Review

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Review

Experimental Evidence of Climate Change Effects on Plankton Community Respiration in European Coastal Waters: Current Insights and Knowledge Gaps in Tested Disturbances and Studied Areas

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Abstract

Plankton community respiration (PCR) plays a central role in aquatic ecosystems, driving the breakdown of organic matter and influencing global carbon cycling through its contribution to the production and consumption of carbon and oxygen. Coastal areas, which serve as critical interfaces between terrestrial and marine ecosystems, are regarded as metabolic hotspots in the oceans, due to their intense biological and biogeochemical activities. Additionally, they are particularly sensitive to the impacts of global climate change. In this regard, this review synthesizes experimental evidence to explore how environmental constraints and climate drivers affect PCR in European coastal waters. In total, 46 studies were found in which PCR was measured during experiments testing the effects of one or multiple global climate change drivers in European coastal waters. Among them, the majority of experiments focused on changes in temperature, nutrient concentrations and stoichiometry, and/or pH, while other stressors were less studied. Many experiments confirmed theoretical predictions, notably regarding the predicted positive effects of increased temperature and nutrient concentrations on metabolism, but more complex responses, often linked to trophic cascade mechanisms and thresholds between positive and negative feedbacks were also often reported. Overall, this review, the first comprehensive synthesis of experimental evidence on PCR in European coastal waters, highlights critical knowledge gaps, notably regarding non- and understudied areas and understudied interactions between stressors that occurs jointly in natural ecosystems. Future research should aim to integrate controlled experiments, long-term monitoring, and modeling approaches to deepen our understanding of PCR dynamics under changing environmental conditions and to predict potential feedbacks to global climate processes.

Keywords: plankton; respiration; climate change; experiments

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1. Introduction

Plankton community respiration (PCR) plays a fundamental role in marine ecosystems by driving the breakdown of organic matter and facilitating carbon cycling. As both autotrophic and heterotrophic plankton organisms metabolize organic compounds, they consume dissolved oxygen (O_2) and release carbon dioxide (CO_2) through aerobic respiration (Robinson and Williams, 2005; Robinson 2019). In contrast, phytoplankton, as the primary producers, convert dissolved CO_2 into organic matter via photosynthesis, producing dissolved oxygen (O_2) as a by-product (Falkowski 1994). These metabolic activities influence the overall efficiency of the ocean's biological pump, a critical mechanism through which carbon is sequestered from the atmosphere and stored in deep ocean waters, mitigating global climate change (Field *et al.*, 1998; Jiao and Azam 2011). Indeed, the balance between plankton production and respiration regulates carbon fluxes within marine ecosystems, and indicates whether a system acts as a net source of O_2, and so a net sink of CO_2, for the atmosphere, or if, conversely, the system acts as a net sink of O2, and a net source of CO_2 for the atmosphere (López-Urrutia *et al*., 2006; Serret *et al*., 2015). Therefore, PCR is a vital component in determining how coastal and open ocean waters act as carbon sinks or sources. Given the sensibility of planktonic processes to environmental changes (Hays *et al*., 2005; Litchman *et al*., 2012), studying PCR and its influence on global biogeochemical cycling appears to be crucial, particularly in the context of global climate change and increased anthropogenic pressures on aquatic ecosystems.

Coastal waters are among the most dynamic and productive regions of the ocean, characterized by complex interactions between terrestrial and marine environments (Cloern *et al*., 2014; Carstensen *et al*., 2015). These areas are influenced by a variety of local environmental conditions, such as freshwater inflows from rivers (Fredston-Hermann *et al*., 2016), nutrient loading from agricultural and terrestrial runoff (Beman *et al*., 2005), and physical factors like tides, currents, and wind-driven mixing (Lizon *et al*., 1995). These interactions create highly variable environments where physical, chemical, and biological conditions can shift rapidly. Coastal waters are also particularly sensitive to global climate change drivers (Harley *et al*., 2006; Rabalais *et al*., 2009). Notably, warming temperatures, ocean acidification, increasing extreme weather event frequency, rising sea levels and changing precipitation patterns, resulting in intensified freshwater and nutrient inputs from land, are altering the structure and function of coastal ecosystems (Harley *et al*., 2006). Finally, coastal waters are key sites of biogeochemical cycling and biodiversity, as their metabolism contributes more to the global biogeochemical cycles than spatially larger but less productive regions of the open ocean, such as oligotrophic gyres (Aranguren-Gassis *et al*., 2013; Serret *et al*., 2015). Therefore, understanding how these dynamic systems respond to both local pressures and global climate change is crucial for predicting future impacts on global biogeochemical cycles and the resilience of marine environments.

Plankton communities are influenced by many of the environmental factors to which coastal waters are sensitive (e.g., Chou *et al*., 2012; Forsblom *et al*., 2019). Therefore, PCR can be highly variable in coastal waters, displaying strong seasonal variations and relationships to environmental conditions (e.g., Agusti *et al*., 2018; García-Martín *et al*., 2019a; Gomez-Castillo *et al*., 2023; Mantikci *et al*., 2024; Prichett *et al*., 2024) and plankton community biomass (Olesen *et al*., 1999; Lozano *et al*., 2021) and structure (Bas-Silvestre *et al*., 2024). In this regard, coastal PCR may be particularly prone to climate change and anthropogenic pressures (del Giorgio and Williams, 2005). However, while monitoring primary production is relatively straightforward, resulting in hundreds of thousands of observations since half a decade and primary production being well-parametrized and integrated into Earth system models (Laufkötter *et al*., 2015), monitoring PCR remains challenging. Budget methods, which rely on *in situ* changes in dissolved O_2 concentration, require expensive and carefully calibrated equipment and complex calculations (Staehr *et al*., 2010; Soulié *et al*., 2021). Direct methods, such as in vitro incubations during which dissolved O_2 concentration changes are measured are labor-intensive and extremely time-consuming, and are susceptible to manipulation biases and "bottle effects" (Robinson and Williams, 2005; García-Martín *et al*., 2011). Consequently, PCR is rarely monitored, and the few available observations are often sparse and not always fully reliable (Arístegui and Harrison, 2002; Regaudie-de-Gioux and Duarte, 2013). This has led to a limited understanding, both temporally and spatially, of climate change impacts on PCR, as well as the parameterization of its drivers and their incorporation into predictive models (Wikner *et al*., 2023). Accordingly, respiration and its related processes have been listed as a highly important knowledge gap in quantifying the effect of climate change on biological carbon storage in the ocean (Grégoire *et al*., 2023; Henson *et al*., 2024).

In this context, controlled-environment experiments could play a valuable role in elucidating the mechanisms behind observed trends (Wernberg *et al*., 2012). While direct measurements are crucial for capturing the complexity of natural systems, experiments remain essential to verify and parameterize causal relationships between key components in coastal ecosystems. Observations typically highlight correlations between environmental conditions and biological processes but cannot confirm causality. Experiments, on the other hand, can uncover underlying mechanisms, though they inevitably simplify the complexities of the systems being studied (Stewart *et al*., 2013).

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In regard of the above, the objective of this review is to provide a comprehensive synthesis of experimental research, examining how environmental constraints and climate change drivers shape PCR in European coastal ecosystems. By focusing on results from controlled experiments, this review aims to elucidate the mechanistic relationships between PCR and environmental factors such as temperature, nutrient availability, and light penetration, alongside climate stressors like ocean warming, acidification, and marine heatwaves. Through an analysis of experimental findings, the review will highlight how these environmental drivers interact to influence PCR, revealing regional patterns and system-specific responses. This experimental perspective will provide critical insights into how future climate conditions may reshape metabolic processes in coastal waters, while identifying key gaps in the studied disturbances and areas and proposing directions for future research to advance our understanding of PCR in the context of global change in Europe.

2. Methods

As this review is focusing on the experimental evaluations of the effects of global climate change on PCR, it is first necessary to define certain terms used in this review. The term "global climate change" refers here to the shifts in global climate driven by anthropogenic emissions of CO_2 and other greenhouse gases, along with its impacts on climatic, oceanographic, and biogeochemical processes. Such impacts encompass global phenomena, such as the ongoing rise in water temperature and decrease in pH, as well as extreme weather phenomena, such as the increase in frequency of marine heatwaves and terrestrial runoffs. In addition, some environmental drivers reflect both global climate change and direct anthropogenic pressures, and are included in the present review. For example, nutrient concentrations and stoichiometry are related to both global climate change (e.g., changes in upwelling processes due to climate change) and direct anthropogenic pressures (e.g., eutrophication due to agricultural waste runoffs). However, stressors related only to anthropogenic activities (e.g., inputs of pesticides) were not taken into account in the present review as they are not directly linked to global climate change.

In addition, this review focusses on scientific peer-reviewed publications. In one instance, the abstract from a presentation at an international conference was used (Serret *et al.*, 2024), as it dealt with a very understudied process (ocean alkalinization) and I was able to access the data from the main author. Additionally, this review only focuses on experiments in which PCR was measured. No limits in the volume of the experimental units were considered, as long as the respiration rate of natural communities was measured. Hence, the experiments in which only one biological compartment (e.g., only phytoplankton) was included were not considered in the present review. Similarly, to ensure that a maximum of studies was considered in the review, no limits were taken into account regarding how PCR was measured, i.e., studies with different approaches and different methodologies (incubations vs. sensor-based). However, it should be noted that both the volume of the experimental units and the method used to measure PCR could play an important role in the comparison of the results between studies. Nonetheless, the goal of the present review was not to try to explain potential discrepancies in results related to methodological questions, but rather to give a global overview on the global climate change effects on PCR in coastal European waters.

Finally, the present review focusses on coastal waters of Europe. Particularly, coastal waters were not here defined from a certain maximum distance from the shore, but rather as marine waters under some influence from the land. As a result, some experiments were included in the present review while they were performed in offshore environments (e.g., in the Tyrrhenian and Ionian Seas, Gazeau *et al.*, 2021) because they specifically tested disturbances arising from the land, e.g., inputs of Saharan dust). Additionally, Europe was considered here only as the geographical region.

In line with all of this, the search for relevant articles was done mainly using the Web of Science (WoS) website (https://apps.webofknowledge.com/, last access: 15 March 2025) maintained by Clarivate. The search was done using several terms in various combinations. These terms included “plankton respiration”, “climate change”, “global climate change”, “warming”, “temperature”, “acidification”, “pCO_2”, “runoff”, “light”, “nutrients”, “ultraviolet”, “UV”, “salinity”, "alkalinization", "metabolism", "plankton metabolism", "ecosystem metabolism", "experiments", "coastal waters". Some papers from 2024 and 2025 were found with an unstructured search in Google Scholar (https://scholar.google.com/, last access: 11 November 2025), as this website includes more recent articles than WoS.

These various searches resulted in over 100 papers, of which many were not suitable for the present review, as they do not explicitly present PCR data, and/or were not focused on the effects of global climate change, and/or did not present results from experiments, and/or were not performed with coastal European waters. All the relevant studies were saved in a specific Zotero (https://www.zotero.org/) library. At the end, 46 studies meeting the review criteria were included. A table summarizing the main information regarding these studies can be found in **Table 1**.

Table 1. Summary of all the studies included in the present review, with their type of disturbance studied, their study site and the broader area of their study site.

	Study	Disturbance	Study site	Area
1	Vaquer-Sunyer *et al.*, (2010)	Warming	Svalbard	Arctic
2	Holding *et al.*, (2013)	Warming	Svalbard	Arctic
3	Wolf *et al.*, (2024)	Warming	Svalbard	Arctic
4	Hoppe *et al.*, (2008)	Warming	Kiel fjord	Baltic
5	Cabrerizo *et al.*, (2021)	Warming	Gulf of Bothnia	Baltic
6	Panigrahi *et al.*, (2013)	Warming	Bothnian Sea	Baltic
7	Lewandowska *et al.*, (2014)	Warming	Baltic Sea	Baltic
8	Wohlers *et al.*, (2009)	Warming	Western Baltic Sea	Baltic
9	Soulié *et al.*, (2022a)	Warming	Thau Lagoon	Mediterranean
10	Vázquez-Domínguez *et al.*, (2007)	Warming	Bay of Blanes	Mediterranean
11	Vaquer-Sunyer & Duarte (2013)	Warming	Majorca	Mediterranean
12	Soulié *et al.*, (2022b)	Warming	Thau Lagoon	Mediterranean
13	Soulié *et al.*, (2023)	Warming	Thau Lagoon	Mediterranean
14	Pulina *et al.*, (2020)	Warming	Cabras lagoon	Mediterranean
15	Maugendre *et al.*, (2015)	Warming; Acidification	Bay of Villefranche	Mediterranean
16	Huete-Stauffer *et al.*, (2018)	Warming	Bay of Biscay	Atlantic

17	Soulié *et al*., (2025)	Warming	Ría de Vigo	Atlantic
18	López-Sandoval *et al*., (2025)	Warming; Nutrients	Ría de Vigo	Atlantic
19	Vaquer-Sunyer *et al*, (2015)	Warming; Nutrients	Baltic Proper	Baltic
20	Tanaka *et al*., (2013)	Acidification	Svalbard	Arctic
21	Spilling *et al*., (2016)	Acidification	Storfjärden, Finland	Baltic
22	Maugendre *et al*., (2017)	Acidification	Bay of Villefranche; Bay of Calvi	Mediterranean
23	Delille *et al*., (2005)	Acidification	Raunefjporden, Norway	Atlantic
24	Egge *et al*., (2009)	Acidification	Raunefjporden, Norway	Atlantic
25	Filella *et al*., (2018)	Acidification; Nutrients	Taliarte, Gran Canaria	Atlantic
26	Martínez-García *et al*., (2013)	Nutrients	Ría de Vigo	Atlantic
27	Vaquer-Sunyer *et al*., (2016)	Nutrients	Baltic Sea	Baltic
28	Olsen *et al*., (2006)	Nutrients	Tvarminne, Blanes Bay, Hopavågen Bay	Baltic, Mediterranean, Atlantic
29	Lagaria *et al*., (2011)	Nutrients	Mediterranean	Mediterranean
30	Duarte *et al*., (2004)	Nutrients	Bay of Blanes	Mediterranean
31	Cabrerizo *et al*., (2022)	Warming; Nutrients	Coastal waters of the Mediterranean and the Atlantic	Mediterranean, Atlantic
32	Martínez-García *et al*., (2014)	Nutrients	Ría de Vigo	Atlantic
33	Baños *et al*., (2022)	Nutrients	Gando Bay, Canary	Atlantic
34	Ortiz *et al*., (2022)	Nutrients	Gando Bay, Canary	Atlantic
35	Cabrerizo *et al*., (2016)	UV; Nutrients	SW Mediterreanean Sea	Mediterranean
36	Lekunberri *et al*., (2010)	Nutrients	Bay of Blanes	Mediterranean

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37	Ortiz et al., (2024)	Nutrients	Gando Bay, Canary	Atlantic
38	Soulié *et al*., (2024)	Terrestrial runoff	Thau Lagoon	Mediterranean
39	Liess *et al*., (2016)	Terrestrial runoff	Thau Lagoon	Mediterranean
40	Soulié *et al*., (2022c)	Terrestrial runoff	Hopavågen Bay	Atlantic
41	Agustí *et al*., (2014)	Light, UV	Majorca	Mediterranean
42	Marín-Samper *et al*., (2024)	Alkalinity	Taliarte, Gran Canria	Atlantic
43	Serret *et al*., (2024)	Alkalinity	Ría de Vigo, Cretan Sea	Atlantic; Mediterranean
44	Mercado *et al*., (2014)	Acidification; Nutrients; Light	Fuengirola, southern Spain	Mediterranean
45	Gazeau *et al*., (2021)	Warming, Acidification, Nutrients	Mediterranean	Mediterranean
46	Vidussi *et al*., (2011)	Warming; UV	Thau Lagoon	Mediterranean

3. Global Change Effects on Plankton Community Respiration

3.1. Temperature Sensitivity and Effect of Warming and Marine Heatwaves

Temperature is a primary driver of metabolic rates, with a direct relationship between temperature and metabolism as described by the Arrhenius Law and which serves as the foundation for the Metabolic Theory of Ecology (MTE) (Brown *et al*., 2004). The MTE uses the fundamental principles of the Arrhenius Law to explain how temperature regulates metabolic processes in ecosystems, influencing ecological functions across all levels of organization (Yvon-Durocher *et al*., 2012; Boscolo-Galazzo *et al*., 2018). According to this theory, PCR is expected to rise with increasing temperature. This was verified at the global ocean scale by Regaudie-de-Gioux and Duarte (2012) and Garcia-Corral *et al*. (2017), who compiled a large dataset of PCR measurements in various regions of the ocean and found a temperature sensitivity of PCR in accordance with the predictions of the MTE. However, this analysis is only based on concurrent measurements of PCR and water temperature, preventing from disentangling the variability in PCR related to temperature to that related to other concomitant environmental forcings. Indeed, temperature effects on PCR can also be nonlinear, as, for example, extreme heat can exceed the thermal tolerance of plankton communities (Chen 2015), disrupting ecosystem functioning. It can especially be the case in coastal areas, where many factors, and notably exchanges with the sediment and the land, can simultaneously affect plankton communities in addition to temperature. Accordingly, some experimental studies showed contrasted effects of changes in temperature on PCR in European coastal waters, sometimes even in contradiction to the predictions of the PCR (Vidussi *et al*., 2011; Soulié *et al*., 2022a).

Warming of the sea surface, either in the form of long-term warming (IPCC 2019; Cheng *et al*., 2022) or episodic marine heatwaves (Frölicher *et al*., 2018), is one the most known consequences of global climate change for the oceans (Smith *et al*., 2023), and also one of the most studied stressors regarding PCR responses toward global climate change (e.g., Cavan and Boyd, 2018; Latorre *et al*., 2023). Coastal waters are considered highly vulnerable to global warming, with sea surface temperatures projected to rise by 3°C by the end of the century in some regions (IPCC 2019), and particularly threatened by marine heatwaves (Garrabou *et al*., 2022; Pastor and Khodayar, 2023; Bashiri *et al*., 2024; Darmaraki *et al*., 2024). In this regard, many studies have experimentally investigated the effect of increased temperature on PCR in coastal waters. Albeit having used different experimental set-ups and studied different systems and communities, most of them highlighted a positive response of coastal PCR to warming, notably in the North Western Mediterranean Sea (Thau Lagoon (Soulié *et al*., 2022b; 2023), Bay of Blanes (Vázquez-Domínguez *et al*., 2007), and Majorca (Vaquer-Sunyer and Duarte, 2013)), in the Baltic Sea (Kiel Bight (Hoppe *et al*., 2008; Breithaupt 2009; Wohlers *et al*., 2009), Öre estuary (Panigrahi *et al*., 2013), South East Baltic Sea (Vaquer-Sunyer *et al*., 2015)), in the North East Atlantic Ocean (Bay of Biscay (Huete-Stauffer *et al*., 2018), Irish Sea (Lefèvre *et al*., 1994), Ría de Vigo (López-Sandoval *et al*., 2025; Soulié *et al*., 2025)), and in the Arctic (Svalbard archipelago (Vaquer-Sunyer *et al*., 2010; Holding *et al*., 2013; Wolf *et al*., 2024)). All the results from these studies tend therefore to confirm the predictions of the MTE, even if they were conducted in complex coastal environments.

However, other studies reported a lack of response, or even a negative effect of warming on PCR, thus contradicting with theoretical predictions and global observations. In the Mediterranean coastal Thau Lagoon, Vidussi *et al*. (2011) reported no significant effect of a +3°C increase on PCR during a *in situ* mesocosm experiment in spring, and suggested a trophic cascade induced by warming and favoring microzooplankton grazing on bacteria, ultimately reducing bacterial abundance and contribution to PCR. In the same location and with similar mesocosm set-ups, Soulié *et al*. (2022a) reported a strong negative response of PCR to a +3°C warming related to a 50% decrease in phytoplankton biomass due to enhanced grazing under elevated temperature during a spring bloom, and no significant effect of +3°C on PCR during of the same year, supposedly due to enhanced competition between heterotrophic bacteria and cyanobacteria under warmed conditions. In another Mediterranean coastal lagoon (Cabras Lagoon, Italy), Pulina *et al*. (2020) reported a decrease in PCR under +3°C and +6°C conditions, which could also have been related to warming effects on heterotrophic bacteria and their grazers. In addition, Maugendre *et al*. (2015) found no significant effect of +3°C temperature increase on PCR in the Bay of Villefranche, NW Mediterranean Sea, potentially due to nutrient-depleted conditions preventing the response of PCR. In the Baltic Sea, +3°C warming, applied either constantly or with fluctuating pulses, was shown to decrease PCR Sea (Cabrerizo *et al*., 2021), certainly due to a strong decrease in phytoplankton biomass under warmed conditions. Lewandowska *et al*. (2014) also reported no significant effect of +3°C warming on Baltic Sea PCR, and suggested a potential trophic cascade mechanism which could have prevented from a stronger response of PCR. Overall, the results from the above-mentioned studies highlight the importance of warming indirect effects, such as changes in the trophic structure of the plankton communities and in nutrient availabilities, which could override the direct positive response of metabolism toward warming in complex systems such as coastal environments. This stresses out the need of experimental studies which incorporates the full natural complexity of coastal ecosystems, and suggests that indirect effects of warming, often neglected, are taken into consideration in global models of the effects of climate change on PCR.

3.2. pH Sensitivity and Effect of Acidification

Ocean acidification, driven by the increasing absorption of atmospheric CO_2 into seawater (Guinotte and Fabry, 2008), has significant implications for coastal ecosystems (Matear and Lenton, 2014), particularly for plankton community respiration (PCR). As CO_2 dissolves in seawater, it forms carbonic acid, lowering the pH and altering the carbonate chemistry of marine environments. As a result of ongoing anthropogenic activities, it is predicted that the global average of the world's ocean pH will continue to decrease, by up to 0.4 by 2100, and 0.77 by 2300 (Turley and Findlay, 2016). This decrease can disrupt metabolic processes in both autotrophic and heterotrophic plankton, impacting PCR directly and indirectly. For phytoplankton, the increase in inorganic carbon availability may directly fuel photosynthesis, and so, indirectly enhances autotrophic respiration (e.g., Qu *et al*., 2021), while acidification can also affect nutrient uptake, and cellular processes (Das and Mangwani, 2015; Bermúdez *et al*., 2016). Heterotrophic organisms may experience changes in metabolic efficiency and energy demands, often leading to changes in respiration rates (Motegi *et al*., 2013; Cripps *et al*., 2016; Davis *et al*., 2017; James *et al*., 2017). However, very few studies have investigated the effect of acidification on respiration in coastal waters at the community level.

Few mesocosm and microcosm experiments conducted in diverse coastal environments (e.g., Mediterranean Sea, Baltic Sea, Svalbard fjords) investigated the effects of elevated CO_2 on PCR. Across these experiments, elevated CO_2 levels generally had no direct impacts on plankton metabolic processes in oligotrophic areas. For example, studies conducted in low-nutrient, low-chlorophyll waters of the coastal Mediterranean Sea (Bay of Villefranche and Bay of Calvi) revealed no significant changes in PCR in response to increased CO_2 (up to 1327 µatm) (Maugendre *et al*., 2017). Similarly, elevated CO_2 (up to 700 µatm), simulating predicted pH conditions of year 2100, did not affect significantly PCR in a mesocosm experiment in Raunefjorden (South of Norway, Atlantic Ocean), even if other metabolic processes, such as the calcification rate of coccolithophorids, were significantly affected (Delille *et al*., 2005). In the same system, increased pCO_2 (1050 µatm) did not affect PCR during another experiment, in which nutrients were added from the start of the experiment (Egge *et al*., 2009). Additionally, in the nutrient-limited Kongsfjorden (Arctic coastal waters, Svalbard archipelago), no significant relationship was found between PCR and 7 levels of pCO_2 (up to 1420 µatm) in a mesocosm experiment, even after nutrient addition (Tanaka *et al*., 2013). Similarly, in coastal Mediterranean waters (North Western Alboran Sea, Southern Spain), elevated pCO2 (1000 µatm) and nutrient concentrations did not alter significantly PCR during a 7-d microcosm experiment, while light availability appeared to be the main controlling factor PCR in this system (Mercado *et al*., 2014).

In contrast, only two experimental studies revealed significant effects of simulated acidification on PCR in coastal European waters. In coastal Atlantic waters of the Canary Islands, increased pCO_2 significantly enhanced PCR after nutrient amendment, while no significant effects were found before adding the nutrients (Filella *et al.*, 2018), suggesting a positive effect of acidification on PCR in highly eutrophic conditions. Conversely, PCR was significantly reduced by almost 40% under high CO_2 levels (up to ~ 1330 µatm) during a mesocosm experiment with nitrogen-limited coastal waters from the Gulf of Finland (Baltic Sea) (Spilling *et al*., 2016), maybe due to a shift toward smaller plankton groups. Overall, the contrasted results obtained from the few studies that have experimentally investigated the effects of ocean acidification on PCR at the community level suggest limited consequences of this stressor, but, most importantly, emphasizes the need of further studies, notably in coastal waters of various nutrient status, to expand our limited knowledge regarding the long-term effect of acidification. It should be noted that ocean alkalinity enhancement, by artificially increasing carbonate ion concentration, is growingly proposed as a nature-based solution to counteract acidification. The environmental consequences of this solution still need to be evaluated at a broad spatial and temporal scales; the first results of Marín-Samper *et al*. (2024) indicated no significant effect of a gradient of alkalinization on PCR during a mesocosm experiment in coastal waters of the Canary Islands (North Eastern Atlantic Ocean), while preliminary results from Serret *et al*. (2024) indicated a reduction of PCR in response to the addition of calcium hydroxide in coastal productive Atlantic waters (Ría de Vigo, Spain) and in the ultraoligotrophic eastern Mediterranean Sea (Crete, Greece).

3.3. Nutrient Sensitivity and Effect of Eutrophication

Nutrient availability, both inorganic (such as nitrate (NO_3^-), orthophosphate (PO_4^{3-}), and silicate (SiO_3^{2-})) and organic (including dissolved organic carbon (DOC), nitrogen (DON), and phosphorus (DOP)), is a key driver of plankton metabolism, influencing both autotrophic and heterotrophic metabolism (Legendre and Rassoulzadegan, 1995). Inorganic nutrients are essential for both autotrophic and heterotrophic metabolism while organic nutrients play a critical role in supporting the microbial loop and heterotrophic processes (Jones *et al*., 2024; Vanharanta *et al*., 2024). Therefore, the interaction between these inorganic and organic nutrient sources, and the nutrient limitation patterns, can significantly alter the structure and function of planktonic communities (Caron *et al*., 2000; Weber and Deutsch, 2010). Nutrient enrichment, for example from the land, either directly from terrestrial runoffs or from watershed and groundwater discharge (e.g., Palma Bay, Mediterranean Sea (Basterretxea *et al*., 2024)), can significantly change the structure of planktonic communities, and by doing so, increase or decrease PCR (e.g., Wilson *et al*., 2024). Nutrient inputs also often result in blooms of larger phytoplankton like diatoms (Spatharis *et al*., 2007), which have high metabolic rates and significantly contribute to carbon fixation (Coggins *et al*., 2023). However, this can also enhance PCR, as observed during spring blooms in temperate coastal waters (the Celtic Sea, North Atlantic Ocean (García-Martín *et al*., 2019b), San Francisco Bay, North Pacific Ocean (Caffrey *et al*., 1998)). Overall, due to these important roles, nutrient availability is often considered as the main factor regulating plankton metabolism (Prichett *et al*., 2024), often surpassing the effects of other parameters, notably temperature (Staehr and Sand-Jensen, 2006; Marañón *et al*., 2018).

In European coastal waters, nutrient availability is either dictated by hydrographic processes, such as coastal upwellings, and anthropogenic inputs, often leading in eutrophication. Eutrophication is the process by which water bodies become enriched with excess nutrients, particularly nitrogen (N) and phosphorus (P), often due to agricultural runoff, wastewater discharge, and other anthropogenic activities (Clarke *et al*., 2006; Rabalais *et al*., 2009). Eutrophication has become an important environmental issue in many coastal waters of Europe, and notably in the Baltic Sea, where it is associated with bad ecological status since several decades (Murray *et al*., 2019). Eutrophication can lead to algal blooms, enhancing PCR, such as reported in a Danish estuary (Jensen *et al*., 1990), particularly when large blooms die off and decompose, fueling heterotrophic bacteria and depleting dissolved oxygen in the water column. This often results in hypoxia (low oxygen levels), which can stress or kill marine organisms and alter the structure of planktonic communities, also changing PCR (Murrell *et al*., 2013; Zhu *et al*., 2016). However, some other coastal waters of southern Europe have experienced oligotrophication – a reduction in nutrient inputs - in the last decades (Mozetič *et al*., 2010; Derolez *et al*., 2020). In addition, global climate change, particularly the increase in temperature, is expected to have profound impacts on the water column stratification— the layering of water due to differences in temperature and density— of water column, which is anticipated to be intensified, especially during the summer months (Li *et al*., 2020). This increased stratification can reduce vertical mixing, limiting the exchange of nutrients between surface and deeper layers and potentially impairing nutrient availability for plankton metabolism in surface waters (Mena *et al*., 2019). Similarly to eutrophication, increase stratification and oligotrophication can significantly alter PCR, as observed for example in a coastal Mediterranean system (Mallorca, Spain) in which oligotrophication resulted in a significant decline of PCR (Agustí *et al*., 2017).

In light of the crucial role eutrophication and oligotrophication – changes in nutrient inputs in general - play in regulating marine ecosystems, many experiments have been conducted to investigate the effects of changes in nutrients on coastal plankton communities. However, differences in the chemical forms of added nutrients, as well as variations in the magnitude and frequency of nutrient inputs, make it challenging to compare results across experiments. Three *in situ* mesocosm experiments, with similar designs and undertaken simultaneously, were performed to assess the effects of added nutrients (nitrate and ammonium) on coastal plankton communities from the Baltic Sea (Tvärminne archipelago, Gulf of Finland), the Mediterranean Sea (Bay of Blanes, North Western Mediterranean), and the Atlantic Sea (Hopavågen Bay, central Norway) (Olsen *et al*., 2006). In all three locations, PCR responded linearly with nutrient loadings, suggesting a common response of PCR toward eutrophication regardless of different environments. Accordingly, positive effects of nutrient enrichment, regardless of the magnitude, frequency or type of loading performed, were found in coastal Mediterranean waters: inputs of phosphorus, silicate, and nitrogen in the Bay of Blanes (Duarte *et al*., 2004), inputs of phosphorus-rich dust in the Bay of Blanes (Lekunberri *et al*., 2010), inputs of nitrogen- and phosphorus-rich dust in oligotrophic waters of the Mediterranean

(Gazeau *et al*., 2021), and inputs of ammonium and orthophosphate in the phosphorus-depleted Ionian basin (Lagaria *et al*., 2011). Similarly, positive effects of nutrient enrichment were also found in coastal Atlantic waters: inputs of nitrogen, phosphate and silicate-enriched deep water in the Canary Islands (Baños *et al*., 2022; Ortiz *et al*., 2022), inputs of nitrogen, phosphate and silicate-enriched deep water at varying silicate:nitrogen ratios in the Canary Islands (Ortiz *et al*., 2024), and, in the Ría de Vigo, with inputs of nitrogen-rich rainwater (Martínez-García *et al*., 2014) or with direct inputs of NH4NO3, Na2SiO3, and Na2HPO4 (López-Sandoval *et al*., 2025).

However, inorganic nitrogen and phosphorus inputs were found to decrease PCR in microcosms carried out with phosphorus-limited coastal Atlantic waters, while no effect were observed with the same experimental set-up in coastal Mediterranean waters, with lower *in situ* phosphorus-limitation (Cabrerizo *et al*., 2022), suggesting that the abiotic conditions to which plankton communities play a role in the observed response of PCR to nutrient loadings. Similarly, no significant effects of dust addition, and inputs of nitrogen, phosphate and organic matter, respectively, on PCR were found in coastal waters from the South Western (Cabrerizo *et al*., 2016) and North Western (Mercado *et al*., 2014) Mediterranean Sea. Furthermore, nitrogen-rich wastewater dissolved organic matter inputs decreased PCR from the coastal Baltic Sea, maybe due to the high lability of the added organic matter that could have fueled bacterial production without enhancing respiration (Vaquer-Sunyer *et al*., 2016). In contrast, the input of organic nutrients enhanced PCR in coastal Atlantic waters (Ría de Vigo, Spain) while the input of inorganic nutrients did not significantly affect PCR during the same experiment (Martínez-García *et al*., 2013). Overall, these results suggest that while increased nutrient availability generally has a positive effect on PCR, the unexpected absence or even negative response of PCR to nutrient enrichment in some cases may indicate complex mechanisms related to shifts in community structure and interactions among organisms. This complexity makes it difficult to predict the effects of climate change-related changes in nutrient availabilities on PCR in coastal waters on a global scale in the future.

3.4. Light and Ultraviolet Sensitivity

Light availability is a fundamental driver of plankton metabolism, directly influencing photosynthesis in phytoplankton (Striebel *et al*., 2023), and indirectly increasing overall plankton community respiration (PCR) through photosynthesis providing organic substrates that support respiratory processes (Pringault *et al*., 2009; Mesa *et al*., 2017). However, exposure to ultraviolet (UV) radiation, particularly UV-B (280-320 nm), can have both inhibitory and stimulatory effects on different components of plankton (Belzile *et al*., 2006; Moreau *et al*., 2014). UV radiation can impair photosynthetic efficiency and damage cellular structures, especially in surface-dwelling plankton, leading to stress-induced increases in respiration rates as cells repair damage (Agustí *et al*., 2014). Therefore, the balance between beneficial and harmful effects of light and UV exposure makes irradiance a complex yet essential factor in determining the metabolic balance of planktonic ecosystems. While Regaudie-de-Gioux *et al*. (2014) and Agustí *et al*. (2014) showed higher respiration rates and shifts toward heterotrophy at the global scale when comparing metabolism estimated in bottles that do not remove UV wavelengths (quartz bottles) versus bottles that do (glass borosilicate bottles), the only study that actually assessed the effects of increased UV radiations on PCR in larger volumes (2260 L *in situ* mesocosms) in European coastal waters reported no significant effects of a 20% increase in UVB radiations on PCR in coastal Mediterranean waters (Thau Lagoon, Vidussi *et al*., 2011).

In many coastal European waters, climate change and anthropogenic activities are increasing the frequency and intensity of terrestrial runoffs, lowering light availability and changing the light spectrum of the water column by bringing colored light-absorbing dissolved organic matter (the so called 'brownification' or 'darkening' phenomenon) (Frigstad *et al*., 2023; Opdal *et al*., 2023; Aigars *et al*., 2024; Solås *et al*., 2024). In Arctic coastal waters, this phenomenon is of extreme importance, notably due to the intensification of glacier melting and consequent huge runoffs of glacier meltwater (van Pelt *et al*., 2019). Accordingly, riverine runoffs were suggested to be the most important factor controlling PCR in some regions of the European Arctic (Vaquer-Sunyer *et al*., 2013). Many experiments have reported significant effects of terrestrial runoffs on plankton community structure in European coastal waters (e.g., Courboulès *et al*., 2023; Garnier *et al*., 2023; Ktistaki *et al*., 2024), however, only few experiments have investigated the effects of such phenomenon on PCR. In Norwegian coastal waters, brownification, simulated by the addition of a highly recalcitrant humic substance, decreased PCR by 27%, while light availability was reduced by 23% (Soulié *et al*., 2022c). Accordingly, an artificial decrease of light (to 32% of the full solar irradiance) significantly decreased PCR in coastal Mediterranean waters (Alboran Sea (Mercado *et al*., 2014)). In contrast, simulated terrestrial runoffs significantly enhanced PCR by 53 to 73% in coastal Mediterranean waters (Liess *et al*., 2016; Soulié *et al*., 2024), despite significant reduction in light availability. However, in both studies, the simulated terrestrial runoff added particulate or dissolved nutrients that fueled plankton metabolism to an extent that suppressed the negative effect due to light attenuation. These studies suggest the existence of a threshold of nutrient enrichment versus light reduction brought by terrestrial runoffs upon which the fate of PCR would depend, making it even more difficult to predict the effects of the increases in intensity and frequency of terrestrial runoffs due to climate change on the long term. In this regard, the limited number of existing studies in which PCR response to experimental light manipulation in natural communities calls for further investigation and experiments.

4. Knowledge Gaps in Studied Disturbances and Areas

Because measuring PCR can be time-consuming, labor-intensive, and expensive, PCR is usually not included in monitoring programs of coastal environments and in climate-change experiments (Breitburg *et al*., 2018; Wikner *et al*., 2023). Hence, available literature on the climate change effects on PCR remains quite scarce, notably in some understudied systems. A recent review on the contribution of PCR on ocean global deoxygenation highlighted the need of better parametrization of the influence of environmental and biological parameters, such as nutrient concentrations and stoichiometry or plankton community structure, on microbial respiration (Robinson 2019). Similarly, current models predicting ocean deoxygenation are still lacking a mechanistic understanding of respiratory oxygen demand to accurately reproduce observe ocean deoxygenation (Oschlies *et al*., 2018). In this regard, experiments can be used to characterize this mechanistic understanding and help resolve the influence of regional processes on global biogeochemical cycles.

The **Figure 1** represents the location of all the experiments testing climate change disturbance that were included in the present review. A clear difference in the extent systems have been studied can be seen from this map, with the Mediterranean and Baltic seas being more studied than other European coastal systems. Notably, no experiments testing the effect of climate change-related disturbances on PCR were published for the Black Sea, some parts of the Mediterranean Sea (e.g., the Adriatic Sea), and some parts of the Atlantic Ocean (e.g., the North Sea) (**Figure 1**). While common responses were identified regarding the effect of certain disturbances on PCR, some system-specific were also highlighted, emphasizing the need of more experimental studies in the understudied and unstudied systems. Regarding the complex relationships between PCR and environmental conditions, these experiments are needed to better our capacity to understand and predict the consequences of the global climate change on biogeochemical cycles.

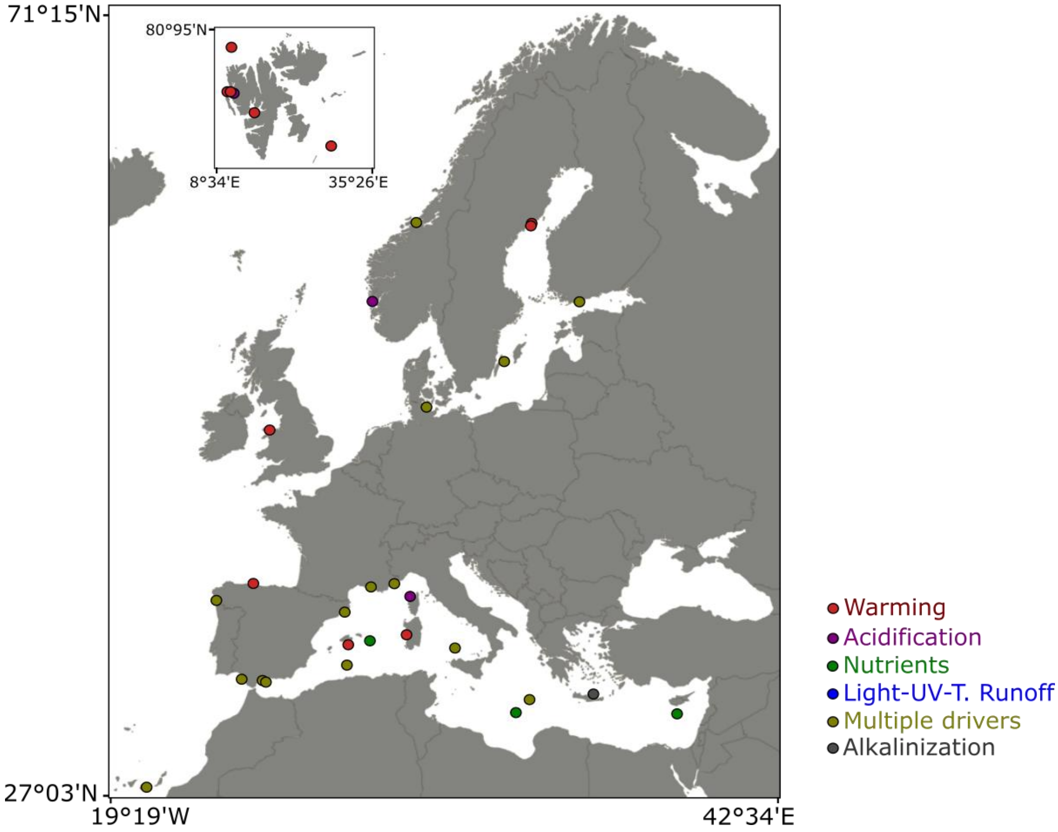

Figure 1. Location of the experiments testing the effects of climate change disturbances on plankton community respiration (PCR) in coastal waters of Europe. The 'multiple drivers' category encompasses locations in which multiple disturbances have been tested (either simultaneously or during different experiments).

Change in temperature is the most studied stressor (24 studies) among all experiments included in the present study (**Figure 2**), in accordance with the importance of water temperature in the regulation of metabolism at a global scale (Regaudie-de-Gioux and Duarte 2012; Boscolo-Galazzo *et al.*, 2018). Even if the positive impact of warming described in global ocean datasets and theoretical predictions was confirmed by experiments in many coastal systems, some studies highlighted contradictory responses of PCR to warming, often related to warming-induced trophic cascade phenomenon altering the biomass of phyto- and/or bacterioplankton. Typically, observations and long-term monitoring cannot parametrize such causal relationships, emphasizing on the need of experimental studies in diverse coastal systems. Changes in nutrient inputs and ratios, including here inputs of nutrients of any sort (terrestrial runoff, artificial inputs, dust inputs..) were the second most studied stressor (18 studies). Global climate change has been proved to greatly affect nutrient dynamics and cycling in the ocean (Hutchins and Capone, 2022), hence the importance of experimentally testing the effects of nutrient changes on PCR. As for warming, while the positive effect of nutrient inputs on metabolism, and so PCR, is straightforward, changes in nutrient ratios can alter community dynamics and interactions, ultimately impacting PCR. This calls for experiments in which nutrient inputs are closely mimicking naturally occurring processes and regional effects of climate change, such as done with Saharan dust inputs in the Mediterranean or changes in upwelling dynamics in coastal Atlantic waters. Finally, ocean acidification is also among the most studied stressors (13 studies) within all the experiments included in the present study. In contrast to temperature and nutrients, the effect of ocean acidification on metabolism at the global scale is difficult to predict. Importance of experimentations testing the effect of acidification on PCR is highlighted by the negative and positive effects found in coastal waters of the Baltic Sea (Spilling *et al.*, 2016) and the Canary Islands (Filella *et al.*, 2018), respectively, while all other studies found no significant effects on PCR. In this regard, other experiments are needed to confirm or infirm such results, and gain understanding in why significant effects were found in such systems but not in other. Other stressors, and notably changes in light and UV availability and spectrum, were not tested in many experiments (7 studies). Therefore, knowledge is still scarce regarding such consequences of climate change; however, certain coastal systems in northern Europe are now increasingly darker (Opdal *et al*., 2024), and knowledge of the effect of such disturbance on PCR is essential to be able to fully understand and predict the response of such systems in the future. Furthermore, experiments in which light is isolated from associated stressors, notably nutrients, are needed to be able to fully characterize the effects of light and disentangle them from potential effects of other environmental factors, as for now, only one study studied the response of coastal PCR to the input of recalcitrant humic substance to simulate coastal darkening so that light reduction and change in water color are simulated without nutrient enrichment (Soulié *et al*., 2022c). In addition to stressors included in the experiments testing PCR in European coastal waters, the effect of some disturbances related to climate change on PCR were never studied to my knowledge, while these disturbances can be locally very important in shaping the ecosystem. For example, salinity has decreased and is expected to continue to decrease in coastal waters of the Baltic Sea, due to increased precipitations and freshwater runoffs (Lehmann *et al*., 2022). Such salinity changes have been shown to shift zooplankton (Hall and Lewandowska, 2022) and phytoplankton (Pilkaitytë *et al*., 2004) community composition, and induce changes in copepod respiration (Soulié *et al*., 2022d), but no study have still investigated the effects of salinity changes on PCR in the Baltic Sea. Similarly, intensification of glacier meltwater runoffs (increased by 11% since the 1980-2000 period) in the coastal Arctic Ocean have been shown to increase and decrease phytoplankton productivity with marine- and land-terminating glaciers, respectively (Ardyna and Arrigo, 2020), but no experimental study has ever been performed to assess the response of PCR toward glacier meltwater, even if such response may play a crucial role in the future Arctic Ocean biogeochemical cycles.

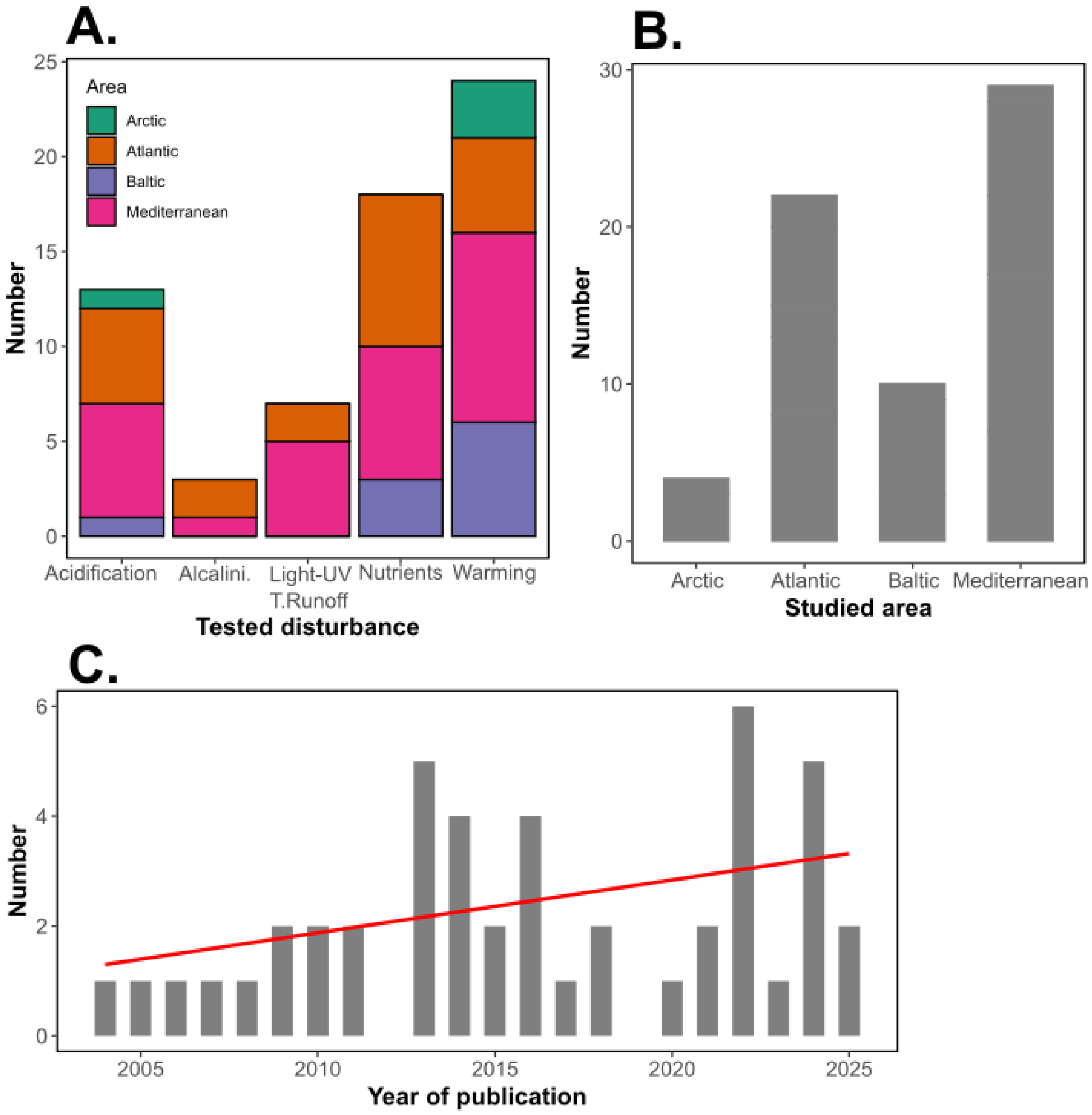

Figure 2. Number of studies describing experiments in which the effects of climate change disturbances on plankton community respiration (PCR) were investigated in coastal waters of Europe, separated based on tested disturbance (**A.**), studied area (**B.**), or year of publications (**C.**).

While studying individual drivers like temperature, pH, and nutrient concentrations provides valuable insights in to the response of PCR and can inform specific mitigation strategies, it's essential to study these factors simultaneously as they often act in combination in natural settings. These simultaneous changes can lead to complex, interactive effects on planktonic communities that might not be predictable based solely on the isolated impact of each driver (e.g., Moreno *et al*., 2022). Among all experiments included in the present review, only 7 studies tested different drivers simultaneously in full factorial designs. These studies can help understand the response of PCR toward simultaneous stressors, similarly to what occurs naturally in coastal waters, and if these disturbances will act antagonistically or synergistically on PCR. Many experiments highlighted complex interactions between stressors, and the effect of stressors applied simultaneously often differs from the addition of single-stressor effects. For example, Cabrerizo *et al*. (2022) showed that the effects of +3°C warming on PCR acted additively to nutrient enrichment in coastal Mediterranean and Atlantic waters, but only under future conditions of pH and UV irradiance. Overall, a more holistic approach, using multi-driver experiments, is crucial for developing effective mitigation strategies that reflect the multifaceted reality of global change.

The present review listed a number of studies assessing the complex responses of PCR in European coastal waters towards various climate change effects, this number following an increasing trend since the early 2000's (**Figure 2**), suggesting that an increasing number of scientists and projects acknowledge the great importance of PCR in the functioning of coastal ecosystems and global biogeochemical cycles. However, this review mainly stresses out the scarcity of studies in which PCR is actually monitored, putting into light understudied regions and stressors, and calling for a better integration of PCR in both experimental studies and long-term monitoring programs. Future research on the effects of climate change on PCR should consider integrating approaches that combine experimental studies, long-term monitoring, and modeling techniques. While experimental studies offer controlled environments to test specific hypotheses on PCR and isolate the effects of stressors, long-term monitoring programs can help capture natural variability and identify trends in PCR while taking into account the full complexity of natural systems. Coupling these approaches with predictive modeling can help bridge the gap between small-scale, short-term experiments and the complex, large-scale dynamics of coastal ecosystems. Such an integrated framework is vital for informing conservation strategies and sustainable management of coastal waters in the face of global climate change.

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