Chapter 5
Ocean Acidification Conditions and Marine Diatoms

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Abstract Ocean acidification doesn't just erode calcium carbonate shells. It can also slow the rate of diatoms to build their beautiful, intricate silica cell walls. Thinner walls mean lighter diatoms making the algae less able to transport carbon to the deep ocean. Diatoms are a key group of non-calcifying marine phytoplankton, responsible for ~40% of ocean productivity. Growth, cell size, and silica content are strong determinants of diatom resilience and sinking velocity; therefore, the effect of diatom species on ocean biogeochemistry is a function of its growth strategy, size, and frustule thickness. In natural environments, pH directly affects the diatom's growth rate and therefore the timing and abundance of species. Consequently, understanding impacts of ocean acidification on diatom community structure is crucial for evaluating the sensitivity of biogeochemical cycles and ecosystem services in the world's oceans.

Keywords Ocean acidification · Biogeochemistry · Diatoms · Growth · Frustule thickness

5.1 Introduction

Ocean acidification is a global threat to the world's oceans, estuaries, and rivers. It is projected to grow as carbon dioxide (CO_2) and continues to be emitted into the atmosphere at record-high levels. The oceans take up CO_2 from the atmosphere and are responsible for absorbing around a third of the CO_2 emitted by fossil fuel burning, deforestation, and cement production since the industrial revolution (Sabine et al. 2004). While this is beneficial in terms of limiting the rise in atmospheric CO_2 concentrations and hence greenhouse warming due to this CO_2, there are direct consequences for ocean chemistry. Ocean acidification describes the lowering of seawater pH and carbonate saturation that result from increasing atmospheric CO_2

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P. Srivastava et al. (eds.), *Insights into the World of Diatoms: From Essentials to Applications*, Plant Life and Environment Dynamics,
https://doi.org/10.1007/978-981-19-5920-2_5

concentrations. There are also indirect and potentially adverse biological and ecological consequences of the chemical changes taking place in the ocean now and as projected into the future (Ridgwell and Schmidt 2010).

Climate affects diatoms in complex ways. As the planet warms due to the increase in carbon dioxide, scientists predict that diatoms will decrease compared to other planktons such as coccolithophores and cyanobacteria (Tatters et al. 2013). In lakes and rivers, a changing climate alters river flow in many parts of the world. The frequency and severity of droughts and floods is changing, which influences diatom species and where they grow. Furthermore, climate controls circulation patterns and thermal stratification of lakes and oceans, which alter diatom species composition (Bach and Taucher 2019). Diatoms affect climate on a global scale. As diatoms photosynthesize, they absorb carbon dioxide from the atmosphere and release oxygen. Although diatoms are very small, they live in the vast oceans, the world over. The effect of fixation of carbon by diatoms and release of oxygen alters the chemistry of the atmosphere. It is well-known that diatoms play a vital role in pelagic food webs and elemental cycling in the oceans (Smetacek et al. 2012). Therefore, understanding the effects of global warming on diatom community structure is essential for considering the sensitivity of biogeochemical cycles and ecosystem services in the world oceans.

5.2 Ocean Acidification

Ocean acidification is the ongoing decrease in the pH value of the Earth's oceans, caused by the uptake of CO_2 from the atmosphere. Friedlingstein et al. (2020) stated that the rate of atmospheric CO_2 levels has persisted to increase and nearly tripled between the 1960s and 2010s. Oceans have mitigated this growth by absorbing about a quarter of CO_2 emissions between 1850 and 2019. As the amount of carbon dioxide in the atmosphere increases, the amount of carbon dioxide absorbed by the ocean also increases. This leads to a series of chemical reactions in the seawater which has a negative impact on marine life and ecosystem functioning (Vargas et al. 2022). As the ocean acidifies, the concentration of carbonate ions decreases. Calcifying organisms such as mussels, corals, and various plankton species need exactly these molecules to build their shells and skeletons (Fig. 5.1). Also, other marine organisms that do not have calcium carbonate shells or skeletons need to spend more energy to regulate their bodily functions in acidifying waters.

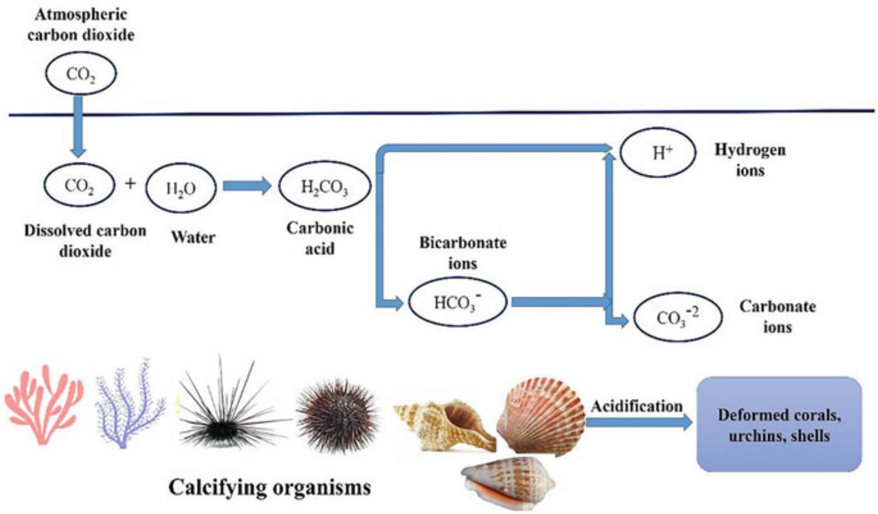

Fig. 5.1 Ocean acidification

5.3 Effects of Ocean Acidification on Marine Diatoms Community

Diatoms are among the most important and prolific microalgae in terms of both abundance and ecological functionality in the ocean. They are within the division of Bacillariophyta and serve directly or indirectly as food for many animals with an assessed contribution of almost 25% to global primary production (Tréguer and De La Rocha 2013). There are at least 30,000 of diatom species which differ in size and ranging from below 3 μm up to a few millimeters (Mann and Vanormelingen 2013). Diatoms are found as single cells or in chains in pelagic and/or benthic habitats and take free-living, surface-attached, symbiotic, or parasitic lifestyles (Mann and Vanormelingen 2013).

Diatom community composition could be affected by different environmental stressors in different ocean areas due to their massive relevance for the Earth system (Tréguer et al. 2018). There have been a number of research articles (Table 5.1) that studied the effects of future CO_2 on marine diatom communities in short-term incubations (Bach et al. 2019; Feng et al. 2009, 2010; Hare et al. 2007; Kim et al. 2006; Tortell et al. 2002, 2008). Also, short-term ocean acidification experiments were done with single species of cultured diatoms (Chen and Gao 2003; Li et al. 2012; Sobrino et al. 2008; Sun et al. 2011; Wu et al. 2010). Few others (Crawfurd et al. 2011; Tatters et al. 2012) have used experimental plans in which isolated diatoms were exposed to different CO_2 conditions for longer periods (more than three months). Most studies indicated that elevated CO_2 led to a measurable increase in phytoplankton productivity, promoting the growth of larger

Table 5.1 Effects of ocean acidification reported on marine diatoms community

Experimental condition	Effects	References
Field incubation experiment, phytoplankton assemblages exposed to CO_2 levels of 150 and 750 ppm (dissolved CO_2 ~3 to 25 μM)	Relative abundance of phytoplankton taxa fluctuated significantly between CO_2 treatments. Abundance of diatoms decreased by about 50% at low CO_2 relative to high CO_2. CO_2 concentrations could potentially impact competition among marine phytoplankton taxa and affect oceanic nutrient cycling	Tortell et al. (2002)
Surface water samples (5 m) were collected at 35 locations. Phytoplankton was concentrated by gravity filtration onto 2.0 mm pore size filters; the fraction of cellular HCO_3 and CO_2 uptake was measured	Diatom species composition is sensitive to CO_2 concentrations ranging from 100 to 800 ppm. Elevated CO_2 led to a measurable increase in phytoplankton productivity, promoting the growth of larger chain-forming diatom	Tortell et al. (2008)
Mesocosm setup and sampling, using different concentrations of CO_2 of 25, 41, and 76 kPa (250, 400, and 750 matm)	Two phytoplankton taxa (microflagellates and cryptomonads) and two diatom species (*Skeletonema costatum* and *Nitzschia* spp.) account for approximately 90% of the phytoplankton community	Kim et al. (2006)
Incubation of phytoplankton communities from two areas under conditions of elevated sea surface temperature and/or partial pressure of carbon dioxide (pCO_2)	Community composition was shifted away from diatoms and toward nanophytoplankton	Hare et al. (2007)
Shipboard continuous culture experiment (Ecostat) was used. Four treatments were tested: 12 °C and 390 ppm CO_2, 12 °C and 690 ppm CO_2, 16 °C and 390 ppm CO_2, and 16 °C and 690 ppm CO_2	Both elevated CO_2 and temperature resulted in changes in phytoplankton community structure	Feng et al. (2009)
Shipboard continuous culture experiment	After 18 days of incubation, increased diatom and *Phaeocystis* abundance. The major influence of high CO_2 was on diatom community structure, by favoring the large centric diatom *Chaetoceros lineola* over the small pennate species Cylindrotheca closterium	Feng et al. (2010)
Natural phytoplankton communities were bounded for 32 days in situ mesocosm with a pCO_2 gradient fluctuating from 380 to 1140 μatm. Nutrients were added to all mesocosms (N, P, Si)	Total diatom biomass was significantly positively affected by high CO_2 after nutrient enrichment. CO_2 effects on diatom biomass and species composition were weak during oligotrophic conditions but became quite strong above ~620 μatm after the nutrient enrichment. Ocean acidification in the subtropics may support the effectiveness of (large) diatoms and cause changes in diatom community composition	Bach et al. (2019)

chain-forming diatom. Future studies will be required to evaluate whether this is also the case for other types of algal communities from other marine systems (Table 5.1).

5.4 Impacts of Ocean Acidification on the Growth of Diatoms

Diatoms in different waters suffer from variations of light and temperature as well as fluctuations in seawater carbonate chemistry. It is predictable that the growing partial pressure of CO_2 (pCO_2) in seawater due to ocean acidification will reduce the cellular requirement of diatoms for energy and resources, therefore stimulating diatom growth and carbon (C) fixation (Tortell et al. 2008). Diatoms show diversified responses to ocean acidification; higher CO_2 concentrations are displayed to enhance (Gao et al. 2012b; Kim et al. 2006; King et al. 2011), have no effect (Boelen et al. 2011) or even inhibit (Li and Campbell 2013; Low-Décarie et al. 2011; McCarthy et al. 2012; Sugie and Yoshimura 2013) growth rates of diatom species. However, raised CO_2 in the ocean increases its availability to algae; the reduced pH can affect the acid-base balance of cells (Flynn et al. 2012). In addition, the higher CO_2 and reduced pH levels can interact with solar radiation and temperature, showing synergistic, antagonistic, or balanced effects (Gao et al. 2012a). Therefore, the mechanisms involved in the responses to ocean acidification of diatoms need to be further explored.

5.5 The Physiological Response of Marine Diatoms to Ocean Acidification

The responses of marine diatoms to ocean acidification are highly variable and species-specific as shown in Table 5.2. Diatoms work greatly efficient CO_2 concentrating mechanisms (CCMs) to reach a high ratio of carboxylation to oxygenation (Raven et al. 2011). They are resistant to high levels of UV radiation (Wu et al. 2012), preferable a low sensitivity to photoinactivation of PSII compared with other phytoplanktons (Key et al. 2010 and Wu et al. 2011), and positively exploit variable light (Lavaud et al. 2007).

Li et al. (2012) estimated the combined effects of ocean acidification, UV radiation, and temperature on the diatom *Phaeodactylum tricornutum* and grew it under two CO_2 concentrations (390 and 1000 μatm); growth at the higher CO_2 concentration increased non-photochemical quenching (NPQ) of cells and partially responded the damage to PS II (photosystem II) produced by UV-A and UV-B. The ratio of repair to UV-B-induced damage decreased with increased NPQ, reflecting induction of NPQ when repair dropped behind the damage, and it was higher under the ocean acidification condition, showing that the increased pCO_2 and lowered pH counteracted UV-B-induced harm. As for photosynthetic carbon fixation rate which

Table 5.2 Physiological response reported of marine diatoms

Diatom species	Type of response	References
Thalassiosira pseudonana	Unaffected	Crawfurd et al. (2011) Yang and Gao (2012) Wu et al. (2014) Shi et al. (2015) Hong et al. (2017)
Ditylum brightwellii	Unaffected	Riebesell et al. (1993)
Nitzschia spp.	Unaffected	Kim et al. (2006)
Chaetoceros brevis	Unaffected	Boelen et al. (2011)
Phaeodactylum tricornutum	Positive	Wu et al. (2010) Hong et al. (2017)
Chaetoceros mueller	Positive	Shi et al. (2019)
Navicula pelliculosa	Positive	Low-Décarie et al. (2011)
Pseudo-nitzschia multiseries	Positive	Sun et al. (2011)
Skeletonema costatum	Positive	Gao et al. (2012b)
Attheya sp.	Positive	King et al. (2011)
Navicula directa	Negative	Torstensson et al. (2012)
Thalassiosira weissflogii	Negative	Mejía et al. (2013)
Nitzschia palea	Negative	Low-Décarie et al. (2011)
Navicula directa	Negative	Torstensson et al. (2012)

increased with increasing temperature from 15 to 25 °C, the elevated CO_2 and temperature levels synergistically interacted to reduce the inhibition caused by UV-B and thus increase the carbon fixation.

5.6 Conclusions and Future Perspectives

Ocean acidification is known to reduce calcification of many calcifying organisms. Different diatom species may have entirely diverse responses to ocean acidification, mostly because of variances in species or phenotypes. The ocean acidification made changes in diatom competitiveness, and assemblage structure may change key ecosystem services; therefore, monitoring community abundance of diatoms over longer timescales is important to gain information on their responses to environmental changes.

References

Bach LT, Taucher J (2019) CO_2 effects on diatoms: a synthesis of more than a decade of ocean acidification experiments with natural communities. Ocean Sci 15:1159–1175. https://doi.org/10.5194/os-15-1159-2019

Bach LT, Hernández-Hernández N, Taucher J, Spisla C, Sforna C, Riebesell U, Arístegui J (2019) Effects of elevated CO2 on a natural diatom community in the subtropical NE Atlantic. Front Mar Sci 6:75. https://doi.org/10.3389/fmars.2019.00075

Boelen P, van de Poll WH, van der Strate HJ, Neven IA, Beardall J et al (2011) Neither elevated nor reduced CO2 affects the photophysiological performance of the marine antarctic diatom Chaetoceros brevis. J Exp Mar Biol Ecol 406:38–45

Chen X, Gao K (2003) Effect of CO2 concentrations on the activity of photosynthetic CO2 fixation and extracellular carbonic anhydrase in the marine diatom Skeletonema costatum. Chin Sci Bull 48:2616–2620. https://doi.org/10.1360/03wc0084

Crawfurd KJ, Raven JA, Wheeler GL, Baxter EJ, Joint I (2011) The response of Thalassiosira pseudonana to long-term exposure to increased CO_2 and decreased pH. PLoS One 6:e26695

Feng Y et al (2009) The effects of increased pCO2 and temperature on the North Atlantic spring bloom. I. The phytoplankton community and biogeochemical response. Mar Ecol Prog Ser 388:13–25. https://doi.org/10.3354/meps08133

Feng Y et al (2010) Interactive effects of iron, irradiance and CO2 on Ross Sea phytoplankton. Deep-Sea Res 57:368–383. https://doi.org/10.1016/j.dsr.2009.10.013

Flynn KJ, Blankford JC, Baird ME, Raven JA, Clark DR et al (2012) Changes in pH at the exterior surface of plankton with ocean acidification. Nat Clim Chang 2:510–513

Friedlingstein P, O'Sullivan M, Jones MW, Andrew RM, Hauck J, Olsen A, Peters et al (2020) Global carbon budget 2020. Earth Syst Sci Data 12:3269–3340. https://doi.org/10.5194/essd-12-3269-2020

Gao K, Helbling EW, Hader DP, Hutchins DA (2012a) Responses of marine primary producers to interactions between ocean acidification, solar radiation, and warming. Mar Ecol Prog Ser 470:167–189

Gao K, Xu JT, Gao G, Li YH, Hutchins DA et al (2012b) Rising CO2 and increased light exposure synergistically reduce marine primary productivity. Nat Clim Chang 2:519–523

Hare CE, Leblanc K, DiTullio GR, Kudela RM, Zhang Y, Lee PA, Riseman S, Tortell PD, Hutchins DA (2007) Consequences of increased temperature and CO2 for algal community structure and biogeochemistry in the Bering Sea. Mar Ecol Prog Ser 352:9–16. https://doi.org/10.3354/meps07182

Hong H, Li D, Lin W, Li W, Shi D (2017) Nitrogen nutritional condition affects the response of energy metabolism in diatoms to elevated carbon dioxide. Mar Ecol Prog Ser 567:41–56

Key T, Mccarthy A, Campbell D, Six C, Roy S, Finkel Z (2010) Cell size tradeoffs govern light exploitation strategies in marine phytoplankton. Environ Microbiol 12:95–104. https://doi.org/10.1111/j.1462-2920.2009.02046.x

Kim JM, Lee K, Shin K, Kang JH, Lee HW (2006) The effect of seawater CO2 concentration on growth of a natural phytoplankton assemblage in a controlled mesocosm experiment. Limnol Oceanogr 51(4):1629–1636

King AL, Sanudo-Wilhelmy SA, Leblanc K, Hutchins DA, Fu F (2011) CO_2 and vitamin B12 interactions determine bioactive trace metal requirements of a subarctic pacific diatom. ISME J 5:1388–1396

Lavaud J, Strzepek RF, Kroth PG (2007) Photoprotection capacity differs among diatoms: possible consequences on the spatial distribution of diatoms related to fluctuations in the underwater light climate. Limnol Oceanogr 52:1188–1194. https://doi.org/10.4319/lo.2007.52.3.1188

Li G, Campbell DA (2013) Rising CO_2 interacts with growth light and growth rate to alter photosystem II photoinactivation of the coastal diatom Thalassiosira pseudonana. PLoS One 8:e55562

Li Y, Gao K, Villafane V, Helbling EW (2012) Ocean acidification mediates photosynthetic response to UV radiation and temperature increase in the diatom Phaeodactylum tricornutum. Biogeosciences 9:3931–3942. https://doi.org/10.5194/bg-9-3931-2012

Low-Décarie E, Fussmann GF, Bell G (2011) The effect of elevated CO_2 on growth and competition in experimental phytoplankton communities. Glob Chang Biol 17:2525–2535

Mann DG, Vanormelingen P (2013) An inordinate fondness? The number, distributions, and origins of diatom species. J Eukaryot Microbiol 60:414–420. https://doi.org/10.1111/jeu.12047

McCarthy A, Rogers SP, Duffy SJ, Campbell DA (2012) Elevated carbon dioxide differentially alters the photophysiology of Thalassiosira pseudonana (Bacillariophyceae) and Emiliania huxleyi (Haptophyta). J Phycol 48(3):635–646

Mejía LM, Isensee K, Méndez-Vicente A, Pisonero J, Shimizu N, González C, Monteleone B, Stoll H (2013) B content and Si/C ratios from cultured diatoms (Thalassiosira pseudonana and Thalassiosira weissflogii): Relationship to seawater pH and diatom carbon acquisition. Geochim Cosmochim Acta 123:322–337. https://doi.org/10.1016/j.gca.2013.06.011

Raven JA, Giordano M, Beardall J, Maberly SC (2011) Algal and aquatic plant carbon concentrating mechanisms in relation to environmental change. Photosynth Res 109:281–296. https://doi.org/10.1007/s11120-011-9632-6

Ridgwell A, Schmidt DN (2010) Past constraints on the vulnerability of marine calcifiers to massive carbon dioxide release. Nat Geosci 3:196–200

Riebesell U, Wolf-Gladrow DA, Smetacek V (1993) Carbon dioxide limitation of marine phytoplankton growth rates. Nature 361:249–251. https://doi.org/10.1038/361249a0

Sabine CL, Feely RA, Gruber N et al (2004) The oceanic sink for anthropogenic CO_2. Science 305:367–371

Shi D, Li W, Hopkinson BM, Hong H, Li D, Kao SJ, Lin W (2015) Interactive effects of light, nitrogen source, and carbon dioxide on energy metabolism in the diatom Thalassiosira pseudonana. Limnol Oceanogr 60:1805–1822

Shi D, Hong H, Su X, Liao L, Chang S, Lin W (2019) Physiological response of marine diatoms to ocean acidification: differential roles of seawater pCO2 and pH. J Phycol 55:521–533

Smetacek V, Klaas C, Strass VH, Assmy P, Montresor M et al (2012) Deep carbon export from a Southern Ocean iron-fertilized diatom bloom. Nature 487:313–319. https://doi.org/10.1038/nature11229

Sobrino C, Ward ML, Neale PJ (2008) Acclimation toelevated carbon dioxide and ultraviolet radiation in the diatom Thalassiosira pseudonana: effects on growth, photosynthesis, and spectral sensitivity photo inhibition. Limnol Oceanogr 53:494–505. https://doi.org/10.4319/lo.2008.53.2.0494

Sugie K, Yoshimura T (2013) Effects of pCO_2 and iron on the elemental composition and cell geometry of the marine diatom Pseudo-nitzschia pseudodelicatissima (Bacillariophyceae). J Phycol 49:475–488

Sun J, Hutchins DA, Feng Y, Seubert EL, Caron DA, Fu FX (2011) Effects of changing pCO2 and phosphate availability on domoic acid production and physiology of the marine harmful bloom diatom Pseudo-nitzschia multiseries. Limnol Oceanogr 56:829–840. https://doi.org/10.4319/lo.2011.56.3.0829

Tatters AO, Fu FX, Hutchins DA (2012) High CO2 and silicate limitation synergistically increase the toxicity of Pseudo-nitzschia fraudulenta. PLoS One 7:e32116. https://doi.org/10.1371/journal.pone.0032116

Tatters AO, Roleda MY, Schnetzer A, Fu F, Hurd CL, Boyd PW, Caron DA, Lie AAY, Hoffmann LJ, Hutchins DA (2013) Short- and long-term conditioning of a temperate marine diatom community to acidification and warming. Philos Trans R Soc B 368:20120437. https://doi.org/10.1098/rstb.2012.0437

Torstensson A, Chierici M, Wulff A (2012) The influence of increased temperature and carbon dioxide levels on the benthic/sea ice diatom Navicula directa. Polar Biol 35:205–214. https://doi.org/10.1007/s00300-011-1056-4

Tortell PD, DiTullio GR, Sigman DM, Morel FMM (2002) CO2 effects on taxonomic composition and nutrient utilization in an equatorial Pacific phytoplankton assemblage. Mar Ecol Prog Ser 236:37–43. https://doi.org/10.3354/meps236037

Tortell PD et al (2008) CO2 sensitivity of Southern Ocean phytoplankton. Geophys Res Lett 35: L04605. https://doi.org/10.1029/2007GL032583

Tréguer PJ, De La Rocha CL (2013) The world ocean silica cycle. Annu Rev Mar Sci 5:477–501. https://doi.org/10.1146/annurev-marine-121211-172346

Tréguer P, Bowler C, Moriceau B, Dutkiewicz S, Gehlen M, Aumont O et al (2018) Influence of diatom diversity on the ocean biological carbon pump. Nat Geosci 11:27–37. https://doi.org/10.1038/s41561-017-0028-x

Vargas CA, Cuevas LA, Broitman BR et al (2022) Upper environmental pCO_2 drives sensitivity to ocean acidification in marine invertebrates. Nat Clim Chang 12:200–207. https://doi.org/10.1038/s41558-021-01269-2

Wu Y, Gao K, Riebesell U (2010) CO2-induced seawater acidification affects physiological performance of the marine diatom Phaeodactylum tricornutum. Biogeosciences 7:2915–2923

Wu H, Cockshutt AM, McCarthy A, Campbell DA (2011) Distinctive photosystem II photo inactivation and protein dynamics in marine diatoms. Plant Physiol 156:2184–2195. https://doi.org/10.1104/pp.111.178772

Wu X, Gao G, Giordano M, Gao K (2012) Growth and photosynthesis of a diatom grown under elevated CO2; in the presence of solar UV radiation. Fundam Appl Limnol/Arch Hydrobiol 180:279–290

Wu Y, Campbell DA, Irwin AJ, Suggett DJ, Finkel ZV (2014) Ocean acidification enhances the growth rate of larger diatoms. Limnol Oceanogr 59:1027–1034

Yang GY, Gao K (2012) Physiological responses of the marine diatom Thalassiosira pseudonana to increased pCO2 and seawater acidity. Mar Environ Res 79:142–151