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RESEARCH ARTICLE

Large potential impacts of marine heatwaves on ecosystem functioning

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Abstract

Ocean warming is driving significant changes in the structure and functioning of marine ecosystems, shifting species' biogeography and phenology, changing body size and biomass and altering the trophodynamics of the system. Particularly, extreme temperature events such as marine heatwaves (MHWs) have been increasing in intensity, duration and frequency. MHWs are causing large-scale impacts on marine ecosystems, such as coral bleaching, mass mortality of seagrass meadows and declines in fish stocks and other marine organisms in recent decades. In this study, we developed and applied a dynamic version of the EcoTroph trophodynamic modelling approach to study the cascading effects of individual MHW on marine ecosystem functioning. We simulated theoretical user-controlled ecosystems and explored the consequences of various assumptions of marine species mortality along the food web, associated with different MHW intensities. We show that an MHW can lead to a significant biomass reduction of all consumers, with the severity of the declines being dependent on species trophic levels (TLs) and biomes, in addition to the characteristics of MHWs. Biomass of higher TLs declines more than lower TLs under an MHW, leading to changes in ecosystem structure. While tropical ecosystems are projected to be sensitive to low-intensity MHWs, polar and temperate ecosystems are expected to be impacted by more intense MHWs. The estimated time to recover from MHW impacts is twice as long for polar ecosystems and one-third longer for temperate biomes compared with tropical biomes. This study highlights the importance of considering extreme weather events in assessing the effects of climate change on the structures and functions of marine ecosystems.

KEYWORDS
dynamic ecosystem modelling, ecosystem functioning, ecosystem modelling, marine heatwave, marine heatwave associated mortality, species thermal stress, trophic structure

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1 | INTRODUCTION

Ocean warming is a key impact driver associated with climate change, affecting marine species from plankton to top predators through changes in their physiology (Cheung, Sarmiento, et al., 2013; Cooley et al., 2022; Pörtner & Farrell, 2008), phenology (Cheung et al., 2009; Dulvy et al., 2008; Durant et al., 2019; Perry et al., 2005; Pinsky et al., 2013; Poloczanska et al., 2013), biogeography (Reygondeau, 2019; Tittensor et al., 2010), trophic dynamics (Boyce et al., 2015; Portner et al., 2014) and ecosystem services such as food provision (Cheung, Watson, & Pauly, 2013). In addition to long-term ocean warming, marine heatwaves (MHWs) are increasing in frequency, intensity and duration (Fox-Kemper et al., 2021; Frölicher et al., 2018; Hobday et al., 2016; Oliver et al., 2018). MHWs are commonly defined as extremely high ocean temperatures that persist from days to months. Technically, MHWs correspond to daily SST anomalies over a specific threshold, usually defined by identifying natural climatological oscillation, observed for five consecutive days or more (Frölicher et al., 2018; Hobday et al., 2016).

The physiological functions of marine ectotherms, which represent more than 95% of marine diversity, are directly impacted by changes in temperature (Pauly & Cheung, 2018; Pörtner & Peck, 2010; Seibel & Drazen, 2007; Smith et al., 2023). These changes affect their metabolism, leading to modifications in body function, growth rate, maximum body size and reproductive rates (Alfonso et al., 2021; Deutsch et al., 2015; Pauly & Cheung, 2018; Poloczanska et al., 2016; Smith et al., 2023). With MHWs, the upper thermal limits of species can be abruptly exceeded, especially for those species living in environments where the water temperature is already near the upper range of their thermal niche (Smale et al., 2019; Smith et al., 2023; Wiens, 2016). To cope with such stressful conditions, organisms resist, migrate or die (Gienapp et al., 2008; Habary et al., 2017; Smith et al., 2023). Organisms may resist when they experience intense thermal stress below their species' thermal limits. These processes include short-term stress responses, such as cellular stress responses to protect and repair cellular macromolecular systems (Somero, 2020), and reducing non-essential metabolic activities, like reproductive investment (Shanks et al., 2020). Thermal stress of MHWs drives shifts in biogeography and species migration, including, for instance, geographical species shifts toward poles and deeper waters (Cheung et al., 2021; Jacox et al., 2020; Lonhart et al., 2019; Smale et al., 2019; Smale & Wernberg, 2013). Organisms may die either when they experience intense thermal stress above their species' thermal limits or when the increased energy demand due to thermal exceeds the metabolic capacity of the species (Lemoine & Burkepile, 2012; Smith et al., 2023). The combination of biological responses associated with MHWs has caused impacts on biodiversity (Cavole et al., 2016; Jones et al., 2018; Wernberg et al., 2016), ecosystem resilience (Arimitsu et al., 2021) and functions (Collins et al., 2019; Smale et al., 2019; Smale & Wernberg, 2013; Smith et al., 2023). MHWs and their ecological effects also impact fisheries (Pershing et al., 2018) and aquaculture (Oliver et al., 2017).

Despite the increasing understanding of the ecological impacts of MHWs on marine ecosystems, various processes of MHWs remain poorly understood. Notably, the relative contributions of MHW characteristics (intensity or magnitude, duration and frequency) to ecosystem responses over time (Gruber et al., 2021) limit our ability to accurately reproduce or predict how MHWs affect and modify the biodiversity and abundance of perturbed marine ecosystems. In this study, we hypothesise that MHWs (intensity/magnitude and duration) impact marine ecosystems' composition and trophodynamics. We developed a dynamic version of the EcoTroph marine ecosystem model (Gascuel et al., 2011; Gascuel & Pauly, 2009), hereafter called EcoTroph-Dyn. The model allows us to represent theoretical user-controlled ecosystems and analyse how the effects of MHWs, occurring during the year's warmest months, propagate through food webs and alter biomass flow from primary producers to top predators in both pelagic and benthic ecosystems. Informed by the estimated thermal niches of fish and invertebrate species (specifically crustaceans, molluscs and shrimp taxonomic groups), we first developed various scenarios of MHW-induced mortality of trophic groups in the marine ecosystems and implemented these scenarios into EcoTroph-Dyn. We then developed a dynamic version of the EcoTroph model (Gascuel et al., 2008, 2011) to simulate a single MHW's impacts on the biomass and production trophic spectra (i.e., distribution of the ecosystem biomass and production by trophic level [TL]). We simulate three theoretical ecosystems (average of biomes environmental conditions) that represent food web functioning in polar, temperate and tropical biomes (sensu Longhurst, 2007). We focus on the impacts of a unique MHW with different durations and intensities and identify the relative effects of MHW-induced change on trophic flow kinetics and trophic efficiency.

2 | MATERIALS AND METHODS

2.1 | EcoTroph under steady-state condition

We used the EcoTroph modelling approach to study the effects of MHWs on marine ecosystems (du Pontavice et al., 2021; Gascuel, 2005; Gascuel et al., 2011; Gascuel & Pauly, 2009). This quasi-physical model represents the functioning of marine ecosystems as a continuous flow of biomass and energy surging up the food webs, from primary producers (low TLs) to top predators (high TLs). In EcoTroph, biomass enters the food web at trophic level TL = 1, corresponding to the photosynthetic activity of primary producers and recycling of nutrients by the microbial loop. Biomass at TLs higher than 2 comprises heterotrophic organisms, including herbivores, carnivores and omnivores such as fish, mammals, crabs, molluscs and cephalopods. Fractional TLs result in a continuous distribution of biomass along TLs (considered here as consumers), defining the biomass trophic spectra (Gascuel et al., 2005). For computation simplification, in EcoTroph, the biomass spectrum is decomposed by an assembly of small TL classes, with each trophic class including all organisms within each class's lower and upper bond. The biomass

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spectrum in EcoTroph generally includes organisms across the water column living in habitats from pelagic to benthic.

EcoTroph computes the flow of biomass as continuous processes through the trophic spectrum, representing organisms' ontogenetic changes in TLs as they grow and abrupt jumps in TLs due to predation events. The aggregated biomass flows are described by a continuous function (Appendix S1) that represents the mean flow of biomass of individual organisms (Gascuel et al., 2008). The biomass flow in EcoTroph is represented by the traditional equations of fluid dynamics. Specifically, the continuous biomass flow, $\Phi(\tau)$, is described by:

$$\Phi(\tau) = B(\tau) \cdot K(\tau) \tag{1}$$

where $\Phi(\tau)$ represents the biomass flow rate at TL τ, expressed in tons per year ($\mathrm{t\,year^{-1}}$). It indicates the quantity of biomass moving through the TL due to processes such as predation or ontogeny. $B(\tau)$ denotes the density of biomass present at TL τ, measured in tons (t) per TL ($\mathrm{t\,TL^{-1}}$). $K(\tau)$, the flow kinetic, is a rate coefficient, which could be interpreted as a turnover rate at TL τ, expressed in TL per year ($\mathrm{TL\,year^{-1}}$). It describes the speed at which the fraction of the biomass at that TL moves to the next level per unit of time. It thus measures the speed of the biomass flow in the food web, from low to high TLs and is inversely proportional to biomass residence time. This latter corresponds to the time each organism stays at a given food web level, depending on its life expectancy.

A discrete approximation of the continuous distribution $B(\tau)$ over TLs is used for mathematical simplification. Hence, the model state variable becomes B_τ (the standing sock of biomass, in metric tons) present at a specific time under steady-state conditions within the TL class $[\tau, \tau+\Delta\tau[$ and Equation (1) becomes (see Appendix S1 for details):

$$B_\tau = \frac{1}{K_\tau} \cdot \Phi_\tau \cdot \Delta\tau \tag{2}$$

where Φ_τ and K_τ are the mean biomass flow (in $\mathrm{t\,year^{-1}}$) and the mean flow kinetic (in $\mathrm{TL\,year^{-1}}$) within the trophic class $[\tau, \tau+\Delta\tau[$, respectively.

Trophic transfers are usually faster at low TLs and in hot waters. Thus, the flow kinetic K_τ can be expressed as a function of TL, using the empirical equation of Gascuel et al. (2008), as:

$$K_\tau = 20.19 \cdot \tau_i^{-3.258} \cdot e^{0.041 \cdot \mathrm{SST_y}} \tag{3}$$

where $\mathrm{SST_y}$ corresponds to the annual sea surface temperature (SST) used as an input parameter (in this study equal to thermal class value, described in Section 2.3.1), allowing us to calculate the flow kinetics for any theoretical biomes characterised by a known temperature.

The biomass flow $\Phi(\tau)$ is not conservative and can be expressed as decreasing function of TL such as (see details in Appendix S1):

$$\Phi(\tau + \Delta\tau) = \Phi(\tau) \cdot \exp(-\mu_\tau) \cdot \Delta\tau \tag{4}$$

where $\Phi(\tau)$ is the biomass flow at TL$=\tau$ (i.e., at the start of the trophic class $[\tau, \tau+\Delta\tau[$), and μ_τ (expressed in $\mathrm{TL^{-1}}$) is the mean natural loss rate within the trophic class, representing the energy that does not get stored within a trophic class and is lost due to non-predation mortality, excretion and respiration. Equation (4) also defines the transfer efficiency (TE) between continuous TLs, corresponding to the estimated fraction of biomass flow transferred from one TL to the next. TE can be expressed as an empirical equation of the sea surface temperature (SST), according to du Pontavice et al. (2021):

$$\mathrm{TE} = e^{-\mu_\tau} = e^{(-2.162+b+(-0.025+a)\cdot \mathrm{sst})} \cdot 1.038013 \tag{5}$$

where a and b are specific parameters for each biome type (du Pontavice et al., 2021) and SST the sea surface temperature of the time simulated.

Finally, EcoTroph defines the biomass flow $\Phi(\tau)$ as the density of production at TL$=\tau$. Therefore, the production P_τ of the trophic class $[\tau, \tau+\Delta\tau[$ is:

$$P_\tau = \int_{s=\tau}^{s=\tau+\Delta\tau'} \Phi(s) \cdot d\tau = \Phi_\tau \cdot \Delta\tau \tag{6}$$

Hence, according to Equations (2) and (6), EcoTroph highlights that biomass stems from the ratio of the production to the flow kinetic. Production is commonly expressed in $\mathrm{t\,year^{-1}}$, which implicitly refers to the conversion of biomass eaten at TL$=\tau-1$ into predator tissues whose mean TL is τ and thus does not explicitly refer to the TL in the production unit. Therefore, in a TL-based approach such as EcoTroph (wherein the width of trophic classes may differ from 1 TL), production must be expressed in $\mathrm{t\,TL\,year^{-1}}$, thus ensuring full consistency of all units used.

In the steady-state version of the EcoTroph model, each trophic class have the same width, conventionally equal to 0.1 TL (Gascuel et al., 2012; Gascuel, 2005) and a range starting at TL$=$2 (corresponding to the first-order consumers), up to TL$=$5.5, an appropriate range to cover all top predators in marine systems (Cortes, 1999; Pauly et al., 1998). This implies that the time needed for the biomass to flow from one to the next trophic class varies, from the low TLs usually characterised by fast trophic transfers to the high TLs marked by slow transfers.

2.2 | Development of a dynamic version of EcoTroph

To examine the temporal dynamics of climatic events such as MHWs, we extended the steady-state EcoTroph to a time-dynamic model version (EcoTroph-Dyn). EcoTroph-Dyn simulated changes in biomass flows at a bi-weekly (14 days) time step to analyse how MHW-induced perturbation propagates over time through the modelled food web and to quantify its cumulative impacts. The choice of a bi-weekly time step represents the average duration of most naturally occurring or experimentally simulated MHWs with observable ecological impacts (Smale et al., 2015).

In EcoTroph-Dyn, we made two main changes over the steady-state EcoTroph to enable the model to undertake time-dynamic simulations of the trophic effects of MHWs. These include changes in modelling flow kinetics and boundaries of trophic classes, as well as the representation of biomass flow in the basic equations.

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2.2.1 | Flow kinetics and boundaries of trophic classes

Biomass spectra in EcoTroph-Dyn were composed of trophic classes with variable widths of TLs. The width of trophic classes $[\tau_i; \tau_{i+1}[$ in modelled biomass spectra were determined based on the estimated mean flow kinetics so biomass could transfer up a trophic spectrum in each time step ($\Delta t = 1/26$ year). Mean flow kinetics is defined as the speed of the trophic flow through the food web and is expressed in TL year^{-1}. Thus:

$$\tau_{i+1} = \tau_i + K_\tau \cdot \Delta t \tag{7}$$

where $\tau_i \in [2; 5.5]$, $\tau_{i=0} = 2$, and K_τ defined by empirical Equation (3).

This equation allows us to define the trophic class boundaries in a reference state, characterised by a baseline mean water temperature for each modelled biomass spectrum (state ① in Figure 1). The baseline mean water temperature is defined as the average sea surface temperature from 1st January 1982 to 31st December 2011 (see Section 2.3.1). When water temperature changes from the baseline, the estimated flow kinetics of the biomass spectrum and the trophic class boundaries are re-computed.

Moreover, MHWs lead to the death of marine organisms, affecting their life expectancy (Smith et al., 2023). In EcoTroph-Dyn, changes in the life expectancy of organisms are represented by the changes in loss rate in the biomass spectrum, that is, the proportion of the biomass that does not stay or move up in the food web (du Pontavice et al., 2021; Gascuel et al., 2008). To account for the MHW's effects on loss rate, the flow kinetic and the resulting width of the trophic class were computed as follows:

$$\tau_{i+1} - \tau_i = K_\tau \cdot \Delta t = 20.19 \cdot \tau_i^{-3.258} \cdot e^{0.041 \cdot \mathrm{SST}_y} \cdot \left(1 + \eta_\tau\right) \cdot \Delta t \tag{8}$$

where η_τ is the MHW-associated additional loss rate, defined according to the method described in Section 2.3.2.

Equation (8) implies that any warming and any MHW's additional losses in the trophic flow reduce the life expectancy of organisms and thus accelerate trophic transfers towards higher TLs or detritus. At each time step, the upper and lower TLs of every trophic class were recalculated given the environmental temperature (SST) that the biomass spectrum is exposed to at time step y and the MHW-associated losses (η_τ).

2.2.2 | Modelling biomass flow in dynamic simulations

EcoTroph-Dyn represents time-dynamic changes in biomass flow by (step 1) computing biomass flow between trophic classes and (step 2) calculating biomass at each trophic class for each time step (represented by ① and ② in Figure 1). To calculate biomass flow (Φ) from trophic class τ to $\tau + \Delta\tau'$ dynamically, we modified Equation (4).

$$\Phi\left(\tau + \Delta\tau', t+1\right) = \Phi(\tau, t) \cdot \exp\left(-\left(\mu_t + \eta_{\tau,t}\right) \cdot \Delta\tau_{,t}\right) \tag{9}$$

where μ_τ (expressed in TL^{-1}, Equation 5) represents the mean natural losses within the trophic class through non-predation mortality, excretion and respiration over a trophic class interval. The $\eta_{\tau,t}$ parameter (expressed in TL^{-1}) represents the mean loss rate caused by the

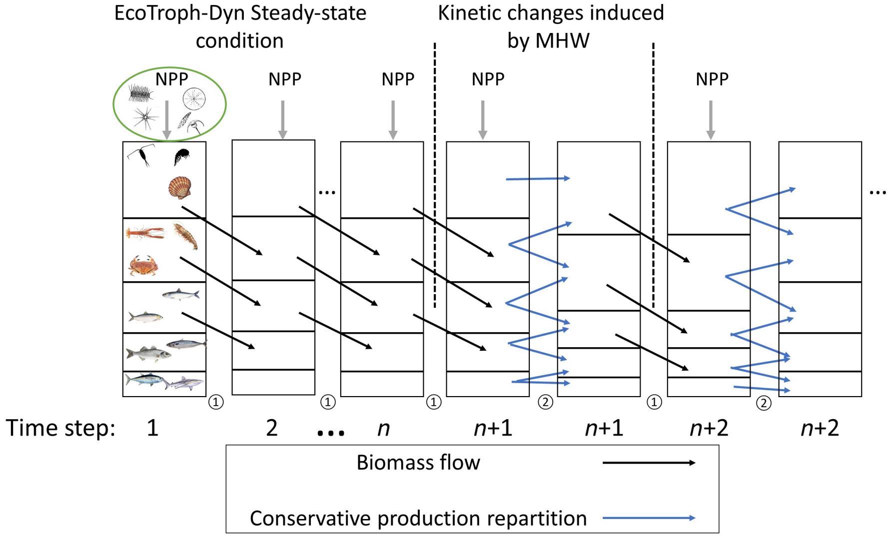

FIGURE 1 EcoTroph-Dyn scheme: The trophic functioning of marine food webs is represented by a biomass flow, with biomass entering the system at trophic level 1 due to net primary production (NPP). Biomass flow reaching each trophic level is then defined by the trophic transfer efficiency. The flow kinetic, temperature and MHW-dependant, is a key parameter to define boundaries of trophic classes and to derive the biomass at each trophic level and time step of the model from the biomass flow. Vertical dashed lines refer to an MHW occurrence, the black arrow represents biomass flow between trophic classes and time step, and the blue arrow represents production redistribution across trophic class boundaries due to an MHW. ① and ② refer to no MHW versus MHW effect, respectively (step 1 and step 2 in the paragraph above).

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instantaneous mortality of species in each trophic class induced by the MHW event.

In Step 2, as the trophic class intervals (τ and $\tau + \Delta\tau$) of each biomass spectra are re-computed at every time step, the production is redistributed into the new trophic class between each time step. The production is allocated proportionally according to the width of the trophic classes. This can be expressed as:

$$P_{\tau'} = \sum_{\tau_i'}^{\tau_{i+1}'} \text{Fraction} \cdot P_\tau \qquad (10)$$

With case 1: $\tau_{i+1}' \geq \tau_{i+1}$:

$$\text{Fraction} = \frac{\tau_{i+1} - \max\left(\tau_i, \tau_i'\right)}{\tau_{i+1} - \tau_i}$$

case 2: $\tau_{i+1}' \leq \tau_{i+1}$:

$$\text{Fraction} = \frac{\tau_{i+1}' - \max\left(\tau_i, \tau_i'\right)}{\tau_{i+1} - \tau_i}$$

Finally, in each trophic class $[\tau, \tau + \Delta\tau'[$ the mean biomass can be expressed as:

$$B_{\tau,t} = \frac{P_{\tau,t}}{K_{\tau,t}} \text{ or } \frac{P_{\tau',t}}{K_{\tau,t}} \text{ if boundaries change} \quad \text{Equation (2, dyn)}$$

2.3 | Development of marine heatwave loss rate algorithm

2.3.1 | MHWs detection and characterisation

To characterise MHWs (climatology, threshold values, intensity and duration), we analysed daily SST observations from the NOAA's AVHRR data (Reynolds et al., 2007; https://www.ncei.noaa.gov/access/metadata/landing-page/bin/iso?id=gov.noaa.ncdc:C00680) to calculate the climatology of temperature, identify extreme temperature thresholds, and determine the intensity and duration of MHWs. We defined MHWs as a discrete, prolonged, anomalously warm water event when the daily SSTs exceed an extreme temperature threshold value for at least five consecutive days (Hobday et al., 2016). The extreme temperature threshold value was calculated for each 1° latitude × 1° longitude spatial cell as the 90th percentile of daily SST from the 30-year historical time series from January 1982 to December 2011. We did not calculate threshold values by season; thus, MHWs events were identified by a single threshold across the year. As a result, we detected MHWs mostly occurring during the year's warmest months (Figure 2a). This approach to identifying the MHWs thresholds represents extreme temperature in the local (spatial cell) context (Oliver et al., 2021). We also calculated a reference average temperature

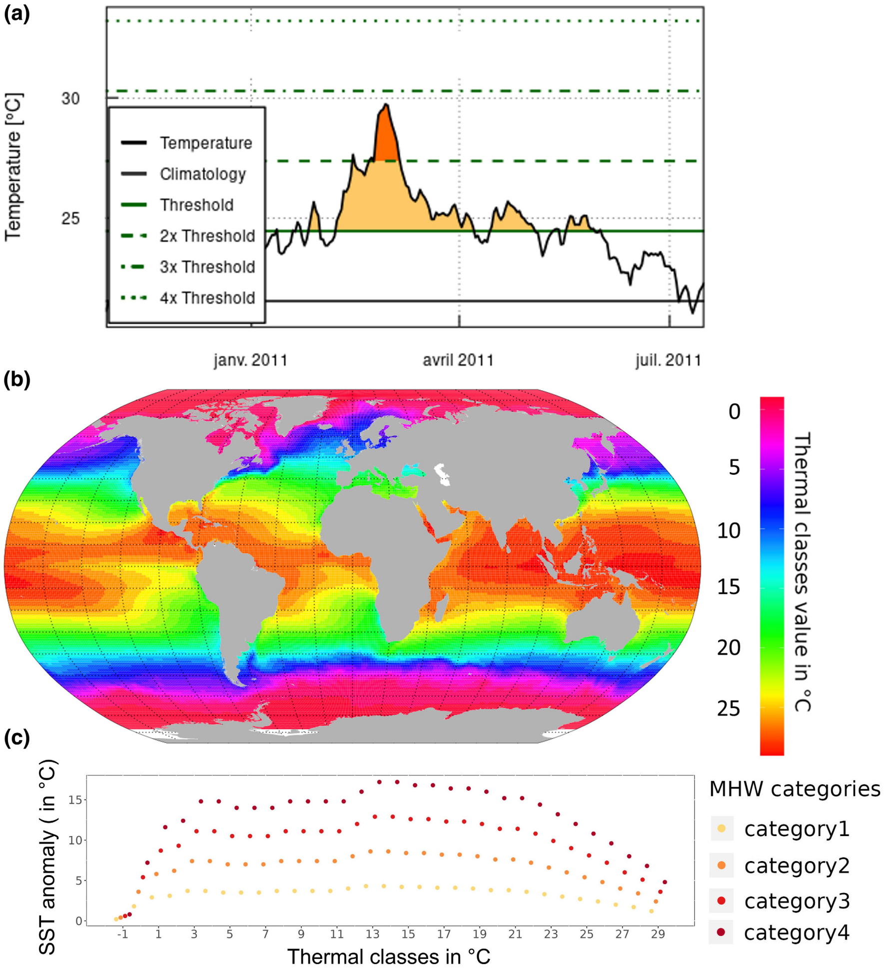

FIGURE 2 MHWs detection and category threshold characteristics across the world ocean and map of ocean averaged temperature by thermal classes: (a) Schematic explanation of MHWs detection for a spatial cell. The solid horizontal green and black lines represent the extreme threshold value and the reference temperature, respectively. (b) A map of thermal classes of 1°C intervals from −1 to 29°C categorised based on the reference temperature at each spatial cell. (c) Average MHW's category threshold per thermal class.

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(SST average) from the same 30-year historical time series for each spatial cell. We used the calculated reference average SST to categorise each spatial cell into 'thermal classes' (TC) of 1°C increment of reference SST average from −1 to 29°C (Figure 2b). We used the R package heatwaveR described at https://robwschlegel.github.io/heatwaveR/ (Schlegel & Smit, 2018) to compute MHWs characteristics in each spatial cell from January 1982 to December 2021. We also calculated the average MHWs category threshold across spatial cells belonging to the same thermal class (Figure 2b,c). MHWs' categories are defined based on multiples of the value represented by the local difference between the climatological mean and the 90th climatological percentile (which is the threshold used to identify MHWs, Hobday, Oliver, et al., 2018). Thus, depending on the local climatological mean, the same MHW category corresponds to different anomalies. For instance, ocean water with a 12°C thermal class exhibits a higher SST anomaly associated with a category 4 MHW than ocean water with a 25°C thermal class.

2.3.2 | Additional loss rate associated with MHW

In this analysis, we included 95 bivalves, 15 cephalopods, 122 crabs and 5241 fish species (see Data availability statement) to access species mean trophic levels and spatial distribution information. For each spatial cell belonging to a given thermal class, we determined the percentage of species exposed to MHW-induced thermal stress. Thermal stress is defined here as the species being exposed to an MHW intensity above the estimated temperature threshold of their thermal niche (95th percentile of the thermal niche; see Appendix S2 for detailed estimation of species distribution and associated thermal threshold methodology). The thermal stress of a species was assumed to be dependent on the category of MHWs that it was exposed to (ranging from category 1 to category 4, corresponding to a specific SST anomaly Figure 2c) and appears to be significantly different (ANOVA, *p*-value <.05) according to the TL class that the species belongs to: (<2.5, 2.5–3.0, 3.0–3.5, 3.5–4.0, 4.0–4.5, 4.5–5.0 and >5.0). See Appendix S3 for more details on the method. TLs <2.5 reach 50% of species thermally stress around one MHW category earlier than other TLs.

To have a continuous representation of the percentage of species undergoing thermal stress as the intensity of MHWs increases, we transformed the discrete MHW's categorisation (Hobday, Oliver, et al., 2018) to a continuous MHW's intensity index as follows:

$$\mathrm{MHW}_{\mathrm{cat},i} = \frac{\text{MHW mean anomaly}, i}{\text{cat1 associated anomaly}, i}$$

where the MHW mean anomaly was calculated as the difference between the MHW mean SST and the reference temperature of each thermal class (*i*), and the 'cat1 associated anomaly' corresponds to the mean threshold value used to identify category 1 MHW in each thermal class (*i*).

We fit the estimated percentage of species undergoing thermal stress with the MHW's intensity index and species' trophic class to a nonlinear function. A Gompertz function was selected after preliminary tests because it better fitted the data than logistic or other mathematical functions with similar shapes. The Gompertz function is expressed as:

$$\%\ \text{of species thermally stressed} = \exp^{-\exp^{\mathrm{b\_tl}_i \cdot \left(\mathrm{MHW}_{\mathrm{cat},i} - \mathrm{lt50\_tl}_i\right)}}; \qquad (11)$$

We estimated the parameters $\mathrm{b\_tl}_i$, $\mathrm{lt}_{50}\mathrm{\_tl}_i$ and $\mathrm{MHW}_{\mathrm{cat},i}$ for each thermal class *i*. The parameters $\mathrm{b\_tl}_i$ and $\mathrm{lt}_{50}\mathrm{\_tl}_i$ correspond to the slope of the function and the index of marine heatwave intensity ($\mathrm{MHW}_{\mathrm{cat},i}$) at which 50% of the species are undergoing thermal stress, respectively.

For each thermal class i (see Appendix S3 for more details on the method), parameters $\mathrm{b\_tl}_i$ and $\mathrm{lt}_{50}\mathrm{\_tl}_i$ were re-expressed according to empirical equations fitted on their first estimates:

$$\mathrm{b\_tl}_i = -1.4511 - e^{0.4223 \cdot (i - 22.4926)} \qquad (12)$$

and

$$\begin{aligned} \mathrm{lt50\_tl}_i &= 3.29 - 0.485 \cdot i + 0.0306 \cdot i^2 - 0.000608 \cdot i^3 \text{ when TL} < 2.5 \text{ and} \\ \mathrm{lt50\_tl}_i &= 3.55 - 0.271 \cdot i + 0.014 \cdot i^2 - 0.000304 \cdot i^3 \text{ when TL} \geq 2.5. \end{aligned} \qquad (13)$$

Finally, we calculated biomass loss rate (η_i) as a linear function of the estimated percentage of species undergoing thermal stress in ocean cells belonging to the same thermal class (*i*):

$$\eta_i = \alpha \cdot \%\ \text{of species thermally stressed}_i \qquad (14)$$

where α is a rate assumed to represent the species' resistance capacity to MHW's conditions, assuming that this resistance reduces the mortality rate due to species' exposure to thermal stress. We explored the sensitivity of the results to the value of α using five resistance capacities. These settings are full resistance ($\alpha = 0$; no mortality due to thermal stress), partial resistance ($\alpha = 0.25$, 0.5, 0.75; 25%, 50% and 75% of the species die because of thermal stress, respectively) and no resistance ($\alpha = 1$; all species die when they are under thermal stress).

2.4 | Marine heatwaves simulations

To assess the impacts of a single MHW, we simulated a full range of theoretical MHWs with an MHW intensity index ranging from 0 to 4 and an MHW duration from 2 weeks to 5 months (1–10 simulation time steps). To understand how trophodynamics affect the effects of an MHW across the food web, we varied the parameters determining flow kinetics, transfer efficiency and biomass loss rate separately and tested their consequences on the model outputs. We applied a constant net primary production (NPP) to all simulations as the objective here was to test the specific effects of an MHW through its direct impacts on species' mortalities. To simulate the effects of an MHW using EcoTrop-Dyn, we perturbed the biomass spectra expected to represent the mean thermal classes of a given biome with an MHW occurring at the fifth time steps, which lasted various times according to the MHW's duration simulated. The MHW perturbation was then removed, and the simulation was run

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under baseline temperature for 262 time steps (11 years) to ensure that biomass spectra returned to their initial levels. To assess the effects of an MHW under different environmental conditions, MHW's simulations were undertaken for three thermal classes that were representative of polar, temperate and tropical biomes identified by Reygondeau et al. (2013) and adapted from Longhurst (2007). We did not intend to mimic the dynamic of the entire biomes but just for a specific thermal class considered representative of the biomes. To find the thermal classes representative of each biome, we averaged the thermal class of each spatial cell belonging to polar, temperate and tropical biomes, respectively. The thermal classes ranged from −1 to 9°C, 2 to 23°C and 16 to 29°C, while the average thermal classes were of 0–1°C, 12–13°C and 25–26°C in polar, temperate and tropical biomes, respectively.

To assess the ecological impacts of the simulated MHWs, we considered two indicators: the time needed for the biomass to recover to the pre-MHW level (expressed in number of time steps) and the average biomass loss (in percentage) over the recovery period. By 'time to recover', we mean the time needed to reach 95% of the original biomass before the MHW event. Both indicators were computed for each trophic compartment (Low TLs ∈ [2;3[, Medium TLs ∈ [3;4[, and High TLs ∈ [4;5.5]) as well as for the entire food web-scale (TLs ∈ [2;5.5]), excluding primary producers, which were simulated using NPP as input.

3 | RESULTS

3.1 | Thermal stress algorithm and MHW-associated loss rate

The global scale thermal stress algorithm (Appendix Figure S3a,b) suggested species inhabiting warm environments are more prone to thermal stress associated with MHW occurrences than species living in colder environments. In thermal class ≥25°C areas, species were already located near the upper-temperature threshold of their thermal niche. For an MHW of Category 1, a large proportion of species appeared already thermally stressed (more than 75% of species), while increasing the intensity of MHWs from Categories 1–2 predicted that close to 100% of species would be under thermal stress (Figure 3). Such high levels of thermal stress remained similar under more intense MHWs. In water comprised in the thermal class of 16–24°C, the majority (78%) of the species are located in regions outside of their upper limit, resulting in a lower percentage of species undergoing thermal stress due to a Category 1 MHW. In water comprised in the thermal classes of 8–15°C, the percentage of species under thermal stress is lower and was estimated to reach 80% only from a Category 4 MHW. Finally, in waters with a thermal class of ≤8°C, almost no species were thermally stressed by any MHW's category lower than category 1.5. However, the proportion of species under thermal stress increased rapidly under higher MHW intensity, reaching around 70% of species under thermal stress when exposed to a Category 4 MHW. The reactions of TLs below 2.5 (Figure 3a) were similar to those of TLs above 2.5 (Figure 3b), with 50% of species experiencing thermal stress (LT_{50}) occurring at a lower intensity of MHW (no change in the curve slope; Supplementary material S3b).

3.2 | Key processes of MHWs' propagation through the food webs

Our simulation showed that an MHW of a given intensity and duration resulted in much higher instantaneous impacts on the consumer biomass in temperate and tropical biomes than in the polar biome. For instance, with an MHW of Category 3 lasting 1.5 months and assuming a resistance capacity of 50% ($\alpha = 0.5$), the total consumer biomass would instantly decrease by 6%, 31% and 36% in Polar, Temperate and Tropical biomes, respectively (dashed orange lines in Figure 4). Because other MHW characteristics led to similar conclusions with different magnitudes in biomass decreases, we have

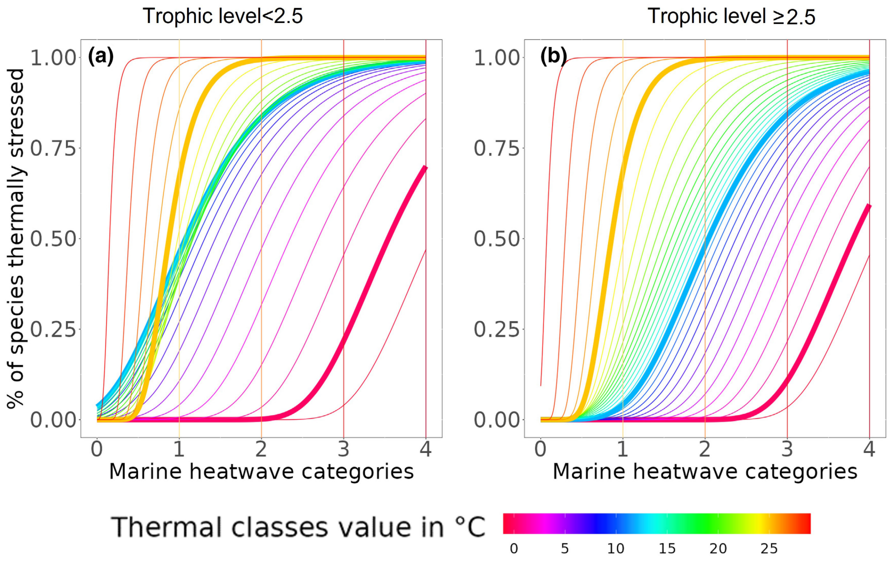

FIGURE 3 Proportion of species undergoing thermal stress: Thermal stress-based algorithm, with the reactions of trophic levels (< and ≥) 2.5 to a MHW event displayed on the (a) and (b) panels, respectively. Vertical lines from left to right correspond to MHW Category 1, Category 2, Category 3 and Category 4, respectively. Thicker lines correspond to the temperature used to simulate polar, temperate and tropical biomes in pink, blue and yellow, respectively.

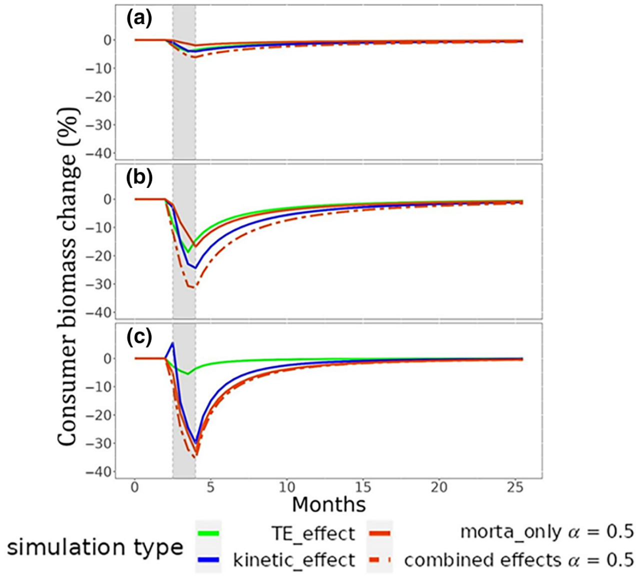

FIGURE 4 Instantaneous total consumer biomass response to an MHW occurrence: Simulation of a 1.5 month duration Category 3 MHW. The unique transfer efficiency effect, unique kinetic effect, $\alpha=0.5$, and combined effects are green, blue, orange and dashed orange, respectively. Grey shade areas correspond to the MHW duration. With (a), (b) and (c) corresponding to polar, temperate and tropical biome simulation, respectively.

chosen these MHW metrics in Figure 4 to represent the role of each trophodynamic process clearly.

The impacts of an MHW on total consumer biomass were driven by changes in trophodynamic parameters, including MHW-associated loss rate and temperature-induced changes in kinetic and transfer efficiency. In the polar biome, there was almost no additional MHW-associated loss rate in the simulated scenario. In contrast, temperature-induced kinetic and transfer efficiency change from the simulated MHWs contributed to a small (4%) instantaneous decrease in consumer biomass. In the temperate biome, changes in transfer efficiency and additional MHW-associated loss rate had a larger influence on total consumer biomass response (−14% and −18%, respectively). However, kinetic appeared to be the primary driver of total consumer biomass reduction by inducing, when considered in isolation, a −24% instantaneous decrease in the total consumer biomass. Finally, in the tropical biome, individually, both kinetic and additional MHW-associated loss rates highly influenced total consumer biomass response to an MHW event (around an instantaneous 30% decrease) compared to transfer efficiency (around an instantaneous 5% decrease). In all cases, the instantaneous biomass spectrum response was larger when simulations considered all drivers together, yet individual driver responses appeared not additive but synergistic.

Looking at biomass spectrum response according to various species' resistance capacity to MHWs, additional mortality played a crucial role in the biomes' magnitude response (Appendix S4). Instantaneous total consumer biomass decreased twice as great in the polar and the temperate biome and fourfold in the tropical biome and under no resistance and full resistance capacity (i.e., $\alpha=0$ and $\alpha=1$, respectively).

3.3 | Marine ecosystems responses

In response to an extreme MHW event, the biomass spectrum impact on each biome was analysed in terms of intensity and duration (Figure 5a), showing that the tropical biome was more affected than the temperate and polar biomes. The polar biome displayed almost no response to a MHW when it was less than category 2 in intensity, regardless of its duration and species' resistance capacity (Appendix Figure S5a). Associate with a Category 3 and 5 months long MHW, an average biomass loss of 7.0%–17.2% was estimated according to $\alpha=0$ to $\alpha=1$. However, Category 3 or stronger MHW caused a higher biomass loss in the polar biome. The temperate biome responded quicker to the MHW perturbation, with a high sensitivity to event duration (isopleth slopes are steeper). A MHW of Category 2 lasting 5 months in temperate areas led to a similar average total consumer biomass loss as an MHW of Category 4 in polar areas. The strongest MHW simulated in the temperate biome (an MHW of Category 4 and last 5 months) led to an average biomass loss of 18.6–30.5 for the same α of 0 and 1, respectively (Figure 5; Appendix Figure S5a). The tropical biome reacted at the first time step to the lower level of MHW's category. A Category 1 MHW lasting 5 months resulted in an average biomass loss of 0 and 32% according to an α of 0 and 1, respectively (Appendix Figure S5a).

Looking at the time needed for the biomass spectrum to recover, the tropical biome was expected to recover faster than the temperate and polar biome (Figure 5b). In polar areas, the biomass spectrum is almost unaffected below category 2 MHW, with a time to recover shorter than 2 months. However, the biomass spectrum needed much more time to recover in case of an extreme category 4 MHW, with time to recover ranking from 9 to 42 months for α between 0 and 1 (Figure 5b; Appendix Figure S5b). In the temperate biome, the time for the biomass spectrum to recover increased in the same trend as the average biomass loss. Lastly, the tropical biome, which showed the highest biomass loss associated with an MHW, recovered the fastest. In response to a MHW of Category 4 lasting 5 months, the biomass spectrum needed between 5.5 and 16.2 months to recover according to $\alpha=0$ and $\alpha=1$, respectively. More generally, whatever species' resistance capacity is considered, the two indicators of biome response to an MHW suggested that the polar biome response to an MHW responded to the intensity or category of the MHW simulated. In contrast, the tropical biome response was strongly linked to the MHW's duration. The response in the temperate biome depended on both MHW's intensity and duration characteristics.

3.4 | Disentangle the signal along the food web

Looking at the food web's different trophic levels for a given α capacity, we observed that the MHW perturbation alters trophic compartments over different time scales (Figure 6). In the temperate biome (Figure 6b), low TLs reacted firstly with a high instantaneous biomass decrease and recovered quickly (Figure 6; Appendix Figure S6a). Medium TLs integrated the perturbation over a more extended period but with a smaller average biomass decrease. Finally, high TLs

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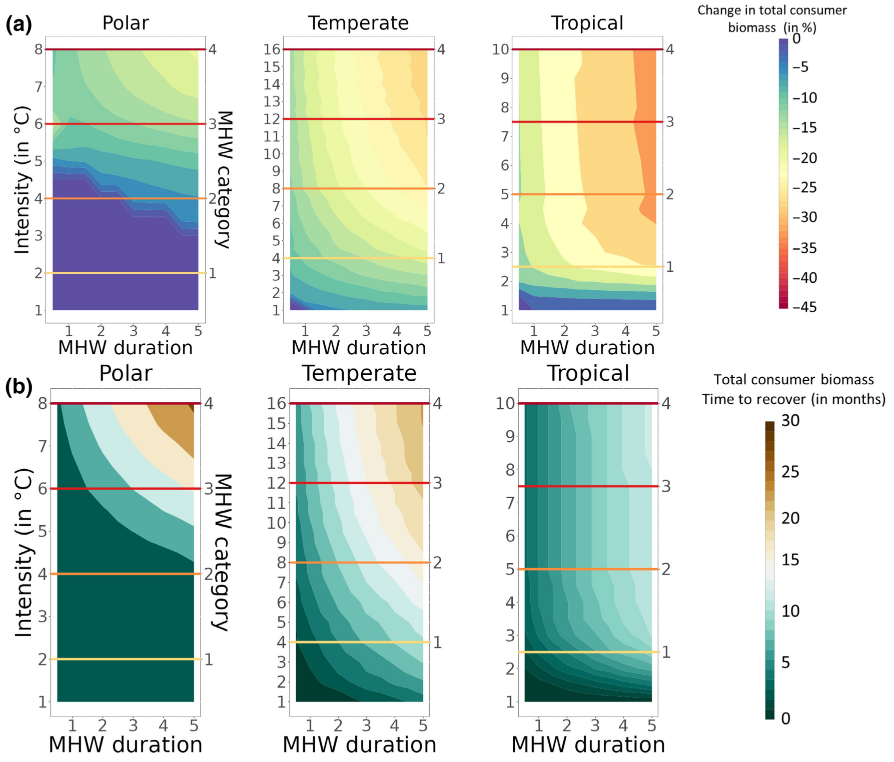

FIGURE 5 Average biomass loss and time to recover associated with MHWs characteristics with $\alpha = 0.5$: (a) corresponds to the average total consumer biomass loss over the period of disturbance, and (b) is the necessary time for the biome to recover 95% of pre-MHW-event biomass. Horizontal lines correspond to the simulated MHW's category in each biome. The left-hand *y*-axis corresponds to the intensity of the MHW in degrees Celsius, while the right-hand *y*-axis corresponds to the category of MHW. The unit of MHW duration on the *x*-axis is months.

were perturbed for the longer time, around tenfold longer than low TLs, with a small average biomass decrease. Given the previous results, it can be assumed that high TLs are the most impacted in the food web.

The responses of the different compartments of food webs across tropical and polar biomes (Figure 6a,c) were analogous to those of the temperate biome, albeit with varying magnitudes. The polar biome, for instance, displayed an approximately twofold smaller average biomass decrease compared with the temperate biome, while perturbation duration was around twice that observed in the temperate trophic compartments.

The average biomass loss of high TLs in response to MHWs was substantial in temperate and tropical environments, while the response was more moderate in polar environments (Figure 7a). For the same MHWs characteristics, high TLs could suffer an average loss of 23% and 25% of their original biomass in temperate and tropical biomes, respectively. However, this biomass loss is related to the time necessary for recovery. In the polar environment, this recovery time was much longer (108 months) compared with temperate (85 months) and tropical (48 months) biomes under an $\alpha = 0.5$ scenario (Figure 7b).

4 | DISCUSSION

4.1 | Various responses to MHWs according to biomes

Biomes respond differently to MHWs events occurring during the year's warmest month, with the overall biome functioning perturbation depending on MHWs intensities and durations. In the tropics, marine species show a narrower thermal safety margin than in poleward biomes (Nilsson et al., 2009; Pörtner & Farrell, 2008; Pörtner & Peck, 2010; Shultz et al., 2016). Therefore, they tend to live closer to their upper thermal limits than temperate and polar species (Begon & Townsend, 2021; Pinsky et al., 2019; Vinagre et al., 2016). Thus, a higher percentage of species undergo thermal stress in the tropical biome compared with the temperate and the polar biome when a low-intensity MHW occurs, and different ecological consequences are

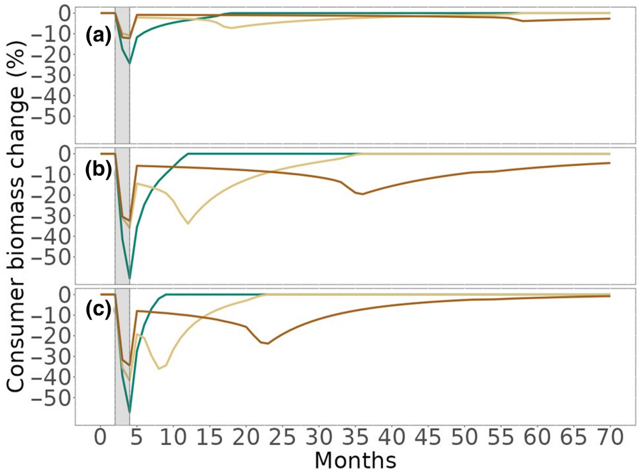

FIGURE 6 Instantaneous biomass changes per trophic group in response to a Category 3 and 1.5 month duration MHW in temperate biome with $\alpha = 0.5$: With low TLs biomass change, medium TL biomass change and high TL biomass change, represented in green, light brown and dark brown respectively. Polar, temperate and tropical biomes correspond to the (a), (b) and (c) panels, respectively.

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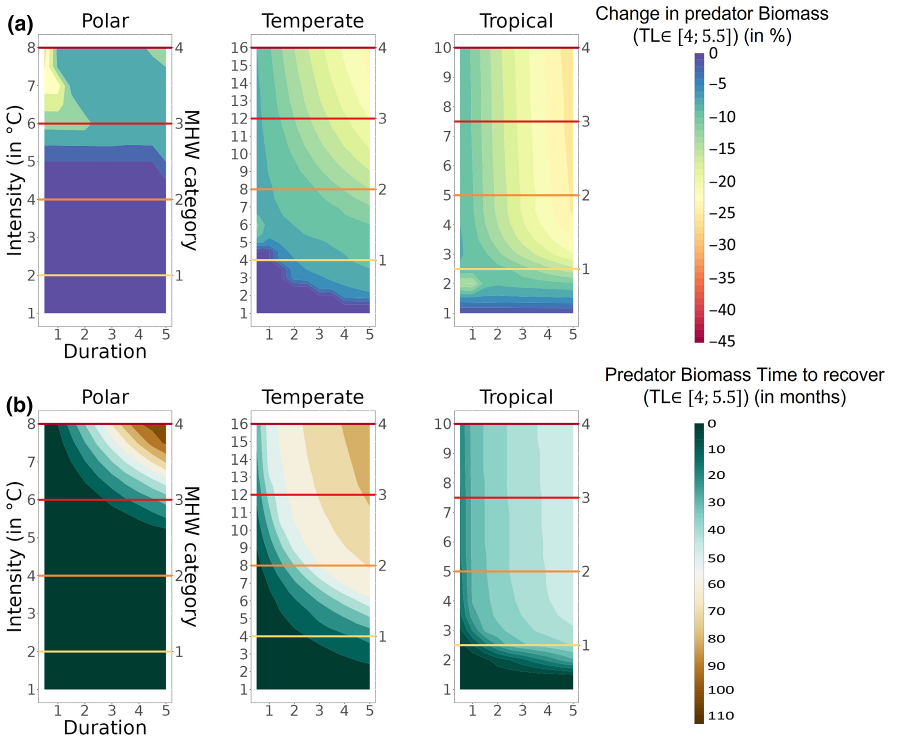

FIGURE 7 High TLs Average biomass loss and time to recover associated with MHWs characteristics with $\alpha = 0.5$: (a) corresponds to the average predator consumer biomass loss over the period of disturbance, and (b) is the necessary time for predator consumer biomass of each biome to recover 95% of pre-MHW-event biomass. Horizontal lines correspond to MHWs categories in each biome. The left-hand *y*-axis corresponds to the intensity of the MHWs in degrees Celsius, while the right-hand *y*-axis corresponds to the category of MHWs. The unit of MHWs duration on the *x*-axis is months.

expected. For instance, the associated biomass loss to a category 2 MHW is always greater in the tropical biome compared to the temperate and polar biome. However, looking jointly at indicators of ecosystem response to an MHW, the temperate biome appears as the ocean areas which endorse the greater perturbation/consequences under $\alpha \leq 0.5$. Conversely, under $\alpha \geq 0.75$ scenario, the tropical biome stands out as the most impacted area.

The polar biome is characterised by long-lived organisms with a limited turnover (i.e., low kinetics, Gascuel et al., 2008) and by a large efficiency in transferring energy along the food web (du Pontavice et al., 2020; Eddy et al., 2021). In such areas, response to an MHW is mainly driven by the intensity of extreme events. Although the magnitude of the MHW-induced instantaneous biomass losses is limited, the recovery time is long (up to 9 years), particularly for high TLs (Smith et al., 2023). In the temperate biome, species have a higher metabolic energy requirement and lower transfer efficiency, which is associated with faster biomass transfer (du Pontavice et al., 2020). The temperate biome is more sensitive to MHWs than the polar biome, with a loss of total consumer biomass of up to 20%, but with a faster recovery time in line with those highlighted by Babcock et al. (2019) and Caputi et al. (2019). In the tropical biome, species have the greater energy request (Smith et al., 2023) and the lowest transfer efficiency associated with fast turnover (du Pontavice et al., 2020). From the less intense category MHW, more than 70% of tropical species are already thermally affected when a Category 1 MHW occurs. Consequently, all MHWs, whatever their intensities, will affect the tropical biome, but with an impact predominantly contingent upon their duration. Notably, an escalation in intensity/magnitude or frequency increases may result in the thermal impact affecting 100% of species, potentially leading to localised depletion of the entire ecosystem. In this biome, biomass loss is expected to be up to 40% associated with $\alpha = 0.5$, which echoes the results from Artana et al. (2024). Furthermore, the stronger biomass decrease across the entire food web and especially low TLs can be related to mass coral bleaching and mass mortality events (Genin et al., 2020; Smith et al., 2023).

The simple occurrence of an MHW, considering all organisms are well adapted to their environmental conditions (in line with $\alpha = 0$ scenario), led to changes in biome structure and functioning (Arimitsu et al., 2021; Harris et al., 2018; Wernberg et al., 2016). In relation to these previous works, we highlight more rapid and less efficient trophic transfers associated with significant losses in the total biomass of consumers, particularly in temperate and tropical biomes. Furthermore, species' resistance capacity associated with α values appears to be a major factor driving the magnitude of biome responses to MHWs (Appendix S4 and S5). According to the resistance scenarios (with $\alpha = 0$ meaning no mortality due to thermal stress and $\alpha = 1$ meaning all species die when they are under thermal stress), major changes in ecosystem structure are estimated in all marine ecosystems: biomass decrease, trophic structure disruption (Appendix S7) and a long time to recover which align with MHWs observed impacts (Babcock et al., 2019; Smale et al., 2019; Smith et al., 2023).

4.2 | Limited resistance capacity to global warming and extreme temperature

Species resistance capacity in our study was considered at the biome scale, although the model processes take place at finer scales. When

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marine ectotherms are exposed to temperatures close to their thermal limits during MHWs, they generally have different physiological and behavioural responses. Examples of heat shock responses include increases in metabolic demand, antioxidative defence, metabolic depression, rising respiratory stress, cellular stress, suppressed immune responses and changing movement rates (Alfonso et al., 2021; Smith et al., 2023; Somero, 2020). These MHWs-induced physiological and behavioural effects would then affect trophodynamic processes, such as increasing mortality and changes in trophic transfer. Some species have demonstrated some capacity to acclimatise to rapid changes in temperature and reduce the acute physiological and behavioural responses under MHWs (Johansen et al., 2021). However, not all organisms have the capabilities to develop these resistance processes. In the case of the year's warmest month MHWs, critical temperatures are generally exceeded, or durations are longer than the period during which resistance processes can be implemented, leaving individuals no other solution than moving to more favourable environmental conditions (if able to) or die (Habary et al., 2017).

At the scale of the biome and food web, we found a significant difference (ANOVA; *p*-value <.05) in species' response to MHWs occurrence according to their TL in line with (Hu et al., 2022). According to TL, the LT_{50}—representing the MHW category where half of the organisms within the TL experience thermal stress—is typically attained approximately one MHW category earlier (i.e., 1.8, 4 and 2.7°C ahead for polar, temperate and tropical biomes, respectively) for individuals of TL <2.5. This trend is particularly notable in ocean temperatures ranging from 5 to 20°C (Appendix Figure S3b). However, in ocean water colder than 5°C or warmer than 20°C, the entire food web responds uniformly to the occurrence of MHWs. This could indicate a good harmonisation of thermal tolerance within ecological assemblages and can explain abrupt changes in the functioning and structure of marine ecosystems in response to MHWs occurrence, as indicated by Trisos et al. (2020). Thus, we have a level of confidence greater than zero in our resistance scenarios, reflecting the greater or lesser sensitivity of biomes to MHW.

Although it may seem unrealistic to create scenarios where only 25% of fewer species have resistance capabilities, this could become plausible in the near future due to the increasing frequency, intensity and duration of marine heatwaves in recent decades (Frölicher et al., 2018; Guo et al., 2022; Oliver et al., 2019; Qiu et al., 2021). Species tend to preserve their ecological niche by retaining the ecological traits and spatial range they have duly acquired; thus, the evolutionary success of species depends on following biomes with similar environmental characteristics rather than on actual adaptive capacity (Crisp et al., 2009; Habary et al., 2017). The ability of species to adapt and resist these short-term (days, weeks and months) and long-term (years, decades and centuries) thermal stresses will determine the survivors of this century and appears to be a crucial issue for the future of marine ecosystems (Johansen et al., 2021). Adapting species is a slow process; thus, the preferred pathway is species acclimatisation (Boyd et al., 2016), but this acclimatisation appears to be limited and unavailable to all organisms. By 2100, under the SSP5_8.5 scenario, it is estimated that sea temperature will increase by about 3.5°C (Kwiatkowski et al., 2020), in association with an increase in the intensity, duration and frequency of MHWs (Oliver et al., 2019; Plecha & Soares, 2020). As such, the percentage of adapted species with resistance capacity is likely to fall sharply, and we may end up with 25% or fewer species resistant to MHWs ($\alpha < 0.25$).

4.3 | MHWs alter the structure and affect the stability of marine ecosystems

All marine biomes have experienced an average of two MHWs events per year over the past 20 years (Oliver et al., 2018; Plecha & Soares, 2020). Therefore, even in the most optimistic case of our simulations, where 100% of species have resistance capacities ($\alpha = 0$), biomes need more time to recover than the return frequency of MHWs events. This raises the question of the resilience of ecosystems. Successive MHWs will affect ecosystems in reconstructions, which are already disrupted, leading to possible irreversible changes in ecosystems' structure (Smale et al., 2019; Smith et al., 2023). A single MHW could lead to a decrease of 0.05 or even up to 0.1 of the ecosystem's mean TL (Appendix S7), which substantially simplifies biomes' food webs with a decrease in large individuals that are usually predators (Pauly et al., 2002) and usually play a fundamental and or regulation role in the ecosystem (Terborgh & Estes, 2013). Our results highlight potential unequal MHW consequences according to food web positioning. High TLs would be more impacted than others, with perturbation time tenfold those of lower TLs concurrent with MHWs observations (Arimitsu et al., 2021; Cavole et al., 2016; Suryan et al., 2021). Critical disruption of ecological assemblage is already occurring and could continue to be observed (Boyd et al., 2016; Portner et al., 2014; Trisos et al., 2020). These whole ecological assemblage disruptions could lead to structural changes such as tropicalisation of ecosystems and changes in species composition (Smale et al., 2019; Wernberg et al., 2013, 2016). Given the position in their thermal niche and the observed consequences of some past MHWs (Pearce et al., 2011; Smale et al., 2019; Wernberg et al., 2013), the tropical biome seems to be more sensitive to MHWs and could undergo deep degradations and/or collapse of most food web. For instance, MHWs occurring since 2016 over the Great Barrier Reef have led to major episodes of coral bleaching (Pratchett et al., 2021). In 2016, an MHW resulted in the catastrophic death of some corals, causing a significant change in ecological functioning (Hughes et al., 2018). Similarly, these changes in invertebrate communities have been associated with changes in the ichthyofauna compartment, highlighting widespread impacts at the ecosystem level (Stuart-Smith et al., 2018). Thus, biomes could be in different resistance scenarios (i.e. different α values), for example, the temperate biome with $\alpha = 0.25$ and the tropical biome with $\alpha = 0.5$, currently, and $\alpha = 0.5$ and $\alpha = 0.75$ in the future for the temperate and tropical biomes, respectively.

4.4 | Implications for managing MHWs' impacts

From our study, we have highlighted that one source of impact of MHWs on trophodynamics is through an additional biomass loss. Thus, utilising the forecasting of MHWs now available (Hartog et al., 2023; Jacox et al., 2022) could help management makers guide the timing of fishery closures to reduce other sources of mortality when MHWs occur. This approach is similar to the management of some invertebrate fisheries in Australia (Caputi et al., 2019). Closing vulnerable fisheries during MHWs, particularly those characterised by low population abundance, species playing a pivotal or those classified as 'endangered species' by IUCN role within ecosystems, would alleviate ecosystems from undue anthropogenic pressure. Similarly, MHWs forecasts could help to manage fisheries better, as has been the case with the lobster fisheries in the Gulf of Maine between 2012 and 2016 (Mills et al., 2013; Pershing et al., 2018). The 2012 MHW event resulted in drastic increases in lobsters' landings, undermining the local and larger-scale economy with a drop of up to 70% in lobster prices. From this event and with the help of forecasting MHWs, the fishery adapted its food chain (Associated Press, 2013; van Allen, 2014) and better responded to the following MHWs in 2016, limiting a drop in lobsters' prices.

Furthermore, we have identified substantial differences in the sensitivity of different biomes and food web compartments to MHWs. Therefore, from a management perspective, it is imperative to identify these sensitive systems and prioritise efforts in formulating management policies to address MHWs occurrences in the future, such as by implementing catch limits (Pershing et al., 2018) and/or targeting alternative species (Hobday, Spillman, et al., 2018).

4.5 | Uncertainties and ways of improvement

4.5.1 | MHWs' assessment methodology caveats

Our study aimed to examine the direct effect that an MHW can have on biomass flows. These direct disturbances in biomass flow are associated with a loss of energy flowing through food webs caused by species' direct mortality in response to MHWs (Gomes et al., 2024; Smith et al., 2023). We focused primarily on MHWs occurring during the year's warmest months, which are generally associated with species exceeding their thermal thresholds (Oliver et al., 2021). While we acknowledge that MHWs during other seasons can significantly impact species phenology (e.g., Ling et al., 2009), considering seasonality results in the detection of a relatively large number of MHWs, some of which may be weak and short-lived, potentially lacking ecological consequences (Oliver et al., 2021). Our approach, therefore, may be considered 'conservative', but it enables the detection of MHWs that generally substantially impact ecosystems' functioning and structure (Oliver et al., 2021). Similarly, this thermal class approach applied in this study does not account for the geographical variation of the model parameters within each thermal class. We consider that MHWs of equal latitude have the same ecological signature on ecosystems, which, while debatable, serves as an informative first approach. The next step to alleviate this constraint could be to apply this mortality model to the entire ocean and study the rates of loss specific to each ecosystem, for example, through a retrospective analysis of the impacts of MHWs on a global scale.

4.5.2 | The thermal stress-based mortality algorithm

Given the projections of climate change and associated MHWs, the study of the adaptation and resistance capacities of species to MHWs are essential to improve our projections of the future of marine ecosystems (Dahlke et al., 2020; Johansen et al., 2021; Pörtner et al., 2017). At a given location, resistance to extreme temperatures is not simply explained by whether a critical temperature value is exceeded (Pörtner et al., 2017; Pörtner & Farrell, 2008; Pörtner & Knust, 2007). Rather, it is a mismatch between the demand for oxygen and oxygen supply that restricts whole-animal tolerance to thermal extremes (Pauly, 2019; Pörtner & Knust, 2007; Pörtner et al., 2017). This capacity to withstand thermal extremes is not static and is intrinsically linked to the duration of exposure, which can also be affected by other stressors (Bigelow, 1921; Kingsolver & Woods, 2016). Furthermore, a species' capacity to resist extreme temperatures depends on many other factors, including location regarding its thermal niche (near leading /trailing range edges or mid-range) and its thermal history (Smith et al., 2023). Noteworthy, this capacity to resist extreme temperature events could depend on additional environmental stressors.

Experimental studies and literature reviews have been conducted to obtain this critical limit value (CTmax) for an important number of species (Bennette et al., 2018; Comte & Olden, 2017; Dahlke et al., 2020; Pörtner & Peck, 2010; Rezende et al., 2014). However, some elements limit the use of these values in real life (Dahlke et al., 2020; Pörtner & Peck, 2010) like (1) Methods used to determine CTmax are not necessarily the same from one species to another and thus cannot be used for comparison purposes. (2) Studies are conducted on time scales that are much shorter than the duration of MHWs and are not directly relevant at the ecosystem scale as other variables, for example, O_2 and pH, are maintained stable. (3) Methods to assess CTmax vary across experiments in their duration, time left for acclimatisation, age and number of individuals tested, or whether for experimentation, individuals are gathered from the field or grown in a laboratory under static conditions. Therefore, it does not appear easy to find these CTmax estimated values comparable.

Furthermore, these CTmax values, as discussed in the previous paragraph, depend on the exposition duration to extreme temperature. Specifically, species' CTmax decreases with time of exposure to extreme temperatures (Bertolini & Pastres, 2021; Bigelow, 1921; Kingsolver & Woods, 2016; Rezende et al., 2014; Villeneuve &

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White, 2024). Rezende et al. (2014) highlighted that marine species' CTmax could decrease by around 10 and 5°C after 12h of experiments with bivalves and fishes, respectively. Similarly, Villeneuve and White (2024) showed that CTmax could decrease by 14°C over 15 days compared with 1 min experiments based on three hypothetical species. Given that MHWs last from days to years, the CTmax values obtained from experiments may be overestimated.

We, therefore, preferred to use thermal data associated with the spatial distribution of each species from the Aqua X project (Asch et al., 2018; Reygondeau, 2019). This provides us with thermal data closer to reality, estimated homogeneously for a large set of species, including both mobile and sessile fish, crabs, cephalopods and bivalves. Noteworthy, we found no difference among taxonomic group thermal limits (in our case, 95th percentile of their thermal niche, (ANOVA, *p*-value >.05) congruent with Vinagre et al. (2019) results and indicates a good harmonisation of thermal tolerance (Trisos et al., 2020).

Acknowledging from case studies that MHWs have a negative impact on the survival of sessile or slow-moving invertebrates (Garrabou et al., 2009, 2022; Mills et al., 2013; Oliver et al., 2017; Smale et al., 2019; Sorte et al., 2010), the results of our study could underestimate the actual impact that MHWs can have at the biomass spectrum scale. For future analyses, the inclusion of additional sessile species from taxa other than those already used will improve the quality/accuracy of estimating the percentage of populations undergoing thermal stress by MHWs.

4.5.3 | Primary production and MHW relation

The two input parameters that drive the response of the EcoTroph-Dyn model are sea surface temperature and primary production. In our simulations, we decided to fix the net primary production only in order to have a better understanding of MHWs. However, associated with MHWs, as under global warming, the abrupt increase in temperature causes an increase in surface water stratification and changes in nutrient availability. At low latitudes, MHWs could be associated with a decrease in nutrients at the ocean surface and, thus, a decrease in phytoplankton growth, leading to an extreme drop in primary production (Le Grix et al., 2022). These two extreme events could have an additional or synergic negative effect on the functioning and stability of marine ecosystems with cascading impacts through the food web depending on which types of phytoplankton marine species prefer to graze on (Bindoff et al., 2019; Cavole et al., 2016; Cheung & Frölicher, 2020). There is a strong agreement in low-latitude regions that MHWs are often associated with an extreme drop in NPP (Gupta et al., 2020; Hayashida et al., 2020; Le Grix et al., 2021). However, in high-latitude regions, there is a lack of consensus between satellite observations and models regarding the impact of MHWs. Therefore, it is possible that the high latitudes ecosystem does not experience a significant reduction in net primary production during MHWs (Garrabou et al., 2022). On the contrary, it is possible that net primary production increases during MHWs at high latitudes because MHWs are often caused by radiative warming, and light energy increases phytoplankton growth (Arteaga & Rousseaux, 2023; Bouchard et al., 2017; LeBlanc et al., 2020).

The study of the relationships between extreme events (e.g., compound events) is very recent (Gruber et al., 2021; Le Grix et al., 2022), and there are still many questions to be answered about their interactions and functioning at the physical level, in particular the quantification of the decrease in NPP associated with MHWs of different intensity and occurring at different locations. Thus, it seemed extremely ambitious to address this issue at the biological level, so we chose to free ourselves from this relationship and thus fixed net primary production in our simulations.

5 | CONCLUSION

In this paper, we have proposed and implemented an approach to assess the potential detrimental effects of individual MHW on ecosystems based on their characteristics. We have identified that ecosystems are not equally sensitive to MHW's characteristics. We also showed that the tropical environment appears to be more susceptible to biomass loss and changes in ecosystem structure in response to those MHW events. Similarly, we have highlighted that the time to recovery is different over biomes and strongly dependent on the rate of trophic transfer. For example, we observed a time to recover in temperate and polar ecosystems that could be one-third and twice greater than in the tropical biome. This work is a first approach, and we recognise the need to develop studies to better understand organisms' responses to repetitive episodes of thermal stress and/or how organisms respond to compound extreme events.

AUTHOR CONTRIBUTIONS

Vianney Guibourd de Luzinais: Conceptualization; data curation; formal analysis; investigation; methodology; resources; validation; visualization; writing – original draft; writing – review and editing. **Didier Gascuel:** Conceptualization; funding acquisition; methodology; project administration; supervision; writing – review and editing. **Gabriel Reygondeau:** Conceptualization; writing – review and editing. **William W. L. Cheung:** Conceptualization; funding acquisition; methodology; project administration; supervision; writing – review and editing.

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CONFLICT OF INTEREST STATEMENT

All the authors have no conflicts of interest to declare.

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DATA AVAILABILITY STATEMENT

Daily SST observations from the NOAA _ AVHRR data are publicly available on the link https://www.ncei.noaa.gov/access/metadata/landing-page/bin/iso?id=gov.noaa.ncdc:C00680. The code for the EcoTroph_Dyn model that supports the findings of this study is openly available at https://doi.org/10.57745/NHVPCR. Species occurrence data and associated trophic levels that support the findings of this study are openly available at https://doi.org/10.57745/PI0N92.

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