkowski et al., 2018, 2019; Lotze et al., 2019), our two simulations show a decline in living organism biomass for all of the simulated compartments (Figure 3b), ranging from around −7% for phytoplankton (nanophytoplankton + diatoms) to −20% for large animals (Table S1; Figures S4 and S5). The decrease in biomass of primary producers was greater in the TW simulation than in the OW simulation, as reflected by the evolution of net primary production (Figure 3a). This decreasing trend with warming is clearly amplified with increasing trophic levels (Figure 3b). Such trophic amplification phenomenon is a well-known feature of marine ecosystem models (MEMs; e.g., Lotze et al., 2019): a rarefaction of preys leads to a more severe decrease of the biomass of their predators. One would therefore expect this amplification process to occur in both runs. However, in the mesozooplankton compartment, the OW and TW simulations diverge (Figure 3b; Figure S6). Trophic amplification between microzooplankton and mesozooplankton is strongly attenuated in the TW case compared to OW, where the relative anomaly of mesozooplankton biomass is not significantly greater than that of microzooplankton (Figure S7). This attenuation in the TW case indicates a top-down control, which would offset the bottom-up amplification process that was clear in the OW simulation.

3.4 | Shifts in trophic regimes

The TW coupling scheme generates top-down effects that modify the trophic regimes worldwide, especially changing the trophic amplification regimes to attenuation or to top-down regimes. To further investigate the possible trophic processes at the origin of the differences observed on Figure 3, we compare the spatial biomass anomalies
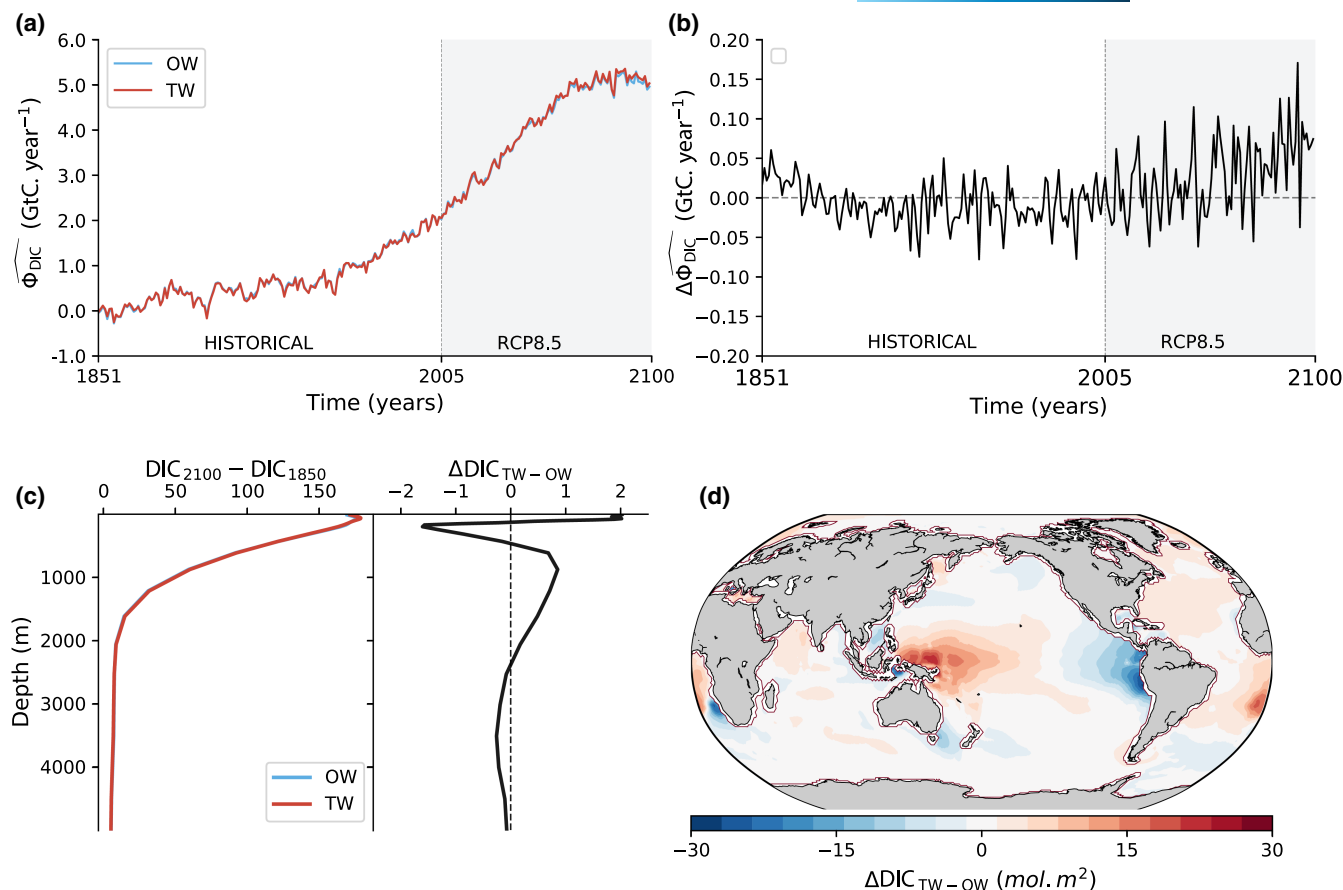
FIGURE 1 Comparison of OW and TW simulations for carbon uptake and dissolved inorganic carbon (DIC) storage. For (a, c), the blue curve is the OW simulation and the red one is the TW simulation. (a) Time series of the mean air–sea inorganic carbon flux (GtC year^{-1}). (b) Time series of the difference in mean air–sea inorganic carbon flux between the TW and OW simulations (TW–OW, GtC year^{-1}). (c) Mean vertical profile of the accumulated total DIC anomaly, ΔDIC (left curve, mmolC m^{-2}), and vertical distribution of the difference in ΔDIC anomaly between the TW and OW simulations (right curve, mmolC m^{-2}), and (d) map of the difference (TW – OW) in depth-integrated DIC anomaly (molC m^{-2}). The OW and TW maps of ΔDIC can be found in the Supplementary Material (Figure S1). OW, one-way; TW, two-way.

of PISCES mesozooplankton with those of the first size classes of APECOSM (i.e., 1 mm–2 cm) that are preying on mesozooplankton. The effects of explicitly accounting for the TW interactions between the lower and upper trophic levels are clearly visible: the distribution of biomass anomalies (mesozooplankton from PISCES vs. small size classes from APECOSM) displays new apparent top-down processes (Figure 4a,c). In the TW simulation at high latitude (>55°), the trophic regimes shift to an apparent top-down regime with pressure increase while in the tropics (10°–25.5°) and at mid-latitudes (25.5°–55°), attenuation and apparent top-down (with pressure release) regimes become recurrent. The spatial distribution gives more insight into the organization of these trophic structure changes (Figure 4b,d): while the OW simulation shows regions that are dominated by amplification, the TW map displays broad coherent areas characterized by a top-down control. In particular, oligotrophic provinces from low to mid-latitudes show largely positive mesozooplankton biomass anomalies co-occurring with collapsing APECOSM biomass, that is, a release of the predation pressure by large organisms on mesozooplankton. On the other hand, the increase in HTLs biomass in APECOSM could be the source of the negative mesozooplankton

biomass anomalies in the Southern Ocean. Interestingly, positive amplification in response to climate change, dominant in the OW simulation, is almost completely replaced in the TW simulation by top-down effects. Note that in the OW simulation the apparent top-down processes cannot be due to trophic interactions since there are no retroactions from HTLs to LTLs in this configuration. They primarily reflect top-down processes within APECOSM (apparent pressure increase) combined with strong climate impacts on large organisms (apparent pressure release).

4 | DISCUSSION

4.1 | Top-down processes, trophic amplification, and implications for climate change impacts on HTLs

Full coupling of HTLs with LTLs in the TW simulation allows for the inception of top-down processes that restrain the emergence of trophic amplification in response to climate change as simulated in the OW simulation.
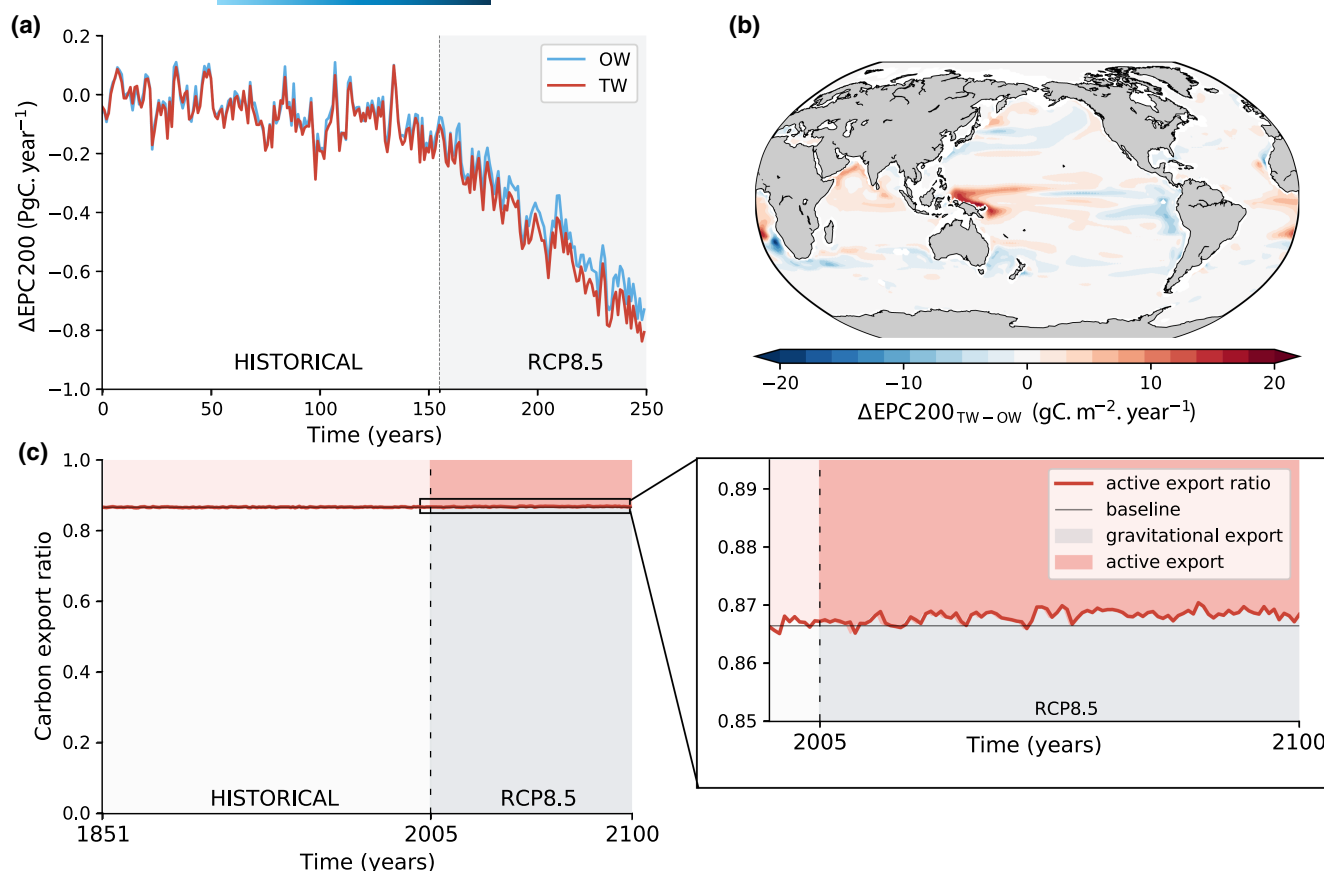
FIGURE 2 Influence of climate change on carbon export in the OW and TW coupling schemes. (a) Time series of the mean carbon export anomaly (PgC per year) at 200 m depth. The anomaly is computed relative to the averaged carbon export over the first 20 years of the historical period (1851–1870). The blue curve corresponds to the OW simulation and the red one to the TW simulation. (b) Map of the difference in export anomaly between the TW and OW simulations (TW–OW, PgC.year^{-1}), and (c) detailed analysis of the export at 200 m for the TW simulation, the grey and red areas represent the proportion of passive and active export, respectively, to the total carbon export. The red line represents the distinction between passive and active export in time, called the active export ratio here. The grey line, named baseline, is the averaged contribution of passive versus active export during the historical time period. A regional analysis of the export can be found in the Supplementary Material (Figure S2). OW, one-way; TW, two-way.

With no retroaction of HTLs onto LTLs, the response of biomass in the OW simulation is primarily driven by trophic amplification and attenuation (Figures 3b and 4). The term trophic amplification has been introduced by Kirby and Beaugrand (2009) to describe the response of a food web to a given hydroclimatic signal, with magnifying biomass responses from LTL to HTL. Trophic amplification has been well characterized in previous studies using HTL models forced by ocean biogeochemical models (e.g., Chust et al., 2014) as well as in the recent FishMIP model ensemble (Lotze et al., 2019; Tittensor et al., 2021). Amplification through the trophic chain in response to climate change has also been demonstrated with a previous version of the OW PISCES-APECOSM end-to-end model (Lefort et al., 2014).

In the TW simulation presented here, HTLs directly feedback onto LTLs through predation and nutrient recycling. These top-down trophic effects cascade down to lower trophic levels, deeply modifying the trophic amplification observed in the OW simulation. This effect is exemplified by the dampened overall decrease in mesozooplankton biomass in the TW simulation (relative to the

OW simulation) (Figure 4; Figures S4–S6; Table S1). Previous studies showed both a reduction in HTLs biomass and the shrinking of HTLs maximum size in response to climate change (Bryndum-Buchholz et al., 2019; Lefort et al., 2014; Pauly & Cheung, 2018), which may generate trophic cascades that favor the growth of mesozooplankton through the release of predation pressure (Frank et al., 2005). Such trophic cascades are also simulated in the fish size spectrum of APECOSM, in both the OW and the TW simulations, where the large and small size classes exhibit a more significant decrease in biomass compared to the intermediate size classes (Figure S8).

Interestingly, the mitigated decrease in mesozooplankton in the TW simulation then propagates to even lower trophic levels with larger simulated reductions in phytozooplankton and microzooplankton biomass (Figure 3; Figures S4–S7; Table S1) as compared to the OW simulation. Finally, the top-down-induced larger reduction in LTLs biomass is also likely responsible for the stronger decrease in HTLs in the TW simulation, in both the historical and RCP8.5 time periods, as top-down effects on plankton can then propagate back up the food web (Travers et al., 2009).
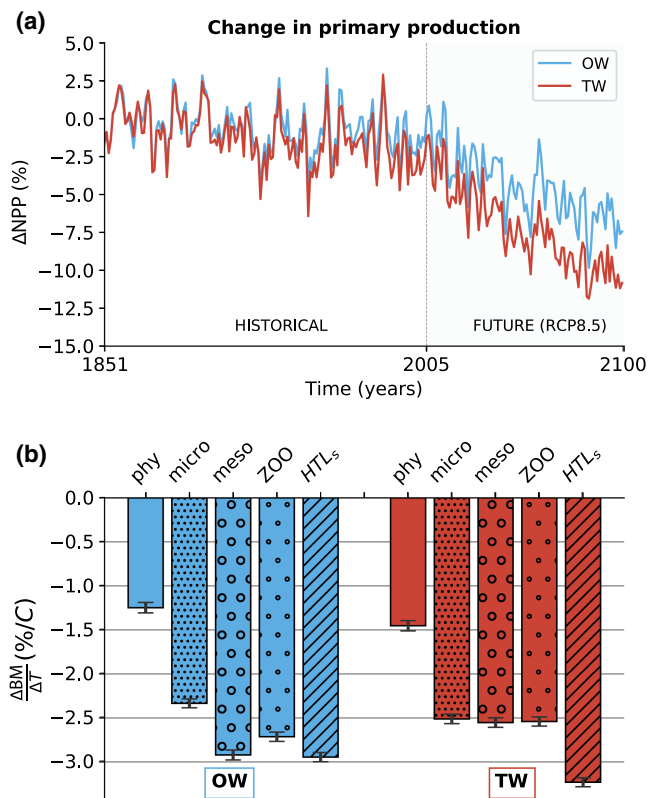
(a) Change in primary production

(b)

FIGURE 3 Generalized impact of HTLs coupling on primary production and LTLs biomass. For all panels, the blue elements correspond to the OW simulation and the red ones to the TW simulation. (a) Time series of the mean net primary production anomaly computed relative to the averaged NPP over the first 20 years of the historical period, (b) barplot representing the global slopes (biomass change per °C) over the RCP8.5 period for each of the five following compartments: Phytoplankton (phyto), microzooplankton (micro), mesozooplankton (meso), total zooplankton (ZOO), and HTLs. The anomalies (Δ) are computed relative to the first 20 years of the historical period (1851–1870). Errors correspond to the normalized variance of the square residuals of the linear regressions. HTL, high trophic level; LTL, low trophic level; OW, one-way; TW, two-way.

The changes introduced by accounting for these trophic feedbacks lead to a decrease in HTL biomass of 3.2% per degree of warming in the TW simulation, as compared to 2.9% in the OW simulation, that is, a 10% amplification of the response (Figure 3b). Our results suggest that the FishMIP projected decline in mean global ocean animal biomass (−19% by 2099 relative to 1990–1999 under high emissions; Tittensor et al., 2021) may be underestimated because none of the models used in FishMIP fully account for HTL to LTL feedbacks. When only analyzing the slopes of the biomass change per degree of warming (Figure 3b), the conclusion that could be drawn from it is that trophic amplification is stronger in the TW framework compared to OW, especially when looking at the slopes of total phytoplankton, total zooplankton, and small HTLs. However, the consideration of bi-directional interactions in the TW simulation brings more dimension to the conclusions that could be drawn from the OW simulation in terms of trophic interactions. The trophic

amplification that seemed to spatially dominate in the OW simulation (Figure 4a) gives way to a much more complex, diverse, and contrasting response (Figure 4c).

Indeed, the geographical structuring of this response is profoundly modified, with a majority of regions characterized by a change in the nature of the trophic regime between the OW and TW simulations. The top-down processes through which the first trophic levels of APECOSM affect mesozooplankton are particularly marked in oligotrophic subtropical gyres where the decrease in HTL biomass even leads to an increase in mesozooplankton biomass (Figure 4d; Figure S5). This counter-intuitive response raises questions on the way HTLs models are forced by input from LTLs models. Indeed, out of the nine HTL models used in FishMIP, four use modeled NPP as a primary input, whereas the five others use phytoplankton and/or zooplankton biomass, or combine plankton biomass with particulate organic matter (Tittensor et al., 2021). In regions where NPP and/or mesozooplankton biomasses do not respond in the same direction to anthropogenic climate change, the choice of the forcing variable introduces significant uncertainties in the way the response of trophic levels to climate change is projected (Heneghan et al., 2021).

4.2 | Potential long-term changes in ocean carbon uptake

The global reduction in the contribution of the active carbon transport to total carbon export is a direct consequence of the decrease in HTLs biomass due to climate change (e.g., Lefort et al., 2014) (Figure 2; Figures S4 and S5). Over the 21st century, the difference in ocean carbon uptake between the OW and TW simulations is very small, representing less than a few % of the global carbon storage in 2100 (Figure 1c). This moderate effect is not a surprise in itself, as the impact of changes in the biological pump on the evolution of the oceanic carbon sink over the 21st century has been shown to be second order in all modeling studies since the pioneering work of Maier-Reimer (1993). Here, export production (whether fully passive in the OW simulation, or combining passive and active processes in the TW simulation) decreases very similarly throughout the simulations, reaching about −12% in 2100 compared to 1851–1870. It is interesting to note that even if the export production, estimated at 200 m, decreases more in the TW simulation than in the OW simulation (by about 6%, Figure 2a), the ocean carbon sink is slightly larger in the TW simulation (Figure 1), highlighting that there is not a simple relationship between changes in export production and its efficiency at sequestering carbon (Koeve et al., 2020).

Even though the impact of HTLs on anthropogenic carbon uptake appears limited in the 21st century, the changes in storage show that more carbon is stored at depth in the TW simulation in 2080–2100 (Figure 1b). This difference is explained by the contrasted vertical signature of passive and active exports, as shown in Aumont et al. (2018) and could lead to carbon sequestration on longer timescales in the TW simulation compared to the OW simulation,
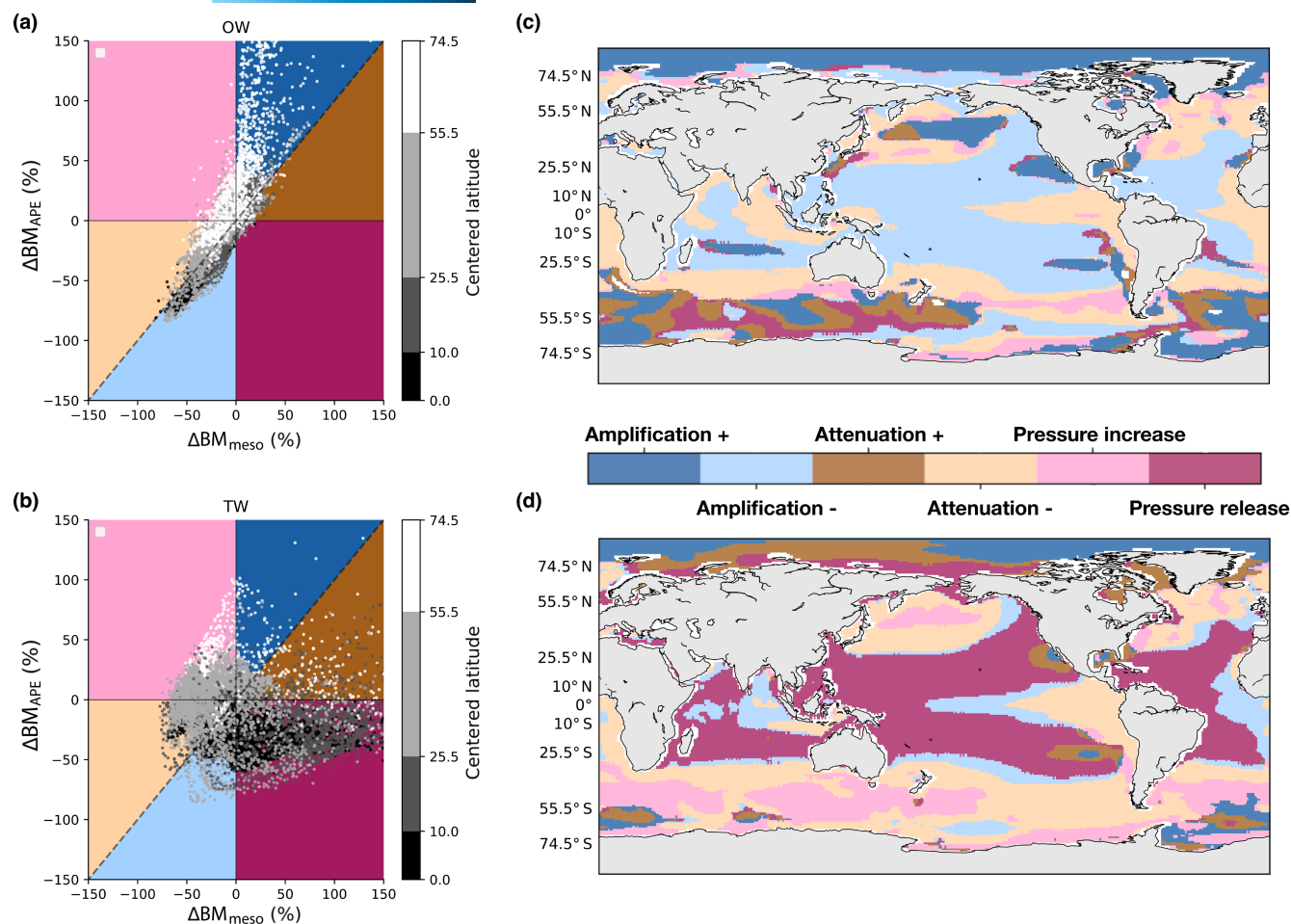
FIGURE 4 Representation of the different trophic regimes between PISCES mesozooplankton and APECOSM small high trophic levels, in both the OW and TW simulations. For both OW (a, b) and TW (c, d): (a, c) show the biomass anomaly in the first five size classes of APECOSM (for all three pelagic communities) as a function of the biomass anomaly of PISCES mesozooplankton. Biomass anomalies are computed as the difference between the mean biomass in the periods (2080–2100) and (1851–1870). The quadrant colors correspond to different trophic regimes that are labelled on the middle color bar. Points are color-coded based on their centered latitude, from equatorial (0—black) to poles (74.5—white) to emphasize possible latitude-related tendencies. The (b, d) show the horizontal distribution of the previously defined trophic regimes. APECOSM, Apex Predators ECOSystem Model; OW, one-way; PISCES, Pelagic Interaction Scheme for Carbon and Ecosystem Studies; TW, two-way.

which could have significant and growing impacts on carbon uptake in the long run (Kwon et al., 2009).

The simulated differences (TW – OW) in ΔDIC at the end of the 21st century are also spatially heterogeneous, reflecting the spatially variable impacts of HTLs feedbacks on carbon export. This is exemplified by the strong simulated contrast between the western and eastern tropical Pacific, both in ΔDIC and in export changes (Figures 1c and 2c). In addition, in response to climate change marine animals move to higher latitudes while their abundance decreases in the tropics, in both observations and simulations (e.g., Hastings et al., 2020; Jones & Cheung, 2015). This phenomenon explains the simulated changes in the proportion of active transport between low and high latitudes (Figure S3). Consequently, the release of predation pressure on mesozooplankton in most of the tropical oceans combined with the reduction of HTLs egestion and excretion fluxes likely contributes to the larger decrease in the export of organic

carbon (Figure 2a). These regional differences in ocean sequestration are critical for modulating the long-term efficiency of carbon storage in the ocean (Siegel et al., 2021).

4.3 | Fishing effects on marine ecosystems and the carbon cycle

The simulations we present here focus on the response of the marine ecosystem to climate change as we assume that there are no other anthropogenic factors affecting the ecosystem, particularly no effect of fishing. Explicit consideration of the interactions between higher and lower trophic levels would make it possible to assess the impacts of fishing-induced mortality of the higher trophic levels on the whole ecosystem and on carbon cycling in an integrated manner. Given the response of LTLs to changes in HTLs biomass in response

to climate change, it is very likely that fishing activity triggers similar types of responses in the ecosystem dynamics. Indeed, as fishing mainly targets large organisms at the top of the trophic chain, its effects would cascade down the food web, hence modifying the size-spectrum of the community in the ocean and the top-down pressure of HTLs onto LTLs (e.g., Heneghan et al., 2019). Previous work has shown that changes in HTLs biomass reverberate onto lower trophic levels biomass and ocean biogeochemistry (e.g., Baum & Worm, 2009; Bianchi et al., 2021; Getzlaff & Oschlies, 2017). We expect the fishing effects to be already significant since analyzes have shown that fishing has caused about a 50% decline in fish biomass during the historical period as compared to about a 5% decline in response to climate change (e.g., Bianchi et al., 2021; Lotze et al., 2019). Combined with climate change, fishing impacts will likely enhance the ecosystem response we model in the TW simulation. A next step using the coupled end-to-end ecosystem model presented here would be to introduce some fishing effect (historical and future scenarios) as a new forcing, which would enable us to estimate quantitatively the effects of fishing on the LTLs but also on the efficiency of the ocean carbon sink. This is even more critical if climate change and fishing act synergistically (Gissi et al., 2021).

5 | LIMITATIONS OF THE STUDY

When analyzing climate projections, the associated uncertainty is classically decomposed into three distinct sources: internal variability, model uncertainty, and scenario uncertainty. The uncertainty linked to internal variability is somehow already included in our study using long simulations and averaging over large regions/long periods of 20 years. The uncertainties related to model and scenarios have been explored for biogeochemical and marine ecosystem projections using the CMIP6 and FishMIP ensembles. In particular, these analysis have quantified the scenario (five different scenarios in Kwiatkowski et al., 2020, two in Tittensor et al., 2021) and model/structure (>10 different ESMs in Kwiatkowski et al., 2020; nine different MEMs in Tittensor et al., 2021) uncertainties. In FishMIP, the MEMs biomass change in response to the IPSL-CM6A-LR projection with the RCP8.5 scenario varies in a 20% range in 2100 between, while the MEMs ensemble mean biomass change varies of about 12% between the mitigation scenario (RCP2.6) and the high-emission scenario (RCP8.5). These structural and scenario uncertainties are thus of the order, or larger, than the differences we simulate between the OW and TW frameworks in our analysis. An intercomparison analysis with models that have been coupled in a TW framework would allow to define the structural uncertainty and if the global mean change would be significantly impacted by the full coupling of the models, but to date only PISCES and APECOSM have run in a TW framework. There is no doubt that using several scenarios would allow us to explore the possible existence of tipping points and non-linearities in the sensitivity of the ecosystem response to climate change. That said, other scenarios have been tested and the model projections show rather linear responses across time and scenarios,

that is, similar response per degree of warming for any given scenario (e.g., Kwiatkowski et al., 2020; Tittensor et al., 2021). Indeed, in our results, the change in biomass integrated over the global ocean shows a linear response per degree of warming (Figure S6). These elements suggest that this scenario enables us to cover the full spectrum of responses that would have been obtained across different scenarios.

Models parametrization also necessarily modulates the organisms response to climate change (e.g., for temperature; Heneghan et al., 2021). Analyzing parametrization uncertainties would imply running several additional simulations (including OW vs. TW, control, historical and projection simulations), which is at that stage too demanding in terms of computing resources. Recent work highlighted that inter-model uncertainty on carbon fluxes and storage is also small compared to other uncertainties (Fu et al., 2022). In addition, studies have highlighted that it is crucial to gather more observations on the processes that are modeled in order to better constrain the response of the ecosystem to climate change (e.g., Rohr et al., 2022; Sailley et al., 2013).

PISCES and APECOSM simulate a poleward migrations of organisms to more favorable conditions in response to climate change (Figures S2 and S5). Observations have also shown that organisms are also likely to adapt to some extent to their changed environment (e.g., Harvey et al., 2014; Miller et al., 2018), which would potentially dampen the difference our simulations show between the high and low latitudes. Understanding local adaptation (niche shifting, by phenotypic plasticity or natural selection depending on the timescale) and evolutionary processes is important to project the ecosystem response to climate change, but our analysis is limited in accounting for adaptation and evolution. The models include a certain plasticity of the organisms, for example in response to temperature, but the functions do not change in time so there is no potential for evolution. In addition, these processes are often species specific and the balance between phenotypic and genotypic responses remains to be established (e.g., Bennett et al., 2019; Poloczanska et al., 2016).

6 | CONCLUSIONS AND RECOMMENDATIONS

Fully coupling the HTLs model to the LTLs model increases model complexity and more than doubles the computation time. According to our results, the complete integration of HTLs seems to only have a small impact on the carbon cycle in this century compared to the CMIP5 inter-model uncertainty (Friedlingstein et al., 2020; Fu et al., 2016). It may thus appear unnecessary to explicitly model HTLs to study the evolution of the globally integrated carbon cycle for this century. However, since fishing is also a strong driver of HTLs biomass, with consequences on LTLs and thus ocean carbon, only a TW coupling can take into account its significant effects on the carbon cycle, even more if it acts synergistically with climate change (Gissi et al., 2021). The TW coupling scheme seems more appropriate for studying longer time scales and regional scales as

it substantially affects the dynamics of the ecosystems. Indeed, modeling the interactions between HTLs and LTLs allows for a better understanding of the dynamical changes induced by climate on the trophic chain. It permits the propagation of trophic cascades through the ecosystem and the subsequent modulation of the community composition (Frank et al., 2005) that affects the ecosystem response to climate change (Goedegebuure et al., 2017), including through primary and export production (Fu et al., 2016). Explicit consideration of the interactions between LTLs and HTLS appears necessary if one wants to analyze ecosystem dynamics and their potential effects on biogeochemical cycles, and to investigate regional differences or changes induced by marine organisms on the carbon cycle on long timescales.

Taking into account TW interactions between HTLs and LTLs enhances trophic amplification between zooplankton and HTLs at the global scale but changes our understanding of ecosystem trophic functioning in response to climate change. In particular, the apparent prevalence of the trophic amplification phenomenon in most recent studies (e.g., Lotze et al., 2019), but also in our study at the global scale (Figure 3b), could be an artifact of the lack of consideration of top-down feedbacks in ecosystem models and/or of the global scale analysis. If this is confirmed by other TW studies, our understanding of the effects of climate change on marine ecosystems and the associated projections could be altered.

Fully coupling LTL and HTL models remains challenging as more data are needed to constrain the model parameters and the interactions between the different trophic levels. In addition, the different HTL models, compared in FishMIP, use either primary production and/or phytoplankton and/or zooplankton biomasses as inputs, which complicates a generalization of the TW framework and the comparison of the trophic interactions.

CONFLICT OF INTEREST
The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT
The data that support the findings of this study are openly available in Zenodo at https://zenodo.org/record/7385454#.Y5cpAC2S3_Q.

ORCID
Priscilla Le Mézo https://orcid.org/0000-0002-5695-4845

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SUPPORTING INFORMATION

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