

Three decades of ocean warming impacts on marine ecosystems: A review and perspective

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ABSTRACT

Ocean warming, primarily resulting from the escalating levels of greenhouse gases in the atmosphere, leads to a rise in the temperature of the Earth's oceans. These gases act as heat-trapping agents, contributing to the overall phenomenon of global warming. In order to gain a comprehensive understanding of how ocean warming impacts marine ecosystems, a thorough literature review was conducted over a span of three decades, involving 2484 initial publications. The systematic literature review screening was facilitated by utilizing Abstrackr's web-based application to efficiently select relevant abstracts, resulting in a final list of 797 publications aligned with the study's objectives. Since the advent of the industrial revolution, greenhouse gas emissions have witnessed an exponential surge, leading to a cumulative increase in atmospheric temperatures at an average rate of 0.08 °C (0.14 °F) per decade since 1880. Over the past 50 years, the ocean has emerged as a primary heat reservoir, absorbing and distributing the majority of the Earth's warming, with more than 90% of the heat gain occurring within its waters. Between 1950 and 2020, the global sea surface temperature (SST) increased by 0.11 °C (0.19 °F). The consequences of ocean warming extend significantly to the environment and climate. It induces the expansion of the ocean, alters its stratification and currents, diminishes oxygen availability, elevates sea levels, and intensifies hurricanes and storms. It also affects marine species' physiology, abundance, distribution, trophic interactions, survival, and mortality and can also cause stress and consequences for human societies that depend on impacted marine resources. Ocean warming is projected to increase from 2 to 4 and 4–8 times under climate scenarios Shared Socioeconomic Pathways 1–2.6 and Shared Socioeconomic Pathways 5–8.5, respectively, with an additional 0.6–2.0 °C added by the end of the century. We summarize its impacts and detailed negative or positive responses on marine taxonomic groups. We also provide critical information to help stakeholders, scientists, managers, and decision-makers to mitigate and adapt while improving biodiversity conservation and sustainability of marine ecosystems.

1. Introduction

Earth's climate system is a complex and highly interconnected system involving the atmosphere, ocean, land surface, snow and ice, small bodies of water, and living organisms (Le Treut et al., 2006). The Earth's climate system varies across time scales, from months to millions of years, and is driven by natural processes, including the Earth's orbital changes, solar variations, volcanic eruptions, earthquakes, and global ocean currents (Alley et al., 2007). Yet, it is regulated by the atmosphere's natural abundance of nature-produced greenhouse gases like water vapor, carbon dioxide (CO₂), methane, and nitrous oxide. These

natural gases play a fundamental role in maintaining and regulating the Earth's climate system (Houghton, 2005).

Before the industrial revolution, the atmospheric CO₂ concentration was 280 ± 10 ppm for several thousand years (Prentice et al., 2001). Since then, a dramatic increase in the atmospheric accumulation and redistribution of human activities has increased greenhouse gases emissions globally. In February 2023, the atmospheric CO₂ concentration reached 422.9 ppm (<https://www.esrl.noaa.gov/gmd/ccgg/trends/monthly.html>). This increase in greenhouse gases is mainly driven by the burning of fossil fuels but also by changes in livestock production, deforestation, and industrial processes such as cement production and

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waste management (Houghton et al., 1990; Sabine et al., 2004; Mikaloff Fletcher et al., 2006; Le Quéré et al., 2010; Abram et al., 2016; Gruber et al., 2019; Yoro and Daramola, 2020). As one of the primary pollutants resulting in the greenhouse gases inventory, CO₂ emissions are modifying the natural climate system and exacerbating anthropogenic climate change, hereafter, ACC (Pachauri and Meyer, 2014). Thus, the accumulation of CO₂ emissions trap heat in the atmosphere leading to a gradual increase in the overall Earth's temperature, referred to as global warming (Alley et al., 2007). Since 1880, the Earth's temperature has risen by an average of 0.08 °C (0.14 °F) per decade (Lindsey and Dahlman, 2021; <https://www.climate.gov/news-features/understanding-climate/climate-change-global-temperature>), with global warming projected to cause significant and faster environmental and ecosystem changes in the coming century (Weart, 2010; Cheng et al., 2021).

As the main component of the Earth's climate system, the ocean contains about 1.35 billion cubic kilometers (324 million cubic miles) of water or about 97% of all the water on Earth. It covers more than 71% of the globe's surface, having a fundamental role and the capability to exchange large amounts of heat, freshwater, and carbon with the atmosphere while providing a large capacity for heat uptake, storage, and transport (Rhein et al., 2013). In the last few centuries, while greenhouse gases emissions have continued increasing (Prentice et al., 2001), the ocean has played a central role in stabilizing the Earth's climate system under ACC conditions. As more greenhouse gases are incorporated into the atmosphere, heat accumulates, which is also absorbed by the ocean, increasing its internal temperatures and referred to as ocean warming (Bindoff et al., 2019).

To better understand the redistribution of the anthropogenic heat uptake in the oceans, it's crucial to quantify its heat balance (Hansen et al., 2005; Meyssignac et al., 2019; Von Schuckmann et al., 2020). Over the past 50 years, the ocean has absorbed ~90% of the atmospheric heat due to the increase in greenhouse gases concentrations, where the ocean's top few meters store as much heat as Earth's entire atmosphere. As a primary consequence of ACC, the ocean has warmed 0.11 °C every decade over the last 50 years. Recent studies estimate that from 1971 to 2010, the warming of the upper ocean accounted for about 63% of the total increase in the amount of stored heat in the Earth's climate system, while warming from 700 m down to the ocean floor has added about another 30% (Rhein et al., 2013). On average, the ocean surface temperature has increased by 0.88 °C from 1850 to 1900 to 2011–2020, with 0.60 °C of this warming occurring since 1980 and an estimated 0.6–2.0 °C increase before the century's end (Fox-Kemper et al., 2021).

As ocean warming continues, the ocean expands, producing sea-level rise, directly impacting the melting of glaciers and the Arctic and Antarctic sea ice and favoring conditions for extreme weather events (Fox-Kemper et al., 2021). Simultaneously, ocean warming makes warmer ocean waters more buoyant, holding less O₂ and reducing the mixing between surface O₂-rich and deep O₂-poor water masses. It also raises the O₂ demand while reducing the available amount for marine organisms to respire. Ocean warming also contributes to the O₂-depletion of ocean dead zones in coastal and open ocean areas, rendering them largely uninhabitable by marine life. As ocean temperature increases at nutrient-poor subtropical ocean gyres, iron availability constrain marine nitrogen fixation in those regions (Hutchins and Capone, 2022; Jiang et al., 2018). These ocean warming-caused changes in the ocean's physics and chemistry are triggering variations in productivity (Moore et al., 2018) and shifts in marine ecosystem composition, functionality, and biodiversity.

Ocean warming has also been accompanied by an increased frequency of discrete periods of extreme regional warming referred to as marine heatwaves (Hobday et al., 2016; Oliver et al., 2018, 2019). These anomalous temperature changes create a high risk of marine ecosystem degradation, forcing species to search for optimal temperatures and food sources while being under stress. Other species move poleward or deeper to escape and find tolerable temperatures (Chaudhary et al.,

2021; Hastings et al., 2020; Proud et al., 2017; Sorte et al., 2010). Ocean warming, in conjunction with marine heatwaves, is also producing mass bleaching and mortality of coral reefs (Donovan et al., 2021; Hughes et al., 2018), influencing the loss of crucial habitat-forming species (Wernberg et al., 2011, 2013), changes in fisheries productivity (Cheung et al., 2012), and declines in economic performance (Free et al., 2019; Poloczanska et al., 2013).

Understanding the consequences of rising emissions of greenhouse gases and the warming of marine ecosystems is a pressing issue in marine ecology (Geraldi et al., 2020). This study aims to review the negative and positive impacts of ocean warming on marine ecosystems, focusing on the major groups, such as viruses and bacteria, phytoplankton, zooplankton, invertebrates, macroalgae, coral reefs, ectotherms, fish, seabirds, and marine mammals. We also review the social, economic, and cultural impacts on societies. Finally, we explore management, conservation, and policy actions to improve marine ecosystems, species, and human societies in light of this ocean warming.

2. Review approach, criteria, and literature representation

A literature review was conducted to identify relevant ocean warming publications using the Web of Science citation database Core Collection. We searched for papers published between January 1, 1991 and December 31, 2021 with the Boolean search terms: "ocean warming" AND (ocean × OR marine) AND ("climate change" OR "climate impact*" OR "climate effect*" OR "climate alteration*" OR "climate implication*" OR "climate shift*" OR "climate extreme*" OR "global climate change" OR "global heating" OR "global warming" OR "climat × varia*" OR climatic OR anthropogenic OR anthropocene OR "human-induced" OR "human-caused" OR "climate-driven" OR "climate-induced change*" OR "climate change scenario*" OR "future climate change" OR "climate anomalies"). Grey literature and non-English publications were omitted from this review. A total of 2484 initial publications were identified for further screening with the Abstrackr (Wallace et al., 2012; Marshall and Wallace 2019; Gates et al., 2020; Giummarra et al., 2020). Abstrackr utilizes a machine learning algorithm to automate article screening and prioritize the most relevant publications. The process begins with a manual review of an initial set of articles. The algorithm learns from the user's screening decisions, identifying patterns and associations between article characteristics and their relevance to ocean warming impacts on marine ecosystems. Using this knowledge, it predicts the relevance of the remaining articles and selects the most informative ones for the user to review. Through active learning, the algorithm continually refines its predictions as more articles are screened. This iterative process, guided by the algorithm's predictions, efficiently identifies articles meeting the predefined criteria, reducing the user's workload. However, it's important for the user to exercise their judgment and validate the algorithm's suggestions. A final list of 797 relevant publications from this screening process from 216 journals was included in this review. Since 1991, an increasing trend in ocean heat content associated with ocean warming reached a maximum in 2021 (Fig. 1, red line), showing a similar trend in ocean warming scientific research, reaching a maximum in 2021 with over 100 publications (Fig. 1, blue bars). Of these 797 publications, 50% were published in nine journals (Geophysical Research Letters, Global Change Biology, Marine Ecology Progress Series, Nature Scientific Report, PLOS One, Frontiers in Marine Science, Marine Environmental Research, Marine Biology, and Coral Reefs). According to the research area criteria of Web of Science, the top three out of 37 relevant publications areas are Environmental Sciences and Ecology, Marine Biology, and Oceanography, which account for 54% of the total publications. Additionally, 55% of the publications belong to four out of 51 categories defined by the Web of Science: Marine & Freshwater Biology, Ecology, Environmental Sciences, and Oceanography. Of the 797 publications, 491 (62%) were utilized to summarize biotic components' negative and positive ocean warming impacts (Supplementary Material 1), and neutral effects

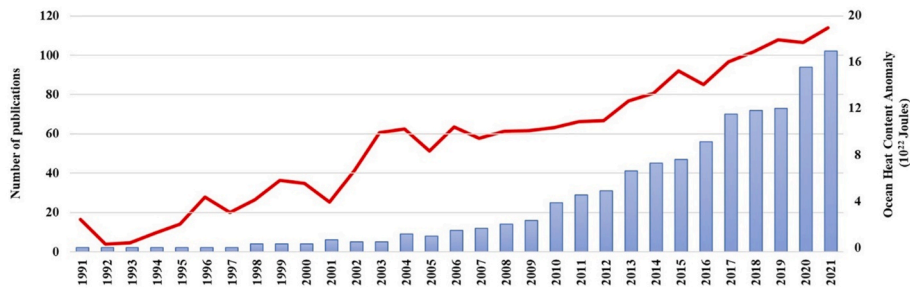


Fig. 1. Number of ocean warming-relevant publications distributed between January 1, 1991, and December 31, 2021 (blue bars, left Y-axis) versus yearly averaged global ocean heat content anomaly (10^{22} J) for the 0–700 m of the ocean (red line, right Y-axis) modified from: <https://www.climate.gov/news-features/understanding-climate/climate-change-ocean-heat-content> (refer to [Supplementary Material 2](#) for details).

mentioned in section 5 (Ocean Warming Impacts On Marine Organisms). The remaining 306 (38%) publications were utilized to summarize abiotic aspects of ocean warming. The positive and negative ocean warming impact criteria considerations are incorporated in [Supplementary Material 2](#).

Moreover, summaries for the ocean warming-impacts were developed across ten taxonomic groups (corals, invertebrates, algae, phytoplankton, viruses and bacteria, zooplankton, fish, ectotherms, seabirds, and marine mammals) for the following 13 criteria ([Fig. 2](#)): i) Abundance (size and biomass), ii) Behavior (activity, performance, feeding, and niche breadth), iii) Biodiversity (species alteration and composition), iv) Distribution (shift and contraction), v) Ecosystem (energy flow, process, functionality, service, habitat, and trophic levels), vi) Infection (pathogens, disease, malformation, necrosis, toxins), vii) Interaction (symbionts, host, competition, and predator-prey), viii) Life cycles (development, growth, and phenology), ix) Physiology (biochemical, metabolism, rates, and performance), x) Population (dynamic and structure), xi) Recruitment (compromise, suppression, and sustainability), xii) Reproduction (fertilization, fecundity, breeding, spawning, and maturity), and xiii) Survival (permanence, mortality, extinction). Diagrams associated with the impact criteria and for the taxonomic groups were developed to represent the ocean warming’s negative ([Figs. 3a,b](#)) and positive ([Fig. 4](#)) impacts on marine organisms.

3. From CO₂ emissions to ocean heat content and the warming of the ocean

Since the industrial revolution, anthropological activities have produced more greenhouse gases emissions than those naturally produced at the end of the last ice age 20,000 years ago. CO₂ emissions have risen exponentially from a pre-industrial level of ~278 ppm to >421 ppm by early 2023. Emissions rose slowly to about 5 billion tons per year in the mid-20th century before skyrocketing to more than 35 billion tons per year by the end of the century. This atmospheric accumulation of human-produced CO₂ has been considered the main ocean heat content driver, accounting for over ~90% of Earth’s excess thermal energy from global warming between 1971 and 2018 ([Cheng et al., 2021](#); [Von Schuckmann et al., 2020](#)). Since the 1950s, the top 2000 m of the global ocean has significantly warmed ([Cheng et al., 2022](#); [Johnson and Lumpkin, 2021](#); [Lyu et al., 2021](#)).

Under the ACC effects, the atmospheric accumulation of greenhouse gases emissions directly increases the Earth’s climate system heat intake ([Stocker et al., 2013](#)). Over the period 1971–2018 (2010–2018), the majority of heat gain is reported for the global ocean with 89% (90%), with 52% for both periods in the upper 700 m depth, 28% (30%) for the 700–2000 m depth layer and 9% (8%) below 2000 m depth ([Von Schuckmann et al., 2020](#); [Johnson and Lumpkin, 2021](#)). The Earth’s

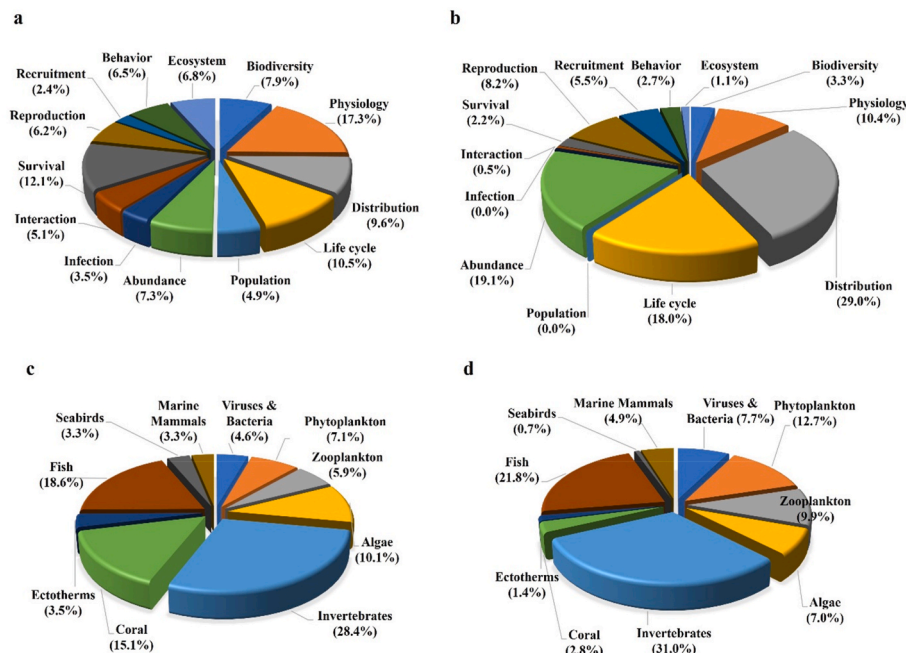


Fig. 2. Proportion of literature reviewed for negative and positive impacts on the 13 criteria (a and b, respectively) and the ten taxonomic groups (c and d, respectively). In each subfigure, multiple articles can be included (refer to [Supplementary Material 1](#) for details).

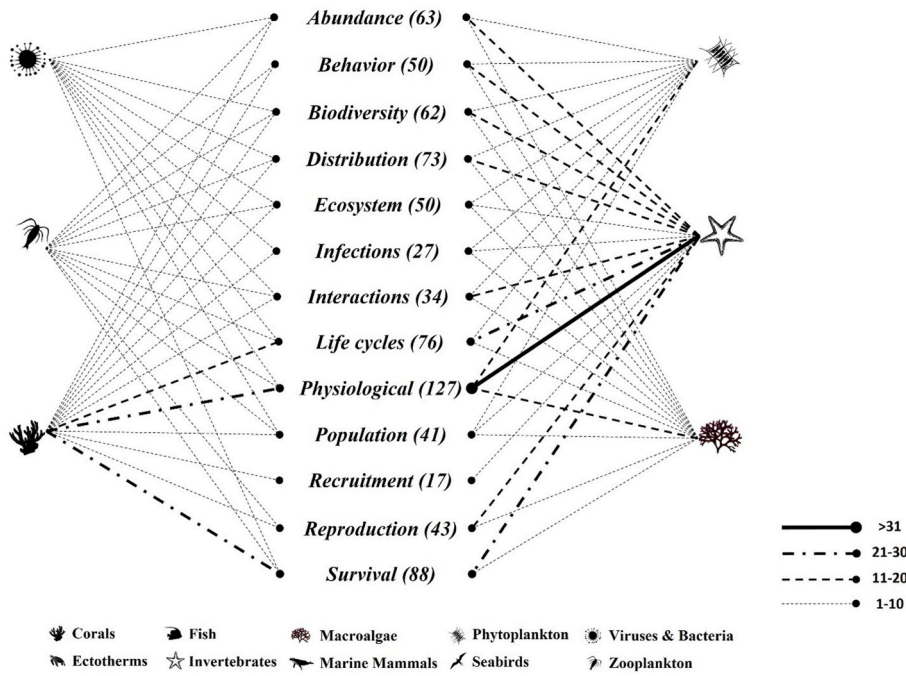


Fig. 3a. Diagram of the number of publications ($n = 421$) referring to negative impacts on six taxonomic groups (corals, invertebrates, macroalgae, phytoplankton, viruses and bacteria, and zooplankton) for 13 criteria (abundance, behavior, biodiversity, distribution, ecosystem, infections, interactions, life cycles, physiological, population, recruitment, reproduction, and survival). The sum of publications ($n = 751$, in parenthesis) relates to the number of studies with more than one criterion per taxonomic group (refer to [Supplementary Material 4](#) for details).

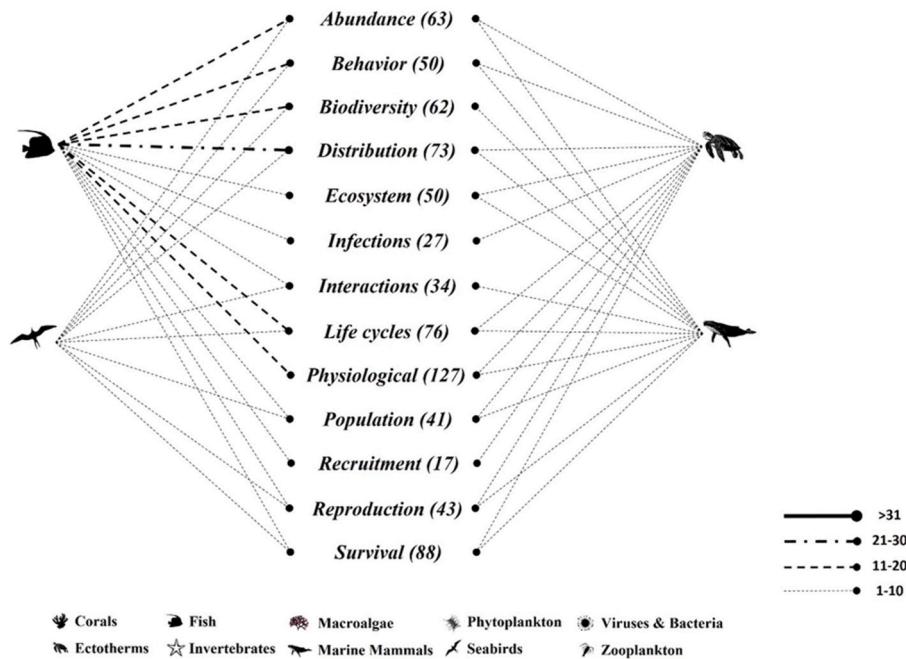


Fig. 3b. Diagram of the number of publications ($n = 421$) referring to negative impacts on four taxonomic groups (fish, ectotherms, seabirds, and marine mammals) for 13 criteria (abundance, behavior, biodiversity, distribution, ecosystem, infections, interactions, life cycles, physiological, population, recruitment, reproduction, and survival). The sum of publications ($n = 751$, in parenthesis) relates to the number of studies with more than one criterion per taxonomic group (refer to [Supplementary Material 4](#) for details).

energy imbalance serves as a fundamental metric to allow the scientific community to assess how well the world responds to the task of bringing climate change under control. This increase in heat intake has been driving ocean and atmospheric warming, with more than 90% of the heat estimated to be stored in the ocean (Strass et al., 2020). Due to its large heat capacity, the ocean dominates the global energy budget for warming, followed by land (6%), melted grounded and floating ice (4%), and the warming of the atmosphere (1%) (Von Schuckmann et al., 2020). Ocean warming is an excellent indicator of how much global warming there is. An increase in ocean warming can also drive ocean heat waves and contribute to extreme weather events (e.g. hurricanes and local storms), disrupt marine ecosystems (e.g. coral bleaching,

productivity), and have significant impacts on ocean-dependent societies (Bindoff et al., 2019; Smith et al., 2021). Sustained warming can also speed up the melting of ocean-terminating glaciers and ice sheets, contributing to the expansion of the ocean and rising sea levels.

On average, between 1993 and 2020, the rate of ocean heat gain was higher in the upper 700 m ($0.37\text{--}0.41\text{ W m}^{-2}$) than in depths of 700–2000 m ($0.15\text{--}0.31\text{ W m}^{-2}$). However, the estimated increase in heat gain from depths between 2000 and 6000 m from June 1992 to July 2011 was much lower, 0.06 W m^{-2} (Lindsey and Dahlman 2021). Additionally, from 1958 to 2019, the Southern and Atlantic Oceans had the highest heat content, accounting for 36% and 33% of the global ocean heat content, respectively, while the Pacific and Indian Oceans

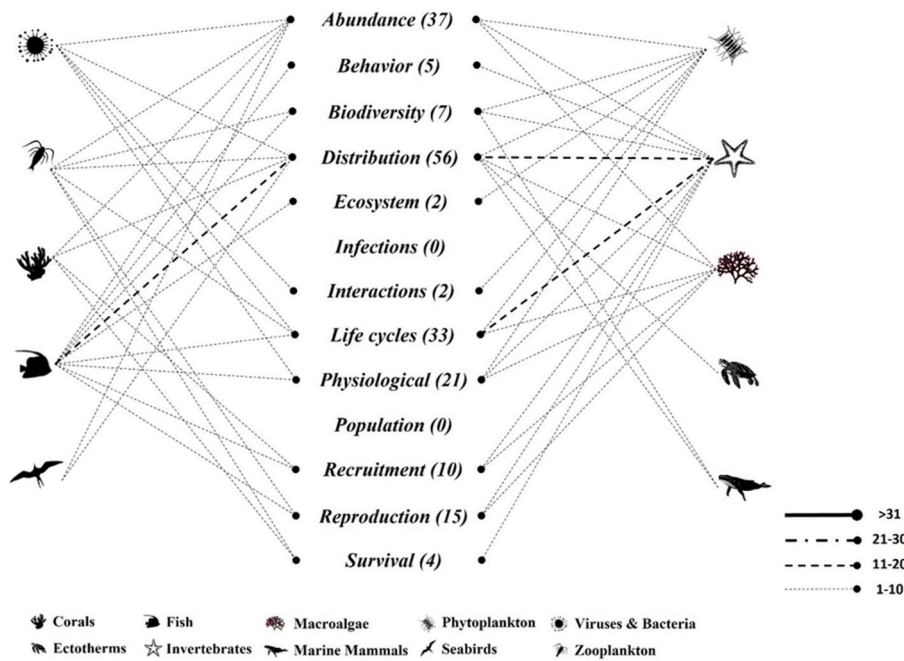


Fig. 4. Diagram of the number of publications ($n = 133$) referring to positive impacts on ten taxonomic groups (corals, invertebrates, macroalgae, phytoplankton, viruses and bacteria, zooplankton, fish, ectotherms, seabirds, and marine mammals) for 13 criteria (abundance, behavior, biodiversity, distribution, ecosystem, infections, interactions, life cycles, physiological, population, recruitment, reproduction, and survival). The sum of publications ($n = 192$, in parenthesis) relates to the number of studies with more than one criterion per taxonomic group (refer to Supplementary Material 5 for details).

accounted for 20% and 9%, respectively. The Southern Ocean, Atlantic Ocean, and Mediterranean Sea showed intense warming mainly associated with changes in ocean circulations (Cheng et al., 2022).

In 2021 and 2022, the world’s oceans recorded their highest heat content since the 1950s, with four basins reporting their highest levels. The “salty gets saltier—fresh gets fresher” pattern is also becoming more pronounced, indicating continued amplification of the global hydrological cycle (Cheng et al., 2023). Ocean depths of around 700 m may warm by an additional 0.2 °C in the next 50 years, continuing to absorb most of the excess heat. These findings significantly affect the Earth’s climate system (Cheng et al., 2022; Fox-Kemper et al., 2021; Salawitch et al., 2017). By 2100, projected warming in the top 2000 m is 2–6 times that observed so far, ranging from low to high-emission scenarios, where the Pacific Ocean is projected to be the most significant heat reservoir owing to its size. Still, area-averaged projected warming remains strongest in the Atlantic and Southern Ocean (Cheng et al., 2022).

From 1950 to 2016, the Indian, Atlantic, and Pacific Ocean basins have warmed at rates of 0.11 °C, 0.07 °C, and 0.05 °C per decade, respectively, with the most significant changes occurring at high latitudes. In 2020, the global average SST was 0.39 °C above the 1981–2010 average, making it the third-warmest year on record after 2016 and 2019. This trend is consistent with El Niño and La Niña years being anomalously warm and cold, respectively, relative to an overall warming trend of 0.10 ± 0.01 °C per decade from 1950 to 2020 (Fox-Kemper et al., 2021).

Ocean warming also impacts ocean stratification as the ocean absorbs heat from the atmosphere, and the surface layer of the ocean warms and becomes less dense. This can increase stratification, as the warm surface layer is less likely to mix with the colder, denser water below. Changes in ocean stratification due to warming have significant impacts on marine ecosystems, as well as on weather and climate patterns. For example, it can affect the distribution of nutrients and dissolved gases, impacting the growth of marine organisms and the ocean’s chemistry. This increase in the upper ocean water column stratification decreases the vertical mixing or overturning of the surface waters, reducing the supply of nutrients to the euphotic zone and the primary productivity (Lozier et al., 2011). The global upper-ocean stratification continued increasing and was among the top seven in 2022 (Cheng et al., 2023). As the SST rises at midlatitudes, the concurrent ocean record

shows that stratification is not unequivocally increasing or mixed-layer depth shoaling (Sallée et al., 2021; Somavilla et al., 2017; Xia et al., 2021). Under these ocean conditions, ocean warming produces a more stable water column which, in turn, can inhibit primary productivity for a significant fraction of the global tropics and subtropics ocean. Furthermore, under a less stratified ocean, ocean warming has significant implications for acoustic transmissions and sound speed (Affatati et al., 2022; Lynch et al., 2018). Some consequences can profoundly affect marine mammals’ communication, feeding, predator avoidance, and navigation (NRC, 2003).

Estimations on how the speed and direction of ocean warming are occurring on the ocean surface and at depths can help explain its impacts on marine ecosystems and species biodiversity. These ocean warming climate velocity estimations can be obtained by following changes in isotherms (e.g. lines of equal temperature). Since 1960, the median climate velocity in the surface ocean has been 21.7 km per decade, with higher values in the Arctic/sub-Arctic and within 15° of the Equator (Burrows et al., 2011). Over the past 50 years, ocean climate velocities have been slower in the mesopelagic (200–1000 m) than in the epipelagic (0–200 m) layers and faster in the bathypelagic (1000–4000 m) and abyssopelagic (>4000 m) layers (Brito-Morales et al., 2020). These differences suggest that deep-ocean species could be exposed similarly to warming effects as surface species. Projected ocean climate velocities for the 2050–2100 period show faster velocities at all depth layers, except at the surface under the most aggressive greenhouse gases mitigation pathway, RCP2.6 (Brito-Morales et al., 2020).

Another ACC disturbance concurrent to the long-term persistent ocean warming is the localized anomalously high temperatures or marine heatwaves. These can extend for millions of square kilometers, persist for weeks to months or even years, and occur from surface to subsurface levels (Hobday et al., 2016, 2018; Oliver et al., 2018, 2019, 2021; Holbrook et al., 2020). ACC is causing an increase in the frequency, intensity, and duration of marine heatwaves and associated impacts over recent decades (Frölicher et al., 2018; Laufkötter et al., 2020; Wernberg, 2021). These marine heatwave events have occurred across all ocean basins and can substantially impact species, ecosystems, and services (Hobday et al., 2016; Oliver et al., 2021; Smale et al., 2019). Overlaying the ocean warming trend, the presence and impact of marine heatwaves can alter the structure of marine ecosystems producing

disturbances that can substantially affect the global distribution and ecophysiological performance of multiple species. Starting at the base of the food chain, they can reduce the growth and survival of phytoplankton and zooplankton and higher trophic levels. Under the impact of ocean warming and marine heatwaves, a latitudinal gradient in species richness with more species in the tropics and richness declining with latitude will continue under ACC, as a decrease in marine species richness at the equator suggest some species' survival is already impacted by the warming of the ocean (Chaudhary et al., 2021).

Ocean warming and other ACC disturbances are estimated to continue to impact marine ecosystems until the goal of climate stabilization is reached. The equilibrium of Earth's energy imbalance has been the goal of the United Nations Framework Convention on Climate Change (UNFCCC) since 1992 and the United Nations Climate Change Conference of the Parties (COP). A key task for the COP is to review the national communications and emission inventories submitted by the Parties. Based on this information, the COP assesses the effects of the measures taken by the Parties and the progress made in achieving the ultimate objective of the convention. Adopted in 2015, an international treaty on climate change, the Paris Agreement, has been discussed yearly at COP events.

In June of 2022, an Ocean and Climate Change Dialogue report laid out ten key messages for governments to consider in the lead-up to the 2022 November COP27. These key messages were: (1) We must protect our ocean AND value its potential as a place for sustainable climate solutions and action; (2) Ocean-based measures offer significant mitigation (cutting greenhouse gases emissions) and adaptation (building resilience to climate change) options; (3) The ocean offers a space for integrated solutions that can be reflected in national climate policies and strategies; (4) Marine technology and marine and coastal nature-based solutions should be integrated to ensure that action is more robust, comprehensive and cost-effective than when using either solution alone; (5) We must use, improve and integrate the latest available ocean science and other knowledge systems; (6) A whole of society approach is needed for ocean-climate action, including to address governance aspects; (7) Funding for ocean-climate action needs to increase and access to funding must be supported; (8) Strengthened finance and other support, including capacity building, must embrace complexity to provide innovative and multidisciplinary solutions; (9) A framework for collaborative efforts across UN Processes would increase institutional support for ocean-climate action; (10) Future ocean and climate change dialogues should focus on distinct topics to deep-dive into specific solutions that strategically support and strengthen ocean-climate action at national and international level and under the UNFCCC process.

Adding to these Ocean and Climate Change Dialogue report messages, the Paris Agreement has set a target to restrict the global average temperature rise to a maximum of 2 °C above pre-industrial levels, with an additional goal to limit it to 1.5 °C. This objective necessitates bringing the Earth's energy imbalance to zero and restoring its system to a quasi-equilibrium state. According to a study with more than 30 researchers from scientific institutions around the world, bringing Earth back towards energy balance would require reducing the amount of CO₂ in the atmosphere from the current levels to approximately 353 ppm to increase heat radiation to space by 0.87 W m⁻² (Von Schuckmann et al., 2020).

4. Ocean warming local to regional impacts

Ocean warming has significant and widespread impacts on the environment, including melting glaciers and ice sheets, resulting in sea-level rise, coastal flooding, erosion, and an increased risk of severe storms (Wang and Lee, 2008; Ades et al., 2019). It affects the physical and chemical conditions of the ocean, altering marine ecosystems and contributing to modifications in biodiversity. Ocean warming also disrupts the local ecological balance by facilitating the expansion of warm-water species and altering ocean currents that regulate the Earth's

climate (Zhang and Wang, 2013). Furthermore, increased absorption of CO₂ by the ocean leads to decreased pH levels, causing increasing acidity that can harm organisms. These changes severely impact the local marine ecosystems, fisheries, and other marine resources, with implications for the broader economy and society. Therefore, it is critical to address and mitigate the local impacts of ocean warming for the long-term sustainability of marine ecosystems and human societies. A thorough analysis of individual and collective disruptions at the local and regional levels is necessary to fully comprehend the implications and effects of ocean warming on marine ecosystems.

4.1. Northern hemisphere

On land, global warming is producing the thawing of Arctic permafrost, shifting some areas from being carbon sinks to carbon sources. The Arctic Ocean, the perception over the last 60 years, has changed from a hostile, sluggish, steady, ice-covered environment with little global impact to a rapid and increasingly changing ocean under ACC conditions (Johnson et al., 2011; Li et al., 2022; Münchow et al., 2011; Polyakov et al., 2010). The Arctic sea-ice summer extent has decreased by nearly 50% over the past decades following the Arctic Ocean regime shift from multi-years of extensive ice cover to mainly seasonal thinner ice cover (Comiso, 2012). This dramatic sea-ice loss is one of the northern hemisphere's most conspicuous signs of warming (Higgins and Cassano, 2009; Parkinson and Comiso, 2013). Through observations and multi-model climate projections, it has been identified that the Arctic Ocean has been increasingly warming nearly four times faster than global warming, a phenomenon known as 'Arctic Amplification' (Shu et al., 2022). Arctic variations include ice retreat's early season enhancement (Steele and Dickinson, 2016), and changes in its energy budget drive this new view of the Arctic Ocean. The warming of the upper ocean in the Arctic contributes to sea-ice loss (Ricker et al., 2021; Shu et al., 2018) and changes in ocean circulation (Lozier et al., 2019; Shu et al., 2021).

The Arctic is becoming one of Earth's regions most susceptible to climate change (Burgard and Notz, 2017; Cheng et al., 2022; Rantanen et al., 2022). These ACC-produced ecosystem changes also increase the arrival of species from warmer areas into the Arctic Ocean, while the local highly vulnerable sea-ice-dependent and low capacity to adapt species decline. All these climate impacts also risk the Arctic indigenous and local communities' livelihoods, health, cultural identities, and heritage sites (Pörtner et al., 2022).

In the last decades, the increasing influence of Atlantic water has been extending northward into the Arctic Ocean, referred to as the 'Atlantification' of the Arctic. As a result, the Arctic Ocean is becoming warmer and saltier, and sea-ice cover is disappearing in the Barents Sea and the Fram Strait. This Atlantification has broad environmental and socioeconomic impacts in the region due to the transport of heat by ocean currents and heat exchanges between the atmosphere and the ocean with implications for future Arctic ACC (Asbjørnsen et al., 2020). It has also been estimated that the upper 2000 m Arctic Ocean warms 2.3 times the global mean rate within this depth range averaged over the 21st century in a global climate model (Shu et al., 2022). While along the Canadian region, ocean warming is also producing changes in ice cover, freshening, sea-ice melting, increasing coastal floods, and accelerating coastal erosion (Costa et al., 2022; Wang et al., 2022). Off Nova Scotia, Canada, the past decade's impacts of ocean warming are producing a catastrophic phase shift from luxuriant kelp beds (biomass has declined by 85–99%) over to rocky reefs dominated by opportunistic turf-forming and invasive algae, presenting a troubling example of the instability of marine systems (Filbee-Dexter et al., 2016).

The northeast Atlantic Ocean has warmed significantly since the 1980s, causing important kelp species to move to different areas due to changes in temperature (Smale et al., 2019). This warming can be traced back to a warming trend that began in the Labrador Sea in the 1960s (Clement et al., 2023; Lazier, 1988; Yashayaev, 2007). Ice loss from the Greenland ice sheet is one of the largest sources of recent sea-level rise

due to atmospheric and ocean temperature trends, leading to irreversible mass loss due to the surface mass balance–elevation feedback (Pattyn et al., 2018). Ocean temperature in several Greenland fjords suggests that ocean warming can cause significant changes in the outlet glaciers (Johannessen et al., 2005). Northern Barents Sea may transition from a cold and stratified Arctic to a warm and well-mixed Atlantic-dominated climate regime with unknown consequences for the Barents Sea ecosystem and its species (Lind et al., 2018). In the Kangerlussuaq glacier in southeast Greenland, ocean warming near the surface can lead to the glacier's retreat because its failure to advance during winter months is due to a weakened proglacial mélange (Bevan et al., 2012). The melting of Greenland's ice sheet and glaciers and its subsequent release of freshwater into the ocean can significantly impact ocean conditions, including sea level rise and marine ecosystems. It can also impact the Atlantic Meridional Overturning Circulation, an important global ocean current system that helps regulate Earth's climate (Rahmstorf et al., 2015).

In California's current ecosystem, the impact of the ACC on ocean warming is leading to changes in coastal ecosystems (Bograd et al., 2022). The recruitment and abundance of abalone, sea urchins, kelp, and other epibenthic species are being affected by ocean warming, leading to unexpected ecosystem interactions between native and non-native species (Kawana et al., 2019; Sorte et al., 2013). Additionally, an anomalous warm condition called “the Blob” was detected in the Northeast Pacific marine ecosystems in October 2013, causing persistent warm-water conditions during the 2015–2016 and 2018–2019 El Niño events (Peterson et al., 2015). It resulted in widespread species shifts, unusual mortality events, and broad impacts on regional commercial fisheries (Di Lorenzo and Mantua, 2016; Michaud et al., 2022; Mogen et al., 2022; Peterson et al., 2017; Rogers et al., 2021). This warm condition reached a record-high SST of 6.2 °C above the historical average in September 2015 along the central California coast (Gentemann et al., 2017). Finally, a higher background SST is expected to enhance the impact of the ACC on the El Niño-Southern Oscillation (Wang et al., 2016) in the North Pacific, leading to greater future impacts (Jia et al., 2021).

Ocean warming also affects marine life in the Mediterranean, especially benthic fauna communities rich in endemic species (Gili et al., 2014). The southeast Mediterranean Sea is highly vulnerable to species introductions due to rapid ocean warming increases (Marbà et al., 2016); while from 1982 to 2015, the overall rate of warming for the Red Sea was 0.17 ± 0.07 °C decade⁻¹, with the northern Red Sea warming between 0.40 and 0.45 °C decade⁻¹, all exceeding the global ocean warming rate (Chaidez et al., 2017).

4.2. Southern hemisphere

In the southern hemisphere, western boundary currents transport heat poleward, creating regions of rapid ocean warming-enhanced eddy generation extensions that have implications for understanding and predicting ocean warming, marine heatwaves, and the impact on the marine ecosystem under climate change (Li et al., 2022). In southeast Asia, Indonesia hosts the greatest tropical coral reef extent within the southern portion of the Coral Triangle. It is a global hotspot for biodiversity (Bellwood and Hughes, 2001), impacted by ocean warming (De Clippele et al., 2023), with species living close to their thermal limits (Stuart-Smith et al., 2015), and that evidenced severe coral bleaching in the past years (Eakin et al., 2019; Hughes et al., 2017). The southern portion of the Coral Triangle has current warming rates of 0.09–0.12 °C per decade, and vertical isotherms are projected to deepen by ca. 30–40 m per decade with similar hotspots of vertical isothermal migrations occurring in the eastern continental margins of Australia, South America, and southern Africa (Jorda et al., 2019). Along Australia's western Pacific Ocean coast, a warming of ~1.8 °C at the site since 1931 suggests that the relative proportion of phytoplankton warm-water to cold-water species has increased (Ajani et al., 2020). In the southeastern

Pacific, ocean warming produced slight shifts in southern distribution endpoints in rocky intertidal species during the last century (Rivadeneira and Fernández, 2005), reducing toxic algal blooms are expected for some harmful algal blooms species (Vellojin et al., 2023).

Since the 1950s, one of the fastest surface warmings has occurred in the Indian Ocean and along coastal boundary currents, where accelerated and complex warming patterns are causing cascading effects on coastal ecosystems. The accelerated warming of these coastal currents is due to the strengthening of subtropical gyres, has cascading effects on coastal ecosystems, and is widely expected to tropicalize further temperate regions (Shears and Bowen, 2017). Within these regions, temperate Australia is a global hotspot for marine biodiversity. Its waters have experienced well-above global average rates of ocean warming, with SST soaring to unprecedented levels. Warming anomalies of 2–4 °C persisted for over ten weeks along >2000 km of coastline (Holland et al., 2021; Wernberg et al., 2013). Along the east coast of Australia, the coastal current has intensified and has become more variable. These patterns result in waters poleward of 32° S warming more than twice as fast as those equatorward of 32° S (Malan et al., 2021).

Unfortunately, the Antarctic, like the Arctic, is strongly impacted by ACC-produced ocean warming, with a similar story about ice melting and feedback creating accelerated warming trends. The Antarctic sea-ice variability is primarily associated with ocean-atmospheric forcing driven by anomalous conditions over the tropical regions of the Pacific and Indian Oceans. The Antarctic ice sheet is the largest reservoir of terrestrial ice and is a significant contributor to sea level rise in a warming climate. During the last decades, warming has already led to changes in the ice regime around Antarctica (Eayrs et al., 2021; Parkinson, 2019). Ice sheets in Antarctica have been affected differently in separate regions. The western Antarctic Peninsula has experienced ice loss, while the Ross Sea has seen an increase in ice sheets. Marine-terminating glaciers in the Antarctic Peninsula have retreated in response to ocean warming, while intense polar cyclones in the Weddell Sea have caused record-low sea-ice extent. In east Antarctica, the Amery ice shelf has increased, but the Totten Glacier has lost ice due to warm water intrusions into its cavities, which could lead to further mass loss in the future (Aoki et al., 2022; Pedro et al., 2016; Pelle et al., 2021; Rintoul et al., 2016; Stammerjohn et al., 2008).

Early predictions suggest Antarctica will have less extensive and thinner sea ice formation than present that may persist for shorter periods (Kacimi and Kwok, 2020), with ice sheet tipping points at or slightly above 1.5–2.0 °C leading to the collapse of major drainage basins due to ice-shelf weakening (Pattyn et al., 2018; Pattyn and Morlighem, 2020). Over the past four decades, ocean measurements in the Ross Sea reveal marked decreases in shelf water salinity and the surface salinity within the Ross Gyre. These changes have been accompanied by atmospheric and ocean warming on Ross Island at depths of ~300 m and thinning of southeast Pacific ice shelves (Jacobs et al., 2002). The ice-ocean interaction significantly impacts the temperature-salinity distribution and the water column stability and impacts further warming and changes ocean currents (Sadai et al., 2020). Through in situ samplings, it has been identified that the Weddell sea ocean warming is spreading with similar long-term temperature trends in the upper 700 m, and a mean heating rate below 2000 m that exceeds the global ocean warming by about five times (Strass et al., 2020).

As ocean warming is heating the Antarctic circumpolar deep water, it threatens the diverse and abundant macrobenthic communities thriving on the continental shelf of the Weddell Sea (Isla and Gerdes, 2019). These impacts can, directly and indirectly, affect coastal benthic organisms, primary production, and food resources for Antarctic benthic consumers (Pineda-Metz et al., 2020). During the Antarctic spring, the growth of algae under extensive areas of sea ice is a fundamental source of local primary productivity that is under the impact of ocean warming (Barr et al., 2017). Under ocean warming conditions, changes in Antarctic sea-ice coverage, seasonality, and thickness have important

consequences with cascading effects across food chains. Such changes relate to phytoplankton phenology and ice algal blooms, shifts in species composition, distribution, and abundance leading to trophic mismatches in both time and space. These changes impact ecosystem structure and function, the breeding and foraging distribution of sea ice-obligate predators such as penguins, and the incursion of sub-Antarctic and/or invasive warmer-climate marine species (Cimino et al., 2016; Clem et al., 2022; McCarthy et al., 2019).

5. Ocean warming impacts on marine organisms

Over millions of years, major global ocean conditions and changes in biodiversity occurred through Earth's paleoclimate glacial and interglacial periods (Andrews, 1998; Hewitt, 2000; Pellissier et al., 2014). However, during the last few hundred years, human-caused CO₂ emissions have produced significant environmental changes through the impacts of global warming. In the marine environment, as the ocean continues absorbing the accumulated atmospheric heat, it is causing changes on multiple scales from individual to communities (Sorte et al., 2013; Vergés et al., 2014) and cascading impacts on ecosystem function (Fraïner et al., 2017; Kortsch et al., 2015; Pinsky et al., 2020). These thermal changes can occur latitudinally and in the water column, directly or indirectly having a cascading effect on multiple aspects of marine organisms and their ecosystem's ecological processes (Beaugrand et al., 2012; Burrows et al., 2011; García Molinos et al., 2016; Hillebrand et al., 2018; Jenouvrier, 2013; Sydeman et al., 2012).

Among the most perceptible ocean warming consequences between marine taxonomic groups is the contraction or expansion of their suitable habitats (Cheung et al., 2010). Their responses to these changes vary between organisms at the base of the marine food web and primary producers (viruses, bacteria, and plankton) to high trophic levels (marine mammals and sharks). Highly adaptable and migratory species with alternatives to optimal thermal ranges may thrive under ocean warming conditions while taking advantage of new environments (e.g. tuna and jumbo squids). Contrarily, less susceptible species (e.g. narrow thermal windows) to the fast-increasing of temperatures will be more vulnerable to the impacts of ocean warming (e.g. corals and ectotherms) with the potential of extinction (Doney et al., 2012). In any case, forced favorable or adverse species' habitat shifts will create new ecological complexity resulting in the establishment of novel communities that differ from those previously existing.

A significant result of ocean warming impacts is the change in marine biodiversity resulting from species shifting poleward or extending or changing their range deeper in the water column (Perry et al., 2005). Species' habitat shifts can affect native species, including the decline and collapse of marine native biodiversity in some areas. Thus, under ocean warming conditions, species range shifts affect rates of ecosystem functioning by altering consumer-resource interactions (Gilson et al., 2021). This new chain of ecological effects can then produce profound consequences, including biogeochemical cycles, primary production, energy flow, and trophic interactions (Falkowski et al., 1998; Field et al., 1998; Occhipinti-Ambrogi 2007; Chavez et al., 2010; Gruber 2011; Beaugrand et al., 2012; Holland et al., 2021; Peng et al., 2022), and in the most extreme cases, alterations to the functioning of entire ecosystems (Jackson and Sala, 2001; Kaschner et al., 2006). That may be the case of the Mediterranean continental shelf, as ~25% of it is predicted to be subject to a total modification of endemic species assemblages (Ben Rais Lasram et al., 2010), with a ~70% species richness decrease predicted by the end of the 21st century (Albouy et al., 2014; Pachauri and Meyer, 2014).

The rapid and severe increase in ocean warming represents a significant and ongoing human-induced disruption that profoundly impacts marine species and ecosystems. The ability of species to adapt and evolve in response to this disruption is crucial for their long-term survival. Marine species exhibit different responses to ocean warming based on their life stages, physiology, and ecological traits, which can






lead to categorizing them as either neutral, winners, or losers. These categories reflect the extent of their susceptibility to ocean warming and its cascading effects on their ecological processes, ranging from individual fitness to population dynamics, community structure, and ecosystem function. This categorization of marine species helps to identify the potential impacts of ocean warming on biodiversity and ecosystem services, which can inform management and conservation strategies. While ecologically significant evolutionary changes typically occur over centuries to millennia, they are happening much faster (Pinsky et al., 2013). In response to environmental changes caused by human activity, contemporary evolution can occur on ecological time-scales of days to years in a wide diversity of ecological contexts. Throughout their life cycles, marine species can display diverse responses to ocean warming. While some species may be positively or negatively impacted, others can exhibit neutral responses to ocean warming. For instance, some species of phytoplankton (Marañón et al., 2014), invertebrates (Byrne 2012, 2013; Detree et al., 2020; Gaitán-Espitia et al., 2014; Ong et al., 2017; Pisani and Greco, 2021), corals (Levas et al., 2015), and fish (Antonucci et al., 2019; Madeira et al., 2021) are examples of marine life that exhibit neutral reactions to ocean warming at different stages of their development. The species that will cope with ACC and evolves are considered the "winner" species, but the more vulnerable species that will suffer from changes in their environment to the point of potential extinction are considered the "loser" species. In either case, the ocean warming consequences can directly or indirectly affect individual organisms to community assemblages and ecosystems (Doney et al., 2012; Hoegh-guldberg, 2010).

An example relating paleo and current climate change and winners and losers species refers to the Antarctic penguin species Gentoo, Adélie, and Chinstrap. During the Last Glacial Maximum, all three species were winners as they responded positively to post-Last Glacial Maximum warming by expanding from glacial refugia, with those breeding at higher latitudes expanding the most. This is because they needed land free of ice to nest and raise their young and ice-free access to the ocean to forage for food. Under the current ocean warming trend, Gentoo penguins are the only one of the three responding to present warming, expanding their range southwards, while the losers, Adélie and Chinstrap penguins, are experiencing a decline in the Antarctic Peninsula, the opposite of their response to post-Last Glacial Maximum warming (Lucas et al., 2014). This example also indicates that species and ecosystems' responses to ocean warming in the paleoclimate reflect what can happen during the present and projected ocean warming impacts on marine species and ecosystems.

5.1. Losers in a warming ocean

In the marine environment, indigenous species use distinct reproductive, dispersal, survival, or combination of strategies during their life history. For some of them, the relationship between ocean temperature conditions and their reproductive strategy, the distance of spreading, and their latitudinal and bathymetrical distribution are well-recognized (Chaudhary et al., 2017; Costello and Chaudhary, 2017; Hastings et al., 2020; Rabosky et al., 2018; Saedi et al., 2019; Tittensor et al., 2010). However, several native species without thermal tolerance to the intensity and spatial extent of ocean warming impacts on their breeding grounds, reproduction, dispersal, survival, or combination of their capabilities have already been identified as "losers" (Doney et al., 2012). These losers are species with populations that decline in abundance and distribution or become extinct. This is the case of some tropical fish, reef-building corals, coral reef fish, mangroves, and seagrasses species, as their richness is declining relative to the increase of ocean warming in their habitats (Chaudhary et al., 2021; Lam et al., 2016; Strona et al., 2021; Tekwa et al., 2022; Yasuhara et al., 2020). Increased local retention of some reef coral larvae and their mortality can weaken connectivity between populations and thus potentially retard recovery following severe disturbances that substantially deplete local

Table 1
 Negative impacts of Ocean Warming on marine species. See [Supplementary Material 1](#) for the full list of literature cited.

Negative Impacts	Taxonomic Group	Publications
Abundance: Size and biomass.		<p>Frainer et al. (2017), Tester (1994), Hillebrand et al. (2018), Veit et al. (1996, 1997), Holbrook et al. (2020), Andrews (1998), Sagarin et al. (1999), Hughes et al. (2017), McFarlane et al. (2000) McFarlane et al. (2000), Hyrenbach and Veit (2003), Schiel et al. (2004), Desaunay et al. (2006), Field et al. (1998), Mackas et al. (2006, 2007), Simpson et al. (2011), Whitehouse et al. (2008b), Beaugrand et al. (2012), Pörtner et al. (2022), Tanaka et al. (2012), Watson et al. (2012), Alsterberg et al. (2013), Hjermann et al. (2013), Kroeker et al. (2013), Acheampong et al. (2014), Pimentel et al. (2014), Vye et al. (2015), Greene (2016), Ben Rais Lasram et al. (2010), Cure et al. (2017), Duffy-Anderson et al. (2017), Lee et al. (2017), Li et al. (2022), Repolho et al. (2017), Swiney et al. (2017), Pratchett et al. (2014), Feng et al. (2019, 2021), Peterson et al. (2015), Ajani et al. (2020), Antonucci et al. (2019), Bedford et al. (2020), Chaudhary et al. (2021), Yeruham et al. (2020), Agrelo et al. (2021), Davis et al. (2021), Gao et al. (2021), Gilson et al. (2021).</p>
Behavior: Activity, performance, feeding, and niche breadth.		<p>Spear and Ainley (1999), McFarlane et al. (2000), Gjerdum et al. (2003), Moline et al. (2004), Le Treut et al. (2006), Mackas et al. (2007), Simpson et al. (2011), Beaugrand et al. (2012), Hoegh-guldberg (2010), McIntyre et al. (2011), Doney et al. (2012), Marshall and Wallace (2019), Strona et al. (2021), Burrows et al. (2011), Harley (2011), Kroeker et al. (2013), Poore et al. (2013, 2016), Wallace et al. (2012), Kizhakudan et al. (2014), Vergés et al. (2014), Nay et al. (2015, 2020), Furness (2016), Gallo and Levin (2016), Nasuchon et al. (2016), Pimentel et al. (2016), Ober et al. (2017), Pisani and Greco (2021), Pratchett et al. (2014), Schmidt et al. (2017), Zhang and Wang (2013), Watson et al. (2018), Comiso (2012), Rossi et al. (2019), Scott et al. (2019), Baldanzi et al. (2020), Kingsburry et al. (2020), Rodriguez et al. (2020), Suarez et al. (2020), Agostini et al. (2021), Coni et al. (2021), Gilson et al. (2021), Listiawati and Kurihara (2021), Raventos et al. (2021), Liu et al. (2021).</p>
Biodiversity: Species alteration and composition.		<p>Tester (1994), Holbrook et al. (2020), Quero (1998), Hughes et al. (2017), Jackson and Sala (2001), Stammerjohn et al. (2008), MacLeod et al. (2005), Grebmeier et al. (2006), Mackas et al. (2006), Graham et al. (2008), Whitehead et al. (2008), Beaugrand et al. (2012), Beaugrand et al. (2012), Moran et al. (2010), Byrne (2012), Kaschner et al. (2011), Oswald et al. (2011), Sorte et al. (2013), Webster et al. (2011, 2016), Wood et al. (2011), Poloczanska et al. (2016), Torstensson et al. (2012), Valdimarsson et al. (2012), Harley (2011), Seth et al. (2013), Russell et al. (2014), Jin et al. (2015), Gross (2016), Listmann et al. (2016), Vergés et al. (2014), Arandia-Gorostidi et al. (2017a), Gravili et al. (2017), Lee et al. (2017), Li et al. (2022), Stuart-Smith et al. (2015), Fowler et al. (2018), Kang et al. (2018), Marshall and Wallace (2019), Teagle and Smale (2018), Isla and Gerdes (2019), Khosravi et al. (2019), Righetti et al. (2019), Rossi et al. (2019), Conti-Jerpe et al. (2020), Copeman et al. (2020), Curtis and McClintock (2020), Frainer et al. (2017), Ramírez-Romero et al. (2020), Villarino et al. (2020), Agostini et al. (2021), Chaudhary et al. (2021), Gislason et al. (2021), Simpson et al. (2011), Vaughan et al. (2021).</p>
Distribution: Shift and contraction.		<p>Field et al. (1998), Murawski (1993), Quero (1998), Spear and Ainley (1999), McFarlane et al. (2000), Harley (2011), Hyrenbach and Veit (2003), Lemoine and Boehning-Gaese (2003), Bush et al. (2004), Gentemann et al. (2017), MacLeod et al. (2005), Rivadeneira and Fernandez (2005), Rogers et al. (2021), Simpson et al. (2011), Rowe et al. (2008), Whitehouse et al. (2008a), Beaugrand et al. (2012), Beaugrand et al. (2012), Yuan et al. (2009), Mantzouni and MacKenzie (2010), Steele and Dickinson (2016), Johnson et al. (2011), Oswald et al. (2011), Tanaka et al. (2012), Valdimarsson et al. (2012), Harley (2011), Alemu and Clement (2014), Potts et al. (2014), Russell et al. (2014), Tiedemann et al. (2014, 2017), Zuo et al. (2014), Leising et al. (2015), Rantanen et al. (2022), Schoeman et al. (2015), Zimmerman et al. (2015), Alabia et al. (2016), Bruge et al. (2016), Butzin and Portner (2016), Gallo and Levin (2016), McCarthy et al. (2019), Ab Lah et al. (2017), Gravili et al. (2017), Li et al. (2022, 2018), Monilor-Hurtado et al. (2017), Ohshimo et al. (2017), Byrne (2012), Marshall and Wallace (2019), Yu and Chen (2018), Diogou et al. (2019), Parkinson and Comiso (2013), Slesinger et al. (2019), Smith et al. (2021), Wernberg et al. (2011), Butler et al. (2020), Frainer et al. (2017), Murphy (2020), Nay et al. (2020), Ben Rais Lasram et al. (2010), Chaidez et al. (2017), Davis et al. (2021), Post et al. (2021), Sabine et al. (2004), Simpson et al. (2011), Thatje et al. (2021), Xu et al. (2021).</p>
Ecosystem: Energy flow, process, functionality, service, habitat, and trophic levels.		<p>Murawski (1993), Andrews (1998), Jackson and Sala (2001), Schiel et al. (2004), Graham et al. (2008), Beaugrand et al. (2012), Keller et al. (2009), Steele and Dickinson (2016), Kaschner et al. (2011), Alsterberg et al. (2013), Collins et al. (2013), Kroeker et al. (2013), Alemu and Clement (2014), Williams et al. (2014), Jin et al. (2015), Manzello (2015), Alabia et al. (2016), Gross (2016), Rosa et al. (2016), Ben Rais Lasram et al. (2010), Chavez et al. (2010), Coles et al. (2018), Fowler et al. (2018), Glynn et al. (2018), Griffiths et al. (2009), Marbà et al. (2016), Peterson et al. (2015), Shalders et al. (2018), Yu and Chen (2018), Khosravi et al. (2019), Peterson et al. (2015), Pouca et al. (2019), Scott et al. (2019), Chiswell and Sutton (2020), Frainer et al. (2017), Karnauskas (2020), López et al. (2020), Rasher et al. (2020), Razak et al. (2020), Clarke et al. (2021), Gao et al. (2021), Roth et al. (2021), Agrelo et al. (2021), Clem et al. (2022), Gilson et al. (2021), Gislason et al. (2021), Liu et al. (2021), Salawitch et al. (2017).</p>

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Table 1 (continued)












Negative Impacts	Taxonomic Group	Publications
Population: Dynamic and structure.		McFarlane et al. (2000), Hyrenbach and Veit (2003), Grebmeier et al. (2006), Graham et al. (2008), Le Quéré et al. (2010) , Wilhelm and Matteson (2008), Beaugrand et al. (2012) , Johnson et al. (2011) , Torstensson et al. (2012), Baker-Austin et al. (2013), Vezzulli et al. (2013, 2015), Guy et al. (2014), Mojica and Brusgaard (2014), Vergés et al. (2014) , Arismendi-Mejia et al. (2015), Kuffner et al. (2015), Mrowicki and O'Connor (2015), Vye et al. (2015), Maffucci et al. (2016), Leal et al. (2017), Kang et al. (2018), Shalders et al. (2018), Isla and Gerdes (2019) , Khosravi et al. (2019), Paula et al. (2019), Rossi et al. (2019), Zacher et al. (2019), Russell (2020), Villarino et al. (2020), Fraïner et al. (2017) , Gislason et al. (2021), Innis et al. (2021), Roth et al. (2021), Salawitch et al. (2017) .
Recruitment: Compromise, suppression, and sustainability.		Holbrook et al. (2020) , Andrews (1998) , McFarlane et al. (2000), Stammerjohn et al. (2008) , Negri et al. (2007), Rogers et al. (2021) , Sorte et al. (2013) , Kipson et al. (2012), Maffucci et al. (2016), Pimentel et al. (2016), Dworjanyan and Byrne (2018), García Molinos et al. (2016) , Newcomb et al. (2019), Baldanzi et al. (2020), García Molinos et al. (2016) , Harley (2011) , Tiedemann et al. (2021).
Reproduction: Fertilization, fecundity, breeding, spawning, and maturity.		Thompson and Furness (1991), Veit et al. (1996), Vilchis et al. (2005), Negri et al. (2007), Rogers et al. (2021) , Simpson et al. (2011) , Le Quéré et al. (2010) , Poloczanska et al. (2016) , Ericson et al. (2012), Byrne (2012, 2013) , Demongin et al. (2010), Chaudhary et al. (2021) , Kipson et al. (2012), Landes and Zimmer (2012), Mayor et al. (2012), Foo and Byrne (2013), Hipfner and Elnor (2013), Acheampong et al. (2014), Boersma and Rebstock (2014), Guy et al. (2014), Kizhakudan et al. (2014), Potts et al. (2014), Arismendi-Mejia et al. (2015), Juarez et al. (2015), Miller et al. (2015), Sandersfeld et al. (2015), Woolsey et al. (2015), Delorme and Sewell (2016), Furness (2016), Barr et al. (2017) , Dworjanyan and Byrne (2018), Leo et al. (2018), Feng et al. (2019, 2021), Lenz et al. (2019), Rossi et al. (2019), Baldanzi et al. (2020), Chirgwin et al. (2020), Hue et al. (2020), Musa et al. (2020), Suarez et al. (2020), Enrique-Navarro et al. (2021), Gonzalez et al. (2021).
Survival: Permanence, mortality, extinction.		Thompson and Furness (1991), Griffiths et al. (2009) , Field et al. (1998) , McFarlane et al. (2000), Reaser et al. (2000), Spencer et al. (2000), Peck (2005), Nozawa and Harrison (2007), Simpson et al. (2011) , Le Quéré et al. (2010) , Peterson et al. (2015) , Poloczanska et al. (2016) , Rantanen et al. (2022) , Demongin et al. (2010), Simpson et al. (2011) , Chaudhary et al. (2021) , Pansch et al. (2012), Watson et al. (2012, 2018), Collins et al. (2013), Fang et al. (2013, 2014), Nguyen et al. (2013), Poore et al. (2013), Pratchett et al. (2014) , Wallace et al. (2012) , Acheampong et al. (2014), Alemu and Clement (2014), Boersma and Rebstock (2014), Carella et al. (2014), Gazeau et al. (2014), Kamyra et al. (2014, 2016), Lam et al. (2016) , Pimentel et al. (2014), Rosa et al. (2014), Rummer et al. (2014), Arismendi-Mejia et al. (2015), Barr et al. (2017) , García Molinos et al. (2016) , Juarez et al. (2015), Manzello (2015), Falkowski et al. (1998) , Maffucci et al. (2016), Smale et al. (2019) , Ben Rais Lasram et al. (2010) , DeCarlo et al. (2017), Horwitz et al. (2017), Luschka and Resell (2017), Monriquez et al. (2017), Pratchett et al. (2014) , Pratchett et al. (2014) , Repolho et al. (2017), Chavez et al. (2010) , Coles et al. (2018), Dias et al. (2018, 2019), García Molinos et al. (2016) , Glynn et al. (2018), Kennedy et al. (2018), Marshall and Wallace (2019) , Rodgers et al. (2018), Mollica et al. (2019), Paula et al. (2019), Putra et al. (2019), Yuan et al. (2019), Balogh and Byrne (2020), Conti-Jerpe et al. (2020), Chaudhary et al. (2021) , Karnauskas (2020), Manullang et al. (2020), Masson-Delmotte et al. (2018) , Minuti et al. (2020), Musa et al. (2020), Razak et al. (2020), Rodriguez et al. (2020), Suarez et al. (2020), Agrelo et al. (2021), Brito-Morales et al. (2020) , Falkowski et al. (1998) , Gao et al., 2021, Levas et al. (2015) , Liberman et al. (2021), Lopez et al. (2021), Nguyen et al. (2021), Rogers et al. (2021) , Sabine et al. (2004) , Wheeler et al. (2021).

populations. Conversely, on isolated reefs dependent on replenishment from local broodstock, increases in local retention may hasten recovery ([Figueiredo et al., 2014](#)). Some other tropical species can potentially respond to ocean warming by having a high capacity to adapt ([Matz et al., 2018](#)) or by producing larvae that can move to new habitats ([Pratchett et al., 2014](#)), but these shifts can be unfavorable as local temperatures increase in the long term, decreasing local biodiversity to the point of substantial marine life losses and risk of extinction across species and ecosystems ([Penn and Deutsch, 2020](#); [Pinsky and Fredston, 2022](#)).

In the northwest Atlantic continental shelf, many benthic invertebrates' ranges have instead shifted toward the equator and into shallower water, causing high mortality ([Fuchs et al., 2020](#)). At higher latitudes and nearer the poles, species tend to invest more heavily in

their offspring and produce non-feeding larvae or bypass the larval stage altogether, producing limited dispersal as they develop quicker and settle closer to their parents. This reproductive strategy means that such species are more vulnerable to ocean warming as moving to new areas will be gradual and slow. Some polar and higher latitude species will be the biggest losers under the ocean warming trend due to their lower dispersal lifestyles under more limited access to cooler waters, which will reduce their spawning and foraging areas ([Griffiths et al., 2009](#); [Isla and Gerdes, 2019](#); [Kędra et al., 2015](#); [Moore and Reeves, 2018](#)). In the Arctic, key prey species' habitat may dramatically shrink if ocean warming continues on its current trajectory, creating potential "losers" such as snails, mussels, and other animals that are important prey for valuable commercial fish species and marine mammals such as Pacific walrus. This decline can reverberate through the entire Arctic food web,

Table 2
Positive impacts of Ocean Warming on marine species. See [Supplementary Material 1](#) for the full list of literature cited.

Positive Impacts	Taxonomic Group	Publications
Abundance: Size and biomass.		Frainer et al. (2017), Andrews (1998), Sagarin et al. (1999), Hughes et al. (2017), Mills (2001), Hyrenbach and Veit (2003), Schiel et al. (2004), Field et al. (1998), Mieszowska et al. (2006), Beaugrand et al. (2012), Steele and Dickinson (2016), Danovaro et al. (2011), Vezzulli et al. (2012), Figueiredo et al. (2014), Gianguzza et al. (2014), Maugendre et al. (2015), Vergés et al. (2014), Ben Rais Lasram et al. (2010), Burrows et al. (2011), Moran et al. (2017), Tarling et al. (2018), Aljbour et al. (2019), Li et al. (2022), Organelli and Claustre (2019), Kawana et al. (2019), Ajani et al. (2020), Antonucci et al. (2019), Flombaum et al. (2020), Yeung and Cooper (2020), López et al. (2020), Gao et al. (2021), Gislason et al. (2021), Mediodia (2021), Vaughan et al. (2021).
Behavior: Activity, performance, feeding, and niche breadth.		Stammerjohn et al. (2008), Fang et al. (2013), Jansen et al. (2016), Vergés et al. (2014), Kim et al. (2020).
Biodiversity: Species alteration and composition.		Whitehead et al. (2008), Peterson et al. (2015), Kaschner et al. (2011), Tose et al. (2017), Kawana et al. (2019), Ben Rais Lasram et al. (2010).
Distribution: Expansion, tropicalization.		Frainer et al. (2017), Quero (1998), Hyrenbach and Veit (2003), Lemoine and Boehning-Gaese (2003), Bush et al. (2004), Byrne (2013), Gentemann et al. (2017), MacLeod et al. (2005), McMahon and Hays (2006), Mieszowska et al. (2006), Simpson et al. (2011), Whitehouse et al. (2008b), Lindsey and Dahlman (2021), Figueiredo et al. (2014), Steele and Dickinson (2016), Byrne (2012, 2016), Johnson et al. (2011), Kerosky et al. (2012), Mackey et al. (2012), Nguyen et al. (2012), Tanaka et al. (2012), Valdimarsson et al. (2012), Pecorino et al. (2013), Jansen et al. (2016), Maffucci et al. (2016), Burrows et al. (2011), Li et al. (2022, 2018, 2019), Tose et al. (2017), Tracey et al. (2017), Cohen et al. (2018), Feng et al. (2018), Neukermans et al. (2018), Tarling et al. (2018), Aljbour et al. (2019), Feng et al. (2019, 2021), Diogou et al. (2019), Espino et al. (2019), Griffiths et al. (2009), Salawitch et al. (2017), Slesinger et al. (2020), Yeung and Cooper (2020), Agostini et al. (2021), Beaugrand et al. (2012), Berdalet (2021), Gislason et al. (2021), Monaco et al. (2021), Salawitch et al. (2017), Vieira et al. (2021).
Ecosystem: Energy flow, process, functionality, service, habitat, and trophic levels.		Loukos et al. (2003)
Interaction: Symbionts, host, competition, and predator-prey.		Arandia-Gorostidi et al. (2017b).
Life cycles: Development, growth, and phenology.		Bhaud et al. (1995), Stammerjohn et al. (2008), Vázquez-Domínguez et al. (2007), Whitehouse et al. (2008a, b), Gianguzza et al. (2011), Pansch et al. (2012), Pecorino et al. (2013), Green et al. (2014), Holland et al. (2021), Pimentel et al. (2014), Sett et al. (2014), Bylenga et al. (2015), Keppel et al. (2015), Falkowski et al. (1998), Gao et al. (2017), Harley (2011), Henschke et al. (2018), Watson et al. (2018), Comiso (2012), Griffiths et al. (2009), Morrongiolo et al. (2019), Organelli and Claustre (2019), Qu et al. (2019), Balogh and Byrne (2020), Li et al. (2022), Sorte et al. (2013), Vidyaratna et al. (2020), Wong and Hofmann (2020), Gouda and Agatsuma (2021), Molto et al. (2021), Raventos et al. (2021).
Physiology: Biochemical, metabolism, rates, and performance.		Field et al. (1998), Vázquez-Domínguez et al. (2007), Pimentel et al. (2014), Schluter et al. (2014), Sett et al. (2014), Arandia-Gorostidi et al. (2017b), Burrows et al. (2011), Gao et al. (2017), Harley (2011), Byrne (2012), Steele and Dickinson (2016), Howald et al. (2019), Qu et al. (2019), Li et al. (2022), Wong and Hofmann (2020), Antonucci et al. (2019), Sorte et al. (2013), Zheng et al. (2020), Booth et al. (2021), Gouda and Agatsuma (2021), Liu et al. (2021).
Recruitment: Success and sustainability.		Andrews (1998), Stammerjohn et al. (2008), Shears and Bowen (2017), Burgard and Notz (2017), Figueiredo et al. (2014), Pearce et al. (2016), Tose et al. (2017), Goode et al. (2019), Kawana et al. (2019).
Reproduction: Development, resilience, and production.		Shears and Bowen (2017), Gianguzza et al. (2011, 2014), Ho et al. (2013), Bhaud et al. (1995), Bylenga et al. (2015), Gao et al. (2017), Gouda et al. (2017), Tose et al. (2017), Byrne (2012), Henschke et al. (2018), Parkinson and Comiso (2013), Schmidt et al. (2020), Spencer et al. (2021).
Survival: Permanence and tolerance.		Pansch et al. (2012), Woolsey et al. (2015), Henschke et al. (2018), Castellan et al. (2019).

impacting Arctic coastal communities that depend heavily on their marine ecosystem for subsistence (Logerwell et al., 2022).

A summary of 421 studies (Table 1) was analyzed to examine the negative effects of ocean warming on ten marine taxonomic groups based on 13 criteria presented in the Review Approach, Criteria, and Literature Representation section. The results indicate that physiology (17.3%), survival (12.1%), and life cycles (10.5%) were the most commonly identified aspects that were adversely affected (Fig. 2a). Invertebrates (28.4%) and fish (18.6%) were found to have the greatest amount of negative evidence, followed by corals (15.1%) and algae (10.1%) (Fig. 2c). The number of publications on negative ocean warming impacts on the taxonomic groups for the 13 criteria (abundance, behavior, biodiversity, distribution, ecosystem, infections, interactions, life cycles, physiological, population, recruitment, reproduction, and survival) are presented in Figures 3a (corals, invertebrates, macroalgae, phytoplankton, viruses and bacteria, and zooplankton) and Fig. 3b (fish, ectotherms, seabirds, and marine mammals).

5.2. Winners in a warming ocean

In contrast, marine species with higher tolerance to fast changes in ocean temperature conditions will benefit from ocean warming impacts during their reproduction, development, dispersal, or survival and will be considered “winners.” Some examples include reef fish communities (Day et al., 2018), shellfish assemblages (Simpson et al., 2011), and species of phytoplankton, seagrass, algae, fish, and even reptiles, marine mammals, seabirds (Hastings et al., 2020), sponges (Bell et al., 2013), penguins (LaRue et al., 2013), and some fishery stocks (Melbourne-Thomas et al., 2022). These winners’ species can potentially increase their abundance and distribution as warmer water moves to higher latitudes and colonize vast distances, as is the case of marine species observed in the last few decades (Chaudhary et al., 2021; Mahanes and Sorte, 2019; Poloczanska et al., 2016). Tropical species that produce large numbers of feeding larvae will be especially better suited to extend their dispersal patterns and population connectivity under ocean warming conditions, increasing biodiversity as they shift to new habitats. Similarly, high-latitude species distributional limited by colder temperatures will also thrive, as they will have access to new habitats, prey, and potentially fewer predators with the intrusion of warmer waters (Fraimer et al., 2017).

This review summarizes 133 studies on the same ten marine taxonomic groups and 13 criteria to identify the positive impacts of ocean warming (Table 2). Under the criteria considered, distribution (29%), abundance (19.1%), and life cycles (18%) as the aspects most identified as beneficial (Fig. 2b), with a greater amount of beneficial evidence studied in other species of invertebrates (31%) and fish (21.8%), followed by phytoplankton (12.7%) and zooplankton (9.9%) (Fig. 2d). The number of publications on positive ocean warming impacts on the taxonomic groups for the criteria and all taxonomic groups are presented in Fig. 4.

6. Conclusions

In the last three decades, the increased dependence on fossil fuels has resulted in a persistent rise in greenhouse gases emissions, particularly carbon dioxide (CO₂), surging by over 51%, leading to a rapid escalation of global warming and heat accumulation in the ocean. This trend has led to rising ocean temperatures from the surface to the deep in all ocean basins while affecting marine ecosystems at various levels, from the Arctic to the Antarctic. The impact of ocean warming, both directly and indirectly, and its interaction with other disturbances such as sea level rise, stratification, acidification, deoxygenation, and eutrophication, is causing a series of physical, chemical, biological, and socio-ecological consequences that are cascading throughout marine life stages and ecosystems. Consequently, since 1991 there has been a surge in research

publications aimed at comprehending the impact of these phenomena on marine ecosystems, with a special emphasis on ocean warming and its context and processes. Most publications examined in this study investigated the impact of ocean warming on marine organisms, particularly invertebrates, fish, corals, algae, phytoplankton, and zooplankton. The majority of these studies analyzed the effects of ocean warming on the physiology, life cycles, and survival of these organisms. Out of the evaluated studies, 78.8% reported negative impacts, 20.1% reported positive effects, and 1.1% observed species with neutral responses to the impacts of ocean warming.

Publications highlight that ocean warming can affect different species at different life stages, resulting in positive, negative, or mixed impacts. Ocean warming is having a noticeable impact on both temperate and colder ecosystems. As temperatures rise, tropical organisms will continue migrating toward higher latitudes, while cold-water species will continue relocating toward deeper water or shifting towards the poles to cope with the changing conditions. These changes could result in complex and unexpected interactions within ecosystems. Species with a restricted thermal range, limited dispersal abilities, and slow adaptation to rising temperatures are vulnerable to adverse effects, such as reduced foraging and spawning areas, decreased population connectivity, and a higher risk of extinction. This group includes various species, such as tropical fish, coral reef fish, reef-building corals, snails, mussels, mangroves, seagrass, polar bears, and other cold-blooded species. In contrast, species with higher thermal tolerance, adaptability, and flexibility to rapid changes in ocean temperature can experience positive effects from ocean warming, enhancing their reproductive and dispersal strategies, distribution, and survival. This group includes several species, such as jellyfish, sponges, tuna, jumbo squids, seagrass, algae, fish (including commercial stocks), and even reptiles, marine mammals, seabirds, and penguins.

Although certain species may seem to derive advantages from ocean warming during particular phases of their life cycle, it is crucial to recognize that altering the equilibrium among different species could trigger a series of repercussions throughout the food chain, resulting in considerable and enduring repercussions for the ocean and its inhabitants. Still, the overall short and mid-term impact of ocean warming and others AAC disturbances on marine ecosystems is negative and can have cascading effects on the entire ecosystem. The impacts of ocean warming on different species can vary significantly, leading to the possibility of modern evolution and the emergence of new ecological interactions and assemblages. Unfortunately, The long-term consequences of ocean warming on ecosystems are still uncertain, but it is expected that the continued warming of the ocean will have significant impacts on species distribution, biodiversity, ecosystem services, and human livelihoods that depend on the ocean’s conditions and marine resources.

It is crucial, then, to continue studying and monitoring the impacts of ocean warming on marine ecosystems to mitigate the potential negative effects and promote the sustainable use of marine resources. International and multidisciplinary efforts are necessary to reduce biases and uncertainties in climate models (Wang et al., 2014), which can be achieved through long-term observations and analysis of Earth’s heat inventory worldwide. The next generation of research should focus on advancing our understanding of paleoclimate evidence, climate processes, and the climate system’s response to increasing radiative forcing. It is also essential to establish robust climatological backgrounds, improve instrument bias correction and quality control, and standardize atmospheric and oceanographic data processing to identify the warming signature accurately. These efforts can help to distinguish between internal variability and ACC trends to improve estimates of equilibrium climate sensitivity and provide more accurate climate projections. Furthermore, these new collaborative efforts can follow international initiatives on in-situ observing systems such as GOOS, Argo, and BGC-Argo fleets or remote sensors such as GOES-R, GeoXO, and PACE to acquire new variables with higher spatiotemporal sampling. By working

together at various levels, from local to global, we can effectively address the swift socio-ecological, economic, and political ramifications of ocean warming and other ACC disturbances on marine ecosystems, species, and the societies that depend on them.

Achieving quasi-equilibrium in Earth's climate system through climate stabilization is crucial to prevent tipping points in marine ecosystems and mitigate the effects of ocean warming and other ACC disturbances. To achieve environmental balance, a collective effort from individuals, corporations, and governments worldwide is necessary to fulfill the Paris Agreement's objective of limiting the global average temperature increase to below 2 °C and capping it at 1.5 °C above pre-industrial levels. This success involves eliminating the usage of fossil fuels (coal, oil, and natural gas), decreasing CO₂ and methane emissions, and shifting towards renewable and sustainable energy sources. Unfortunately, at the November 2022 COP27, discussions did not result in a formal agreement to phase out global fossil fuel use, including. Failure to reduce or eliminate the use of fossil fuels within the next few years will result in the ocean absorbing more atmospheric heat, leading to catastrophic consequences for the planet. Ocean warming will continue, resulting in thermal expansion and increased volume, leading to higher sea levels and chaotic hazards to coastal regions worldwide, including increased frequency and severity of flooding, erosion, saltwater intrusion, and damage to infrastructure and property. Additionally, the increased absorption of CO₂ will decrease seawater pH, intensifying ocean acidification and posing severe risks to marine environments such as intertidal zones, coral reefs, coastal wetlands, and mangroves. These habitats are essential nurseries for numerous marine species, making their preservation imperative from the direct and indirect impact of ocean warming. Losing these critical habitats can have far-reaching impacts on the entire marine food web, ultimately affecting human livelihoods and coastal communities that depend on these ecosystems for sustenance and income.

In March 2023, as this review was being prepared, nations reached a groundbreaking agreement known as the High Seas Treaty after decades of negotiations. This multilateral treaty aims to protect and restore marine nature by designating 30% of the world's oceans as protected areas by 2030. Although this is a commendable accomplishment, the newly proposed protected areas under this treaty and the existent protected and unprotected marine ecosystems will continue facing catastrophic consequences if CO₂ emissions keep increasing and the Paris Agreement's goal of limiting global warming is not met. Hence, it is critical to continue advocating for sustainable ocean management to avoid disastrous marine ecosystem outcomes.

Authors statement

All authors contributed to writing and editing the article. RMV led the investigation, conceptualization, methodology, statistics, visualization, and the writing of the original and final draft. JA and EAT helped in the conceptualization, writing, reviewing, and editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

This is a literature review, all information is publicly available.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.dsr2.2023.105318>.

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