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Regulation of marine plankton respiration: A test of models

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Plankton respiration is a major process removing oxygen from pelagic environments and constitutes one of the largest oxygen transformations in the sea. Where the O_2 supplies due to dissolution, advection and oxygenic photosynthesis are not sufficient, hypoxic, or anoxic waters may result. Coastal waters with limited water exchange are especially prone to have low oxygen levels due to eutrophication and climate change. To support marine environmental management in a period of rapid climate change, we investigated the current knowledge of regulating plankton respiration based on field and experimental studies reported in the literature. Models for regulation of plankton respiration was tested on a three-year field data set. Temperature is the most reported predictor positively influencing plankton respiration (mean r^2 = 0.50, n=15). The organic carbon supply driven by primary production has a similar coefficient of determination but fewer reported relationships (mean r^2 = 0.52, n=6). Riverine discharges of dissolved organic carbon can override the influence of primary production in estuaries precluding effects of nutrient reductions. The median predictions of respiration regulation produced by current models vary by a factor of 2 from the median of observed values and extreme values varied even more. Predictions by models are therefore still too uncertain for application at regional and local scales. Models with temperature as predictor showed best performance but deviated from measured values in some seasons. The combined dependence of plankton respiration on temperature, phytoplankton production and discharge of riverine organic carbon will probably lead to increased oxygen consumption and reduced oxygen levels with projected climate change. This will be especially pronounced where increased precipitation is expected to enhance riverine discharges of carbon compounds. The biologically mediated transfer of carbon for long-term storage in deeper layers will slow down. Implementation of plankton respiration measurements in long-term ecological monitoring programs at water body and basin scales is advocated, which would enable future multivariate analyses and improvements in model precision across aquatic environments.

1 Introduction

1.1 Biological and microbial carbon pump concepts

The development of large volumes of sea water with low oxygen concentrations (hypoxic) or where oxygen is absent (anoxic) is of increasing concern for society and for the sustainability of marine ecosystem services (Diaz and Rosenberg, 2008; Rabalais et al., 2010; Zhang et al., 2010; Carstensen et al., 2014; Breitburg et al. 2018). Outgassing due to elevated temperatures and enhanced respiration rates of marine organisms are two major processes that decrease oxygen concentrations in aquatic systems (Oschlies et al., 2018). In addition to removing oxygen, respiration also contributes to elevated atmospheric carbon loads by producing CO_2 (Figure 1) (Rivkin and Legendre, 2001; Sanders et al., 2016). Current estimates show that less than 1% of carbon assimilated in the sea will end up in deep waters over millennia and thus be removed from biosphere cycling. More than 90% of sedimenting carbon is mineralized back to the atmosphere as CO_2 by respiration (Henson et al., 2011; Bach et al., 2019; Fender et al., 2019; Giering et al., 2020). Consequently, the regulation of respiration and associated oxygen consumption will be crucial to accurately model marine and global carbon cycles and to assess the ability of biological and microbial carbon pumps to mitigate CO_2 levels in the biosphere (Dang, 2020). This knowledge is also crucial for stakeholders and environmental managers who are responsible for sustaining ecosystem functions, biodiversity, and chemical compositions in the sea.

Therefore, we investigated the current understanding of the regulation of plankton respiration using reported general models applied on a coastal multi-year data set of plankton respiration from the well-studied Öre Estuary located in the boreal zone (The

FIGURE 1
Schematic view of the role of respiration in the biological and microbial carbon pumps in the sea. Respiration drives oxygen consumption and mineralization of organic carbon pools to CO_2 and its emission to the atmosphere. Understanding respiration regulation is therefore crucial for the carbon budget of the atmosphere and the capacity of the ocean to assimilate carbon. Phyto-, protozooplankton and prokaryotic plankton are crucial for operating these processes together with mesozooplankton.

Baltic Sea, Vikström and Wikner, 2019; Vikström et al., 2020). The boreal zone constitutes the next largest land carbon reservoir on the planet (Pan et al., 2011), and a substantial load of organic carbon is discharged to the coastal zone (Reader et al., 2014). Coastal waters are important due to high marine biodiversity and productivity, load of terrestrial organic carbon by river discharge and that limited water exchange increases risk of hypoxia in some coastal areas (e.g., the Baltic Sea). Pelagic respiration is dominant in the water column and is the focus of this study, while benthic respiration comprises one-fourth of total marine respiration in estuarine waters (Hopkinson and Smith, 2005). In deeper oceanic environments, pelagic respiration is expected to be even more dominant due to degradation of sedimentary matter by bacterioplankton (Cho and Azam, 1988). Plankton respiration will thereby have a major impact on the marine carbon distribution between the organic fraction and CO_2 in both coastal and offshore environments.

1.2 Role of respiration in BCP

The "biological carbon pump" (BCP) is defined as the assimilation of CO_2 and synthesis of biomass by autotrophic plankton, followed by sedimentation of dead and aggregated cells as well as faecal pellets produced by grazing zooplankton to deeper water layers (Figure 1). The major transformation of biomass to CO_2 occurs in surface waters, and less than 10% is transported to deeper waters (Henson et al., 2011). The potential transformation by prokaryotes of the bioavailable carbon substrates reaching the deep water to recalcitrant compounds is named the "microbial carbon pump" (MCP). Direct evidence for the generation of recalcitrant compounds is methodologically challenging, and only limited experimental evidence has been reported thus far (Jiao et al., 2010). The combined action of BCP and MCP has been proposed as a mechanism of the biosphere to remove CO_2 from the atmosphere, a mechanism that is proposed to be bioengineered to speed up CO_2 removal.

BCP and MCP are efficiently counteracted by respiration throughout the entire water column (Robinson, 2019). Prokaryotes not only mineralize dissolved and particulate organic matter in the surface layer but also colonize, dissolve and degrade sedimenting aggregates and faecal pellets (Cho and Azam, 1988; Azam and Malfatti, 2007). Determinations of mainly free-living prokaryotic respiration are relevant, as the contribution from respiration by particle-associated prokaryotes seems limited (Belcher et al., 2016), possibly due to the efficient dissolution of aggregates. Microorganisms perform this degradation of organic matter and thereby dominate oxygen consumption in the sea, where phyto- and bacterioplankton account for approximately 33% each, and protozooplankton accounts for 24% (Figure 2, Robinson et al., 2005). The respiration by microbial plankton in the water column is thereby a major cause of the small fraction of carbon reaching the deep ocean, which originally formed in the marine photic zone. Consequently, oxygen consumption contributing to hypoxia and emission of CO_2 will mainly be caused by microbial activity in the pelagic realm. For coastal
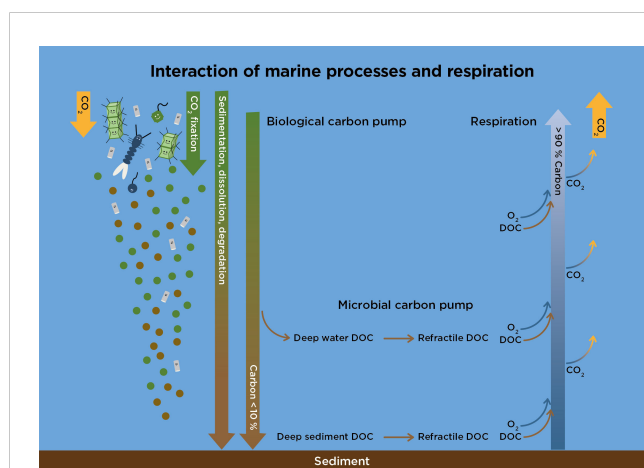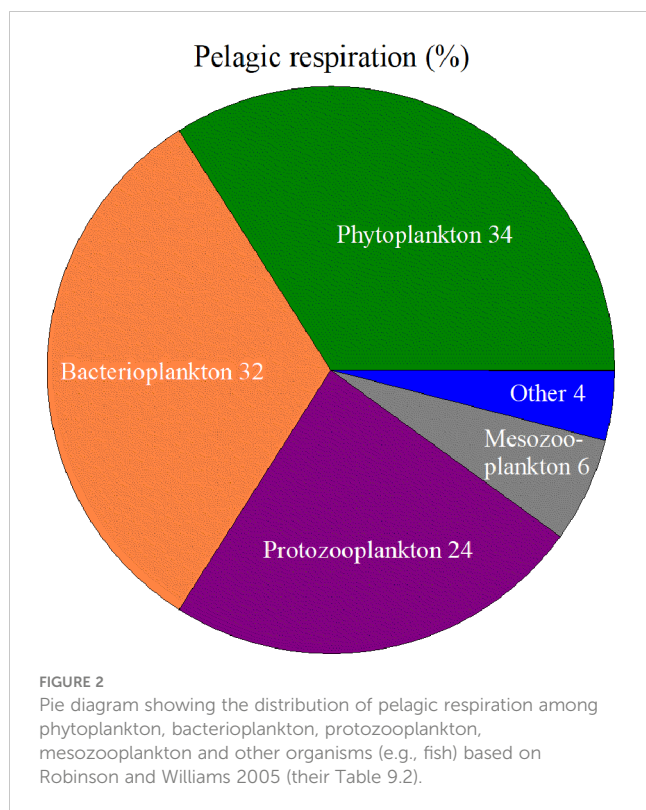
FIGURE 2
Pie diagram showing the distribution of pelagic respiration among phytoplankton, bacterioplankton, protozooplankton, mesozooplankton and other organisms (e.g., fish) based on Robinson and Williams 2005 (their Table 9.2).

and estuarine environments, it is relevant to point out that planktonic respiration is already a major process that converts organic carbon to CO_2 in shallower waters (i.e., > 40 m bottom depth) (Sandberg et al., 2004; Hopkinson and Smith, 2005).

A better understanding of the controlling factors of plankton respiration and how it will be affected by projected climate changes is therefore important. We compile the current understanding of how oxygen consumption is regulated with a particular focus on plankton respiration in the boreal zone. Fish respiration was not investigated, as it constitutes a relatively small part of pelagic respiration (Figure 2, Robinson et al., 2005). Mesozooplankton abundances in Winkler bottle volumes are too low (typically < 150 ml) to contribute to these measurements. Additionally, mesozooplankton respiration constitutes a small share of pelagic respiration (Figure 2, Robinson et al., 2005).

2 Methods

2.1 Study design

Reports providing empirical evidence for how pelagic oxygen consumption is regulated were compiled from the current literature, reviews, and book sections. Models related to pelagic oxygen consumption were also searched in articles using physical-biogeochemical models to project the effects on oxygen status caused by climate change. Pelagic oxygen consumption consists primarily of plankton respiration, including bacterioplankton (i.e., prokaryotic plankton, Figure 2). Benthic respiration and NH_4 oxidation (e.g., nitrification) were not investigated.

The reported mathematical functions with predictors, coefficients of determination (r^2) and coefficients of precision were collected. The r^2-values were used as a measure of the strengths of relationships. When log transformed data were used to define the statistical relationship those relationships were given lesser rank than relationships obtained with untransformed data to predict plankton respiration on regional or local scales.

Selected equations modelling plankton respiration were tested for their predictive powers using a three-year field dataset (Vikström et al., 2020) and a study of bacterioplankton respiration (Vikström and Wikner, 2019), both collected from a boreal estuary in the northern Baltic Sea.

Reported assessments of the expected effects of current climate change projections on oxygen consumption and oxygen concentrations in the references were compiled.

2.2 Collection of references

A comprehensive compilation of the scientific knowledge of aquatic respiration contained in the book by Williams et al. (2005) was used to cover older references. An earlier compilation of bacterioplankton respiration was found in Robinson (2008).

The Web of Science was searched using the following syntaxes: (TS=respiration OR (TS=oxygen AND TS=consumption)) AND (TS=marine OR TS=Sea) AND (TS=climate AND TS=Change) (date of search: 15th September 2022) and (TS=respiration OR (TS=oxygen AND TS=consumption)) AND (TS=marine OR TS=Sea) AND (TS=control AND TS=Regulation) (date of search: 16th September 2022)

References in the authors' EndNote libraries and paper copy libraries from three decades of research were another source for collecting references.

2.3 Search strategy

Articles and chapters were searched for figures that showed relationships between oxygen consumption or respiration versus different predictors. Only marine environments were investigated. The equations for relationships should be reported with at least the coefficient of determination provided. It was also ideal when the statistical significances, number of values and precisions of derived coefficients of the fitted model were reported.

Reports of Q_{10}- or activation energy-values (E_a) for plankton and bacterioplankton respiration were compiled from estuaries and ocean ecosystems.

The texts were screened for titles, subtitles, or conclusions regarding oxygen consumption regulation. In addition, reported assessments of the effect of climate change on oxygen consumption and oxygen status were compiled.

Predictors where significant relationships from several investigations were available were selected for further analysis. Here, the equations reported were compiled and ranked according to their r^2 values as indications of model fit. Ease of prediction was seen as key for application to environmental management.

2.4 Data sources

A three-year multiple season dataset of planktonic respiration that was measured with optode sensors (the OPTOCS method, n=191, Vikström et al., 2020) and bacterioplankton respiration data from two seasons (n=42, Vikström and Wikner, 2019), estimated with the same method. The two datasets are from the boreal Öre Estuary (northern Baltic Sea), with high riverine carbon input and encompasses complementary data such as primary production ($^{14}CO_2$ incorporation), bacterioplankton community growth rates (^{3}H-thymidine incorporation), bacterioplankton carbon contents, temperatures, dissolved organic carbon and nutrients. The datasets were used for testing the different models found in the literature in a coastal boreal environment.

One significant relationship was reported as an r^2 value by Hopkinson and Smith (2005) but lacked derived equations or associated statistical information. To add this model to the analysis, data were extracted from their Figure 8.9 (WebPlotDigitizer, https://apps.automeris.io/wpd/) and were added to Table 1.

2.5 Data analysis

To evaluate the explanatory degrees of models (i.e., Figure 3), the category "plankton respiration" included one "phyto"- and "picoplankton" category each. Additionally, one "planktonic and benthic" category was joined with the plankton category. Discrete values from different depths were used for model testing unless the model was designed for integrated values, where the observed values were integrated in the same manner. Boxplots were used to describe the levels and distributions of values when more than one case occurred. Determinations of model capabilities to predict plankton respiration in the dataset with observations were performed in R Studio (version 2022.07.01 + 554, R_Core_Team, 2021) and packages therein. The conformity between the observed and predicted values of the different models was assessed by boxplots across seasons and residual root mean square error (RMSE) values (Sokal and Rohlf, 1995). Boxplots indicate conformity for both the level and distribution of data, while the RMSEs show residual variances that are not explained by the models. When using temperature as the main driver, the measured temperature at the time of estimation of respiration was used. Complementary data were extracted from the dBotnia database (dBotnia, 1994), which are identical to those reported by Vikström et al. (2020). For the model by Eilola et al. (2009), bioavailable detritus was modelled as $0.75 \times [DOC]$ assuming 50% of marine DOC to be bioavailable and POC constituting 25% of total organic carbon (Forsgren and Jansson, 1992; Sandberg et al., 2004). Bacterioplankton abundances and growth rates were available in the authors' datasets and are presented in Vikström and Wikner (2019). The measurement of oxygen consumption by optodes sensors (OPTOCS method) enables extraction of initial air saturations and oxygen concentrations from individual runs and was used here for Equation 7 (Table 1). Model fits were evaluated by the root mean square error values calculated for each model (Equation 1) and are presented in Supplementary Table S2.

TABLE 1 Functional relationships and their coefficient of determination (r^2) for different quantities of pelagic respiration compiled from the indicated references.

Equation No.	Equation	Explanatory factor	r^2	p	n
3	$PR=0.005e^{0.086T}$	Temperature	0.87	<0.01	14[7]
4	$R=4.94(\pm 2.30)GPP^{0.74\,(\pm 0.087)}$	Gross primary production	0.72[a]	0.041,<0.001	29[5]
5	$PR=0.33(\pm 0.070)T$	Temperature	0.63[a,b]	<0.001	15[6]
6	$\Sigma R= 4.57 + 0.73\Sigma NPP$	Net phytoplankton production	0.54	0.02	65[8]
7	$R=-23+0.51NPCP$	Net plankton community production	0.48	<0.001	46[9]
8	$R=f(T)C_r(O_2/(O_2+k_1))$	Temperature and oxygen conc.	–	–	–[4]
9	$PR=0.002e^{0.15T}\times[DOC+POC]\times0.0019$	Temperature and organic carbon supply	–	–	–[10]
10	$\log_{10}R=1.0(\log_{10}P)^{0.78(\pm 0.02)}$	Gross primary production	0.66	–	874[1]
11	$\log_{10}BR=3.69(\log_{10}BG)^{0.58}$	Bacterioplankton growth	0.56	<0.001	286[2]
12	$\log_{10}BR=0.05T-0.59$	Temperature	0.32	<0.001	286[2]
13	$\log_{10}BR=1.62(\log_{10}BA)^{0.81}$	Bacterioplankton abundance	0.27	<0.001	260[2]
14	$\log_{e}\rho=26.49-0.589/kT$	Temperature	0.20	<0.001	205[3]
15	$\log_{10}BR=0.02(\log_{10}DOC)^{0.80}$	Dissolved organic carbon	0.18	<0.001	167[2]

Models are sorted on untransformed and logarithmic values and then descending level of the r^2-value within those categories. The measured quantities are ecosystem respiration (R), plankton respiration (PR), bacterioplankton respiration (BR), and specific prokaryotic respiration (ρ). The standard errors of coefficients are shown in parentheses, probabilities of type I errors (p) and numbers of cases (n) are presented where reported. References are given as exponents next to the n values.
[1]Duarte and Agusti (1998), [2]Robinson (2008), [3] López-Urrutia and Morán (2007) (k is Boltzmann's constant), [4]Bendtsen and Hansen (2013) (k_1 is pelagic O_2 half-saturation constant), [5]Hopkinson and Smith (2005), [6]Panigrahi et al. (2013), [7]Smith and Kemp (1995) (Mid bay, upper layer), [8]Williams (1998) (Σ=depth integrated values), [9]Smith and Kemp (2001), [10]Eilola et al. (2009), -=not reported, [a]Adjusted r^2. [b]Values (26% of total n) recalculated and corrected for observed oversaturation of oxygen.
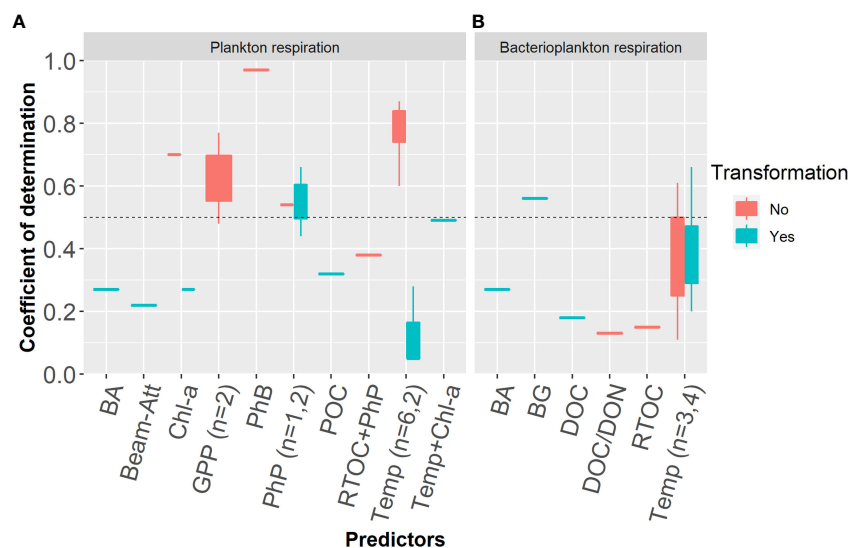
FIGURE 3
Boxplots showing the distributions of the coefficient of determination (r^2) of environmental predictors for plankton respiration **(A)** and bacterioplankton respiration **(B)** reported in the literature. The dashed horizontal black line represents the level for 50% of the explanation. Categories without any boxplot distributions represent values from a single study. The numbers of observations for categories exceeding 1 are shown. The predictors bacterioplankton abundance (BA), beam attenuation (Beam-Att), chlorophyll-a (chl-a), phytoplankton biomass (PhB), phytoplankton production (PhP), particulate organic carbon (POC), riverine total organic carbon (RTOC), temperature (Temp), bacterioplankton growth (BG), dissolved organic carbon (DOC) and dissolved organic nitrogen (DON) are shown.

$$RMSE = \sqrt{\frac{\Sigma(Measured - Predicted)^2}{n}} \qquad \text{Eq. 1}$$

3 Results and discussion

A total of 36 references were found that included empirical information regarding plankton respiration regulation (Supplementary Table S1). Three of those lacked coefficients of determination and were removed from the data analysis of r^2. The publication years of the collected articles covered 1991 to 2020. One-third of those came from books that previously reviewed the subject field. In addition, 4 references reporting different coupled physical-biogeochemical models were reviewed.

3.1 Models for regulation of respiration

As a primary strategy to investigate the current knowledge of plankton respiration regulation, we reviewed some of the models that were applied to simulate the marine carbon cycle. However, in several references the equations used for oxygen consumption were not provided, alternatively based on mass balance calculations or on relationships coupled to nitrogen cycling (Neumann et al., 2002; Savchuk, 2002; Eilola et al., 2009; Meier et al., 2011b). Among reported equations, the Swedish Coastal and Ocean Biogeochemical model (SCOBI) calculate pelagic oxygen consumption based on detritus mineralization and temperature (Eilola et al., 2009). Bendtsen and Hansen (2013) provided a model for oxygen consumption that is included in Table 1, referring to White et al.

(1991); Pomeroy and Wiebe (2001) and Lomas et al. (2002) regarding temperature control of pelagic respiration. Their relationship uses a temperature sensitivity-dependence (Q_{10}-value) and half-saturation constant for oxygen concentrations that differs from most other relationships presented in Table S1. They also calculated benthic respiration in a similar manner using different parameter values. The inclusion of oxygen concentration is scientifically motivated but rarely used, as many studies of plankton respiration are performed in well oxygenated environments. However, in environments showing hypoxia, this predictor becomes crucial for proper modelling of oxygen consumption. However, no quality measure of the relationship by Bendtsen and Hansen (2013) is provided, such as the explanation degree or other measures of fit to observed data.

3.2 Experimentally derived regulation of respiration

3.2.1 Character of references

Few studies have directly addressed the regulation of plankton respiration. Research with a focus on respiration has been directed toward the trophic balance between pelagic respiration and carbon fixation (Duarte and Agusti, 1998; Williams and Le, 1998; del Giorgio and Duarte, 2002; Williams et al., 2004) and more recently, climate change effects (Lopez-Urrutia et al., 2006; Vazquez-Dominguez et al., 2007; Sarmento et al., 2010; Panigrahi et al., 2013). One study that directly addressed the regulation of bacterioplankton respiration showed a relationship to DOC (Alonso-Saez et al., 2008), and several studies of respiration in Chesapeake Bay also provide valuable results that are relevant to the

regulation of plankton and bacterioplankton respiration (Smith and Kemp, 1995; Smith and Kemp, 2001; Smith and Kemp, 2003). Relationships among respiration and various predictors are also reported in an outstanding review and synthesis of respiration studies in aquatic environments (Williams et al., 2005). For bacterioplankton respiration, a book section by Robinson (2008) provided a comprehensive background. Given the limited community of distinguished researchers in the field who are included in the reference list, earlier reviews of respiration and our own research activity in the field in the past two decades, the risk of having overlooked key reports is assessed to be low.

3.2.2 Explanatory power of predictors

Studies reporting significant relationships with different predictors were compiled to assess the current knowledge of plankton respiration control (Table S1). The reported coefficient of determination (r^2 univariate, R^2 multivariate) were used as measures of the explanatory powers of the relationships. A plot of r^2 versus predictor provides an overview of the current understanding of plankton and bacterioplankton respiration regulation (Figure 3). Due to varying types of respiration that were measured and distributed as untransformed or transformed values, the number of cases for each combination with predictors become low. The ambient temperature in the sampled environment is the most reported governing predictor (grand mean r^2 = 0.50, n=15). Reports using untransformed values for plankton respiration are typically obtained in more homogenous environments and show higher coefficient of determination than those based on logarithm transformed values (i.e., cross-ecosystem studies). Analyses of temperature regulation based on untransformed values alone were performed on aggregated basins or environments that were deemed similar (i.e., estuaries) and resulted in a grand mean r^2 of 0.61 (n=9). Cross-system analyses, which are typically based on logarithm transformed values prior to statistical tests, show a lower mean r^2- value of 0.32 (n=6) for temperature. Coefficient of determination based on untransformed values are higher (r^2 = 0.74, n=6) than when based on logarithm transformed values for plankton respiration, but not so for bacterioplankton respiration. Given the lower coefficient of determination and that back-transformed coefficients are associated with wider confidence intervals, the uncertainties for relationships based on logarithm transformed values are substantial. Increasing imprecision when transforming a predictive function from logarithmic to untransformed measures is of concern when applied to local water bodies or when doing basin scale planning within marine environmental management.

The supply of carbon substrates as a regulator of plankton respiration is also reported, albeit with fewer cases (r^2 = 0.52, n=6). Those encompasses different predictors, such as gross primary production (GPP), net primary production (NPP), net plankton community production (NPCP) and riverine DOC (rDOC). The coefficient of determination are comparably high based on the untransformed values for GPP alone (r^2 = 0.63, n=2), representing estuarine environments. One report of a significant relationship with phytoplankton biomass (i.e., chlorophyll-a) from

the Gulf of Riga had the highest r^2 value reported for a predictor but re-analysis resulted in a lower value (r^2 = 0.65, year 1995 data) (Olesen et al., 1999). This value was close to one case of a high explanation for chlorophyll-a based on untransformed values reported from the Chesapeake Bay (r^2 = 0.70) (Smith and Kemp, 2001). The predictive power of phytoplankton abundance may reflect its importance as a source for carbon substrate supplies *via* zooplankton exudation, faeces pellet production and dissolution. A lack of effects of mineral nutrients (e.g., NO_3 and PO_4) on bacterioplankton respiration was reported in a one-year field study (Lemée et al., 2002). The relationship with the supply of organic carbon substrates (including plankton biomass) is directly relevant for assigning eutrophication as a cause of hypoxia development. The high coefficient of determination between plankton respiration and gross primary production from estuaries is the most powerful relationship reported of this type (r^2 = 0.77, n=29, untransformed) (Hopkinson and Smith, 2005).

When comparing results and models from different studies both the environmental conditions and methodology applied may influence the results. Still models for regulation of plankton respiration is typically presented as being generally applicable, and ideally should be so, motivating validation in any environment at this stage. Field studies dominated the data set of 37 studies (Table S1) investigated, with only two microcosm studies and one mesocosm and model study each. Spatial and temporal scale of studies vary and could also influence models. Sampling varies from individual stations, *via* coastal transects to compilation of marine data across sea areas. Temporal scales from days to several years occur. 18 studies were done in estuarine environments, most of them in the boreal zone. Studies representative of oceanic environments amounts to 13. Temperature should have a similar basic effect in most environments, but likely influenced by the level of the ambient water temperature and type of organic matter present. This can be one cause of deviating precision of the models. Estuaries will be directly influenced by input of terrestrial organic matter from rivers with some bioavailable fraction and a large humic component. The influence of riverine discharge is lacking in identified models but shown as a major driver in a Baltic Sea estuary (Vikström et al., 2020). The autochthonous productivity in meso- and eutrophic environments appear to systematically increase plankton respiration, although continued increase (Duarte and Agusti, 1998; Williams and Le, 1998) or levelling off (Hopkinson and Smith, 2005) at higher productivity rates differ between studies.

3.2.3 The dual influence of temperature

Distinguishing between the effects of temperature and substrate supply is challenging. An increase in temperature (T) increases the probability of elements and molecules colliding and thereby the chemical reaction rate (k) at a given activation energy (E_a) for a chemical reaction:

$$k = Ae^{-E_a/RT} \qquad \text{Eq. 2}$$

where R is the molar gas constant and A is a collision frequency constant (Dickerson and Geis, 1979). Temperature thereby affects

both enzyme catalysis of reactions by conformational change of the enzyme, and the chemical reactions of the creation and/or breakage of chemical bonds in or between the substrates. Consequently, organisms, especially bacterioplankton, should also experience elevated temperatures as an extended pool of available substrates. Higher temperature makes many chemical reactions more energetically favorable and thereby more substrates should be possible to use for metabolism. To better approach the issue of confounding predictors, we advocate that future research include multivariate collection of data accompanied by multivariate statistical analyses, including predictor influence measures and correlations. Reports where different predictors have been challenged in multiple stepwise regressions are scarce, and it is therefore not possible to assess whether higher coefficient of determination can be achieved using several predictors. Panigrahi et al. (2013) reported results from a multiple regression with temperature and chlorophyll-a, where only temperature remained once the data were adjusted for samples with oxygen oversaturation (>100%).

3.2.4 Riverine DOC as a source of substrates

Riverine discharge of DOC drives a significant share of plankton respiration in the boreal northern Baltic Sea with high freshwater influence (r^2 = 0.38, n=46) (Vikström et al., 2020). Riverine DOC exceeds the carbon supply from estuarine phytoplankton carbon fixation by 4-fold and explains part of the high plankton respiration levels during winter with negligible phytoplankton production (i.e., baseline respiration, del Giorgio and Williams, 2005). Other reports of significant plankton respiration at zero phytoplankton production prevail (Williams and Le, 1998; Du and Shen, 2015), although this was not further discussed by the authors. Thus, riverine DOC can supply coastal respiration with carbon substrates when discharges are sufficient and should be considered together with primary production in coastal areas.

3.2.5 Bacterioplankton growth as a predictor

Bacterioplankton respiration shows a coupling to bacterioplankton growth that is recommended as a preferred predictor (Robinson, 2008). This finding reflects that favorable growth conditions for bacterioplankton in general promote their respiration. When using bacterioplankton biomass growth as an environmental indicator, this can provide valuable information for managers on the trophic status and indicate the level and development of oxygen consumption. In this context, the observation that bacterioplankton respiration lacks a relationship to prokaryotic diversity is relevant (Reinthaler and Herndl, 2005) and is supported by other reports of functional redundancy in prokaryotic communities (Fernandez-Gonzalez et al., 2016). However, a recent report in contrary demonstrate significantly different respiration rates between lineages, but still a positive relationship to growth rate (Munson-McGee et al., 2022). For other questions such as climate change effects, external environmental predictors are of more value for projecting net outcomes for bacterioplankton respiration. As bacterioplankton

growth estimates also have marked uncertainty and evaluated factors are $\log_{10}$-transformed, the predictive value of those equations for managing the marine environment is limited (Figure 3 and 4). In addition, uncertainty estimates of the derived coefficients are rarely provided in the covered literature regardless of the predictor involved, which precludes assessments of model precision.

3.2.6 Maintenance activities contribute to respiration

Complicating the relationship between bacterioplankton respiration and growth, the contribution of maintenance respiration of prokaryotes is probably of a sufficient extent to influence plankton respiration regulation in the field (Carlson et al., 2007; Vikström and Wikner, 2019; Verma et al., 2022; Wikner and Vikström, 2023). This should also apply to other planktonic organisms (e.g., Norberg and DeAngelis, 1997) but is not discussed in a review of zooplankton respiration (Hernández-León and Ikeda, 2005). The influence of maintenance respiration should weaken the relationships with growth-related predictors. Temperature plausibly influences maintenance respiration as well, but other factors in the environment that regulate maintenance activities of organisms should also contribute. Activities such as
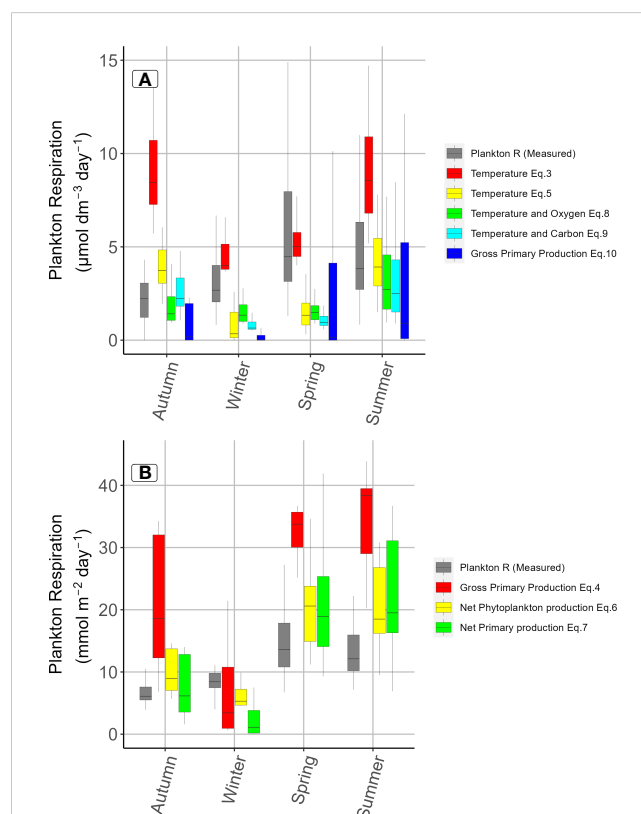

FIGURE 4
Comparison of observed values for plankton respiration in a boreal estuary and modelled values based on indicated functions from the literature (Table 1). Boxplots show the median values, interquartile range (25-75%) and the 0-25% and 75-100% quartiles. Models based in discrete **(A)** or integrated values **(B)**, respectively, are shown in separate panels.

maintaining osmotic potential inside cells requires energy metabolism *via* increased ATP synthesis. Nutrients (e.g., nitrogen and phosphorus) are also required for the synthesis of osmolytes, repair of nucleic acids, enzymes, and other cell constituents. However, as elements for maintenance metabolism can be recycled intracellularly and be independent of biomass increase, a share of pelagic respiration should be uncoupled from external nutrient supply. A better understanding of maintenance activities in plankton is recommended for future research to increase our knowledge of maintenance respiration regulation.

3.3 Fit of relationships to a multiyear dataset

3.3.1 Prediction of plankton respiration

The ability of selected relationships to predict a three-year annual dataset of respiration rates from the boreal northern Baltic Sea at the four major seasons were tested (Table 1, Vikström et al., 2020, Figures S1-S13). The power of models to predict respiration were assessed by median and spread of values in boxplots and by root mean square errors between predicted and observed values (Figures 4, 5). Low values of RMSE indicate good predictive power (Sokal and Rohlf, 1995), while match between observed and modelled data sets regarding median and spread were assessed visually. All functions deviated from the observed values for plankton respiration at some season (Figure 4). Temperature and oxygen (Eq. 8) and temperature and carbon (Eq. 9) showed good match on both level and spread with observed values in autumn and summer, while being clearly lower than observed values in winter and spring. Also, net phytoplankton production (Eq. 6) and net primary production (Eq. 7) showed good match regarding the median, but generally larger spread than observed values (c.f., integrated values). Temperature alone (Eq. 3)

matched the median well in winter and spring, while being markedly higher at other seasons. Noticeably, the other temperature equation (Eq. 5) was instead closer to observed values in summer and autumn, but lower in winter and spring, showing a correlation to Eq. 3 but on a markedly lower level. For discrete values, 4 of 5 models showed good match during summer while being more scattered other seasons. Gross primary production (Eq. 4) deviated most for integrated values, despite showing a high r^2-value to data in the original article.

The analysis of root mean square error (RMSE) encompassed all seasons (Table S2). Model Eq. 5, 8, 10, 9, and 3 showed low RMSE values in ascending order (3.3-4.0 µmol dm^{-3} d^{-1}). All these coincided with models performing well in the box-plot analysis above. However, models with low RMSE were also associated with the highest number of cases tested (*n*>178 per model). For phytoplankton production, related tests could only include 51 cases, and the difference in *n* may have contributed to the different RMSE observed.

Even if many predicted distributions of plankton respiration remain within a factor of 2 relative to the observed values, substantial deviations occur that contribute to uncertainty in projecting the effects due to climate change and anthropogenic disturbance. Therefore, none of the tested equations could model the observed respiration rates in the northern Baltic Sea with sufficient accuracy and precision in all seasons. A statistically significant relationship between plankton respiration and temperature has previously been reported for the reference estuary (Panigrahi et al., 2013, Table S4). That relationship was based on a multiple regression using samples from 5 m depth (i.e., volumetric data), where chlorophyll-a, phytoplankton production and dissolved organic carbon was removed from the initial model. In a later study, including influence of riverine discharge of total organic carbon and phytoplankton production integrated over the
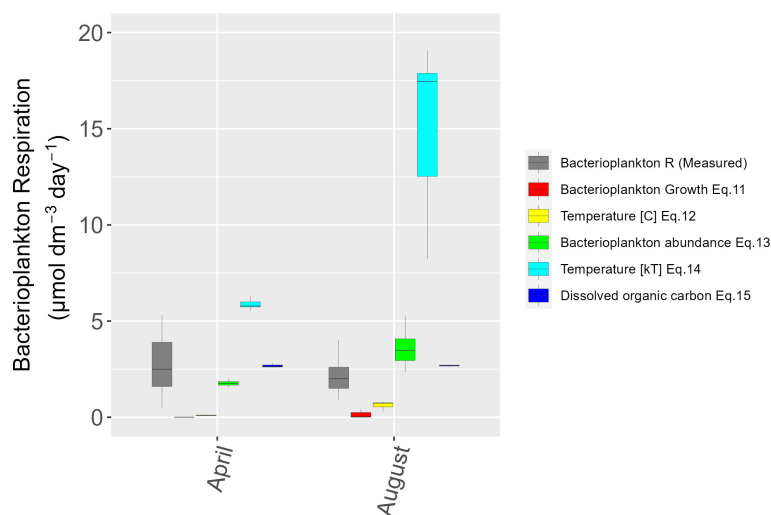

FIGURE 5
Same as Figure 4 but for bacterioplankton respiration.

water column, the sum of those factors (i.e., carbon input) was the only required predictor based on a multiple regression, (Vikström et al., 2020, their Figure 4). Water temperature, chlorophyll-a and dissolved organic carbon were removed from their initial model due to too low influence on plankton respiration. But also those relationships show a moderate predictive ability.

3.3.2 Prediction of bacterioplankton respiration

Modelling bacterioplankton respiration showed the best fit to the observed data for the predictors, DOC and bacterioplankton abundance in April but both had a markedly narrower range of values (Figure 5). The exception was bacterioplankton abundance reproducing the spread well in August, albeit at a higher median value. The observed bacterioplankton respiration rates came from another dataset from the same boreal estuary (Vikström and Wikner, 2019). DOC and bacterioplankton abundance were also the predictors showing the lowest RMSE values (Table S2). Significant maintenance respiration at low values of bacterio plankton growth (0.004-0.1 µmol dm^{-3} d^{-1}) could possibly explain an underestimation by this model in the oligotrophic and comparably cold environment of the boreal estuary with high loads of terrigenous organic matter (Vikström and Wikner, 2019). The analysis of a global data set by (López-Urrutia and Morán, 2007) also find that bacterioplankton respiration is maintained at depleted trophic state while bacterial growth decrease, together reducing the growth efficiency. Taken together, the current models for bacterioplankton respiration also deviates from observed data regarding level, distribution, or both attributes. Consequently, uncertainty in current models precludes precise (< ± 20% CV) prediction of future bacterioplankton respiration in the tested water body.

3.4 Temperature sensitivity of plankton respiration

Given that temperature is a commonly reported and a comparably strong predictor of respiration, current reports of the temperature sensitivity of plankton and bacterioplankton respiration were compiled (Table 2). The Q$_{10}$ values for plankton respiration showed a median value of 3.2 (range 1.8-26). Variations occur between measurements within the same study and these are to some extent related to season (e.g., Panigrahi et al., 2013). Colder ambient temperatures tend to promote higher values but may also be explained by rates closer to the detection limits of current methods, where comparably small difference in untransformed units may mean multiple increases in rates. High inputs of riverine dissolved organic carbon together with low temperatures are also suggested to explain the high Q$_{10}$ values in the northern Baltic Sea (Nydahl et al., 2013; Panigrahi et al., 2013). The DOC concentrations in the northern Baltic Sea are 5-fold higher than those in oceanic waters (Voss et al., 2021). Excess bioavailable carbon substrates should promote larger increases in respiration rates with increasing temperature. Plankton respiration seems to be more temperature sensitive than phytoplankton production and bacterioplankton growth (Lefevre et al., 1994; Vazquez-Dominguez et al., 2007; Panigrahi et al., 2013).

3.5 Effects of climate change on oxygen consumption

Reported assessment of climate change effects on oxygen consumption and concentrations in the current literature were compiled (Table 3). There is a consistent view in these reports that

TABLE 2 Q$_{10}$-values for oxygen consumption and respiration reported in the literature.

Variable	Q$_{10}$/E$_a$-value (-, eV)	Range Q$_{10}$/E$_a$	Ambient tempera-ture (°C)	Environment	Citation
Plankton respiration	2.8/-	1.4-24/-	1.0-6.7	Antarctic Ocean	Robinson and Williams (1993)
Plankton respiration	3.2/-	–	3.25	Antarctic Ocean	Vosjan and Olanczukneyman (1991)
Plankton respiration	5.1/-	4.2-10.6/-	9.0-16.0	Atlantic NE coast	Lefevre et al. (1994)
Plankton respiration	2.5/-	0.77-8.4/-	-1.5-1.0	Atlantic NW coast	Pomeroy et al. (1991)
Mesopelagic respiration	3.65/-0.90	–	8.7-14.9	Atlantic South and Indian Ocean	Mazuecos et al. (2015)
Plankton respiration	9/-	0.01-1115/-	-0.2-17.7	Estuary	Panigrahi et al. (2013)[b]
Microbial respiration	26/-	12-2370/-	12.0-15.0	Estuary	Nydahl et al. (2013)
Plankton respiration	2.4/-	1.9-2.8/-	4.4	Mesocosm	Hoppe et al. (2008)
Microbial respiration	-/-0.56	–	-1.0-28.5	Global Ocean	Lopez-Urrutia et al. (2006)
Plankton respiration	-/-0.32	–	-0.1-35	Global Ocean	Lopez-Urrutia et al. (2006)
Plankton respiration	6.8/-	5.9-7.1/-	23.0-24.0	Mediterranean Sea	Robinson (2000)
Microbial respiration	1.9/-	–	12.5-15.5/25.0-27.3	Mediterranean Sea Coast	Vazquez-Dominguez et al. (2007)

-, not available. [a]Mean of reported range. [b]Values (26% of total n) recalculated and corrected for observed oxygen oversaturation.
Cases are sorted by environment for comparison.

TABLE 3 Compilation of the effects of climate change assessed in the literature on oxygen consumption and concentrations.

Environment	Study type	Climate change effect on O_2		Reference
		Consumption	Concentration	
Coastal Mediterranean Sea	Manipulated field samples	↑	–	(Vazquez-Dominguez et al., 2007)
Ocean	Compiled field data	↑	–	(Robinson, 2008)
Ocean	MTE[†]-analysis of field data	↑	–	(Sarmento et al., 2010)
Baltic Sea	Model assemble	↑	↓	(Meier et al., 2011b)
Coastal Baltic Sea	Microcosm experiment	↑	↓	(Nydahl et al., 2013)
Kattegat	OXYCON model	↑	↓	(Bendtsen and Hansen, 2013)
Coastal Baltic Sea	Manipulated field samples	↑	↓	(Panigrahi et al., 2013)
Ocean	Review	–	↓	(Oschlies et al., 2018)

[†]Metabolic Theory of Ecology.
Arrows indicate the direction of change. Dashes indicate not reported assessments.

oxygen consumption will increase, and oxygen concentrations will decrease if the current climate projections for temperature are realized. This is in accordance with the evidence that temperature is a major predictor for respiration (Figure 3, Table S1, Figure 6). A literature survey of prokaryotic strains (n=239) and their thermal performance curve support an increase in prokaryotic respiration at higher temperature (Smith et al., 2019), but was mainly related to terrestrial taxa and lacked assessment of changes in substrate supply. Coupled physical-biogeochemical models driven by regionalized meteorological data from global climate simulations also show that oxygen consumption will increase in the Baltic Sea (Meier et al.,

2011a). Both direct effect of temperature on plankton respiration and an increased supply of organic matter *via* higher primary production due to nutrient loads contribute to the increase. A mesocosm study from this sea area provides further support for increased plankton respiration and projects a reduction in the biological pump of organic matter to deeper water layers (Wohlers et al., 2009). However, that projection is based on that primary production increase is an outcome of climate change, while the net outcome of climate change for primary production varies with the marine environment. In contrast to the Baltic Sea scenario, a net 12-26% decrease in global primary production is projected when accounting
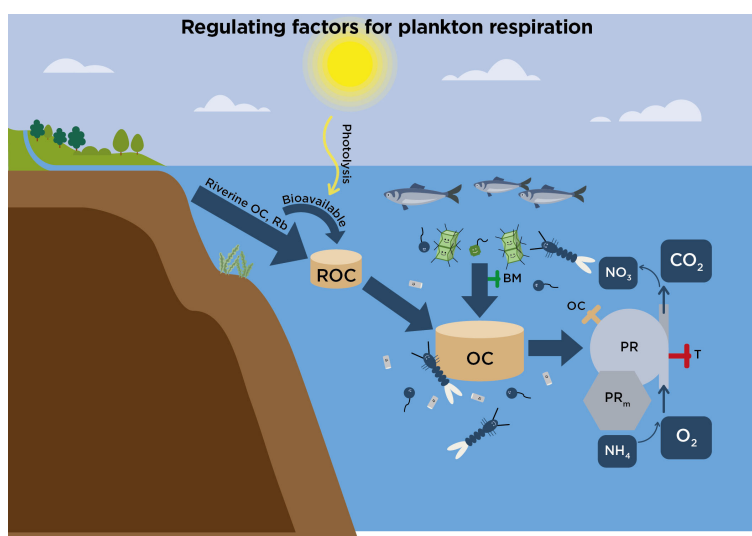

FIGURE 6
Conceptual diagram showing how plankton respiration (PR) is mainly controlled by temperature (T, red valve), and supply of bioavailable organic carbon (OC, yellow valve). OC is provided by excretion from grazing zooplankton and fish, phytoplankton and macroalgal exudation and detritus degradation. Coupling between respiration and biomass (BM, green valve, i.e., Chl-a) may reflect its importance for generating OC *via* zooplankton excretion and viral lysis. Supply of organic matter from riverine DOM discharge (ROC) can be significant in estuaries and contribute to formation of OC. Photolysis increase bioavailability of refractile humic substances. ROC drives basal respiration (PR$_b$). Oxidation of NH_4 to NO_3 contribute with a smaller share in the marine environment. The significant contribution of maintenance respiration (PR$_m$) to plankton respiration is also indicated.

for changes in nutrient availability (Couespel et al., 2021). Confidence in effect of climate change on primary production also influence reliability in projection of its effect on oxygen consumption.

In the northern Baltic Sea, primary production is also expected to decline but because of elevated precipitation and discharges of organic carbon (Andersson et al., 2015). In environments where precipitation is projected to increase due to climate change, terrestrial organic carbon, nitrogen and phosphorous discharged will also be elevated. Phytoplankton and macroalgae can use these elevated supplies of nitrogen and phosphorous for growth unless counteracted by reduced light penetration or global insolation (i.e., increased cloudiness). Reduced primary production under elevated freshwater discharges has been demonstrated on basin and multiannual scales in the northern Baltic Sea, explained by reduced light irradiance and intensified competition for limiting mineral nutrients (Wikner and Andersson, 2012). Terrestrial organic carbon from boreal watersheds is colored due to humic substances that hamper light penetration in the water column. Part of the terrestrial organic carbon can also be directly bioavailable to aquatic biota (20%, Pettersson et al., 1997) and should become more bioavailable by photolytic cleavage (Bertilsson et al., 1999), promoting bacterioplankton growth and respiration. Increased competition between bacterioplankton and phytoplankton for limited mineral nutrients will therefore further reduce primary production. The projected climate changes with warmer waters and higher precipitation in the northern Baltic Sea are consequently expected to enhance plankton respiration without an increase in primary production (Meier et al., 2011b; Andersson et al., 2015).

The expected effects of climate change in the Baltic Sea are in accordance with assessments conducted on the global scale. López-Urrutia and Morán (2007) conclude that global warming will lead to an increased flux of CO_2 from the ocean to the atmosphere. Sarmento and Descy (2008) claim that our knowledge and experimental evidence make it probable that bacterioplankton respiration and losses to grazers will increase, making microorganisms even more dominant in a warmer ocean. Robinson (2008) also concluded that bacterioplankton and thus total respiration will increase with the projected temperature increases. Further support for this view is provided by Oschlies et al. (2018), who projected that warming of waters will not change the integrated oxygen loss but will shift the respiration of organic matter closer to the surface, reducing the oxygen concentration there.

Given the significance of temperature as a predictor, a tentative quantitative estimate of the temperature effect on plankton respiration can be calculated based on the reported temperature sensitivity (i.e., Q_{10}-value, Table 2). Rearranging the Q_{10}-function reported by (Sherr and Sherr, 1996) to

$$\frac{R_2}{R_1} = Q_{10}^{(T_2 - T_1)/10} \qquad \text{Eq. 16}$$

the effect of increased temperature (T_2-T_1) on increase in plankton respiration (R_2/R_1) can be calculated. Using the median Q_{10}-value from Table 2 of 3.2 and the Representative Concentration Pathway (RCP) scenario 2.6 with projected 1°C increase in water temperature, a 12% increase in plankton respiration is projected

(Table S3, IPCC, 2019). For the RCP8.5 scenario, leading to a 4°C increase in water temperature, the result is 59% increase in R. Those projections assume that the supply of organic carbon for fueling plankton respiration is not limiting this increase. Even a 12% increase in plankton respiration can cause hypoxia to develop over longer periods, or enhance current hypoxic waters to anoxia, assuming similar or reduced ventilation of the water column. Reduced oxygen concentration would influence many biogeochemical processes dependent on the redox potential with potential profound impact on the environmental status.

The authors above, however, simultaneously stress the uncertainties in current models regarding oxygen consumption and respiration. In line with the conclusion in this compilation, Robinson (2008) infers that the uncertainty in bacterioplankton respiration regulation is still too large to make meaningful projections. Additionally, Oschlies et al. (2018) state that the current understanding of oxygen consumption is insufficient for confident modelling of climate change effects. The literature thus concordantly stresses the paucity of knowledge regarding plankton respiration. The long-term projections mentioned above should therefore be viewed as educated guesses.

Ideally, a model for regulation of plankton respiration would apply to all water environments if accounting for major regulating factors properly. This justifies our investigation of models reported up to date on a well-studied boreal estuary. We conclude that current models do not predict plankton respiration sufficiently well but emphasizes that characteristics of the tested environment may influence this conclusion. Similar test with data from other water environments is advocated. To advance our knowledge of respiration in the sea, improved model performance across water environments can increase the confidence in future advice for management. The systematic measurements of oxygen consumption, primary production and temperature should be implemented in long-term ecological and monitoring programs covering several years, also advocated by Breitburg et al. (2018). Collaboration with biogeochemical modelers is advocated for experimental design. Selected representative high-frequency sampling sites should cover all seasons with at least monthly sampling. Here, multivariate statistics and time series analysis, possibly combined with artificial intelligence technique should be employed at local basin or water body scales, while avoiding the application of logarithm-transformed relationships. In estuaries, measurements of river discharge of organic carbon and nutrients is needed. Harmonization of methodology and terminology would facilitate cross-ecosystem syntheses. For future applications by environmental management agencies, simple and precise predictors and clear guidelines are needed and can be achieved by concerted efforts between environmental monitoring and research.

Data availability statement

The original contributions presented in the study are included in the article/Supplementary Material. Further inquiries can be directed to the corresponding author.

Author contributions

JW, KV and AV designed the study and contributed to literature search. JW composed introductory and conceptual figures, made Table 1 and S1. AV synthesized degree of explanation and made corresponding figures. KV made modelling of selected equations based on available data sets and completed data into figures and tables. JW was the main author and KV and AV contributed in writing. All authors contributed to the article and approved the submitted version.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2023.1134699/full#supplementary-material

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