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# Fate of Mediterranean Scleractinian Cold-Water Corals as a Result of Global Climate Change. A Synthesis

Cornelia Maier, Markus G. Weinbauer,  
and Jean-Pierre Gattuso

## Abstract

This chapter addresses the question as to how Mediterranean cold-water corals might fare in the future under anthropogenically-induced global climate change. The focus on three most prominent scleractinian cold-water corals species, the two branching and habitat-forming forms *Madrepora oculata*, *Lophelia pertusa* and the solitary cup coral *Desmophyllum dianthus*. We provide an introduction to climate change principals, highlight the current status of the marine environment with regard to global climate change, and describe how climate change impacts such as ocean acidification are predicted to affect key calcifiers such as scleractinian cold-water corals in the Mediterranean region. A synthesis of the experimental cold-water coral studies conducted to date on climate change impacts: The present state of knowledge reviewed in this chapter takes into account the number of experiments that have been carried out in the Mediterranean as well as for comparative purposes in other parts of the world, to examine the effects of climate change on the corals. We assess the statistical robustness of these experiments and what challenges the presented experiments. A comprehensive multi-study comparison is provided in order to inform on the present state of knowledge, and knowledge gaps, in understanding the effects of global climate change on cold-water corals. Finally we describe what the fate could be for the important scleractinian coral group in the Mediterranean region.

## Keywords

Mediterranean cold-water coral · Climate change · Ocean acidification · Temperature · Calcification · Respiration

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## 44.1 Introduction 37

### 44.1.1 Global Climate Change 38

Climate change refers to a change in weather conditions over a longer period of time, taking place from decades to millions of years and usually referring to (regional) rise or fall of mean temperatures, changes in precipitation and parameters such as the frequency of extreme weather events. Throughout Earth's history long-term climate change and climate events have taken place as a consequence of internal or external forcing of the naturally occurring climate system. The most recent, relatively short-term change in the global climate however, has been more dramatic and due to anthropogenically produced greenhouse gases that have acted on the climate system by reducing the heat radiation to space. Anthropogenically induced global warming trend had already been described in the late nineteenth century (Arrhenius 1896). At that time, the contribution of industrially produced CO<sub>2</sub> was thought to have minor effects with respect to the overall natural climate dynamics and it was believed that the observed warming would at least be partially beneficial to human prosperity: "...there is good mixed with the evil. ..., we may hope to enjoy ages with more equitable and better climates, especially as regards the colder regions of the earth..." (Arrhenius 1908). Since this time research to investigate climate change impacts has intensified and there is now strong evidence, that besides the increase in temperature, our global climate has become less stable with more frequent and intense weather events due to the present day atmospheric levels of CO<sub>2</sub> concentration being higher than at any time during the last 2.6 million years (Lewandowsky et al. 2016). Since pre-industrial times, atmospheric CO<sub>2</sub> increased from 280 to 400 ppm and a further doubling is projected until the end of the century (IPCC 2013). This rate of change is unprecedented with an anthropogenic CO<sub>2</sub> release rate being 14,000 times faster than the natural net release of CO<sub>2</sub> (Zeebe et al. 2016).

### 44.1.2 The Role of the Oceans

The oceans play an important role in global climate through gas and heat exchange and it is this thermal capacity of the oceans that moderates the climate and slows down global warming. Heat exchange with the ocean affects the upper ocean layers more strongly than the deep ocean and up to 90% of the additional heat and about one third of anthropogenic CO<sub>2</sub> released since pre-industrial times has been absorbed by the oceans. Since the 1970s ocean temperatures too have increased by 0.11 °C per decade in the upper 75 m and by 0.015 °C at 700 m water depth (Levitus et al. 2012; Rhein et al. 2013). An apparent ‘hiatus’ in global warming and sea surface heat uptake during the last 15 years had been identified (IPCC 2013), while the deeper ocean has contributed significantly to an additional and recent heat sequestration. This factor explains the observed slowing down of atmospheric warming during the last decade (Hansen et al. 2011; Meehl et al. 2011; Chen and Tung 2014; Cheng et al. 2015; Yan et al. 2016; Desbruyères et al. 2016; Bova et al. 2016), with recent research substantiating the ongoing ocean warming trend (Kosaka and Xie 2013; Karl et al. 2015; Lewandowsky et al. 2016; Fyfe et al. 2016; Song et al. 2016; Hausfather et al. 2017). Global change not only affects the general heat content and warming of the oceans, but has widespread consequences related to the temperature dependent state of water as solid ice, liquid or vapour. Changes in sea level, salinity and freshwater content show strong regional trends dependent on the ratio of evaporation, precipitation, river discharge and melting of glaciers and ice caps (Church et al. 2011; Pierce et al. 2012; Levermann et al. 2013; Rhein et al. 2013). Since the 1950s the contrast between high- and low-salinity regions has increased by 0.13 (Rhein et al. 2013). These changes in seawater temperature and salinity affect the density and volume of seawater causing changes to the steric sea level (Antonov et al. 2002; Llovel et al. 2014), circulation of water masses and to ocean currents (Purkey and Johnson 2010; England et al. 2014; McGregor et al. 2014).

### 44.1.3 Ocean Acidification

Anthropogenic CO<sub>2</sub> released to the atmosphere is partially taken up by the oceans and acts as a major net sink for anthropogenic carbon (Revelle and Suess 1957; Orr et al. 2001; Sabine et al. 2004; Landschützer et al. 2016). Since pre-industrial times about 25–30% of atmospheric CO<sub>2</sub> has been absorbed by the oceans. The rising partial pressure of CO<sub>2</sub> (pCO<sub>2</sub>) has major consequences as CO<sub>2</sub> reacts to carbonic acid in solution resulting in the reduction of ocean pH termed ocean acidification (OA). There is an increasing awareness that climate change is altering the physical and biogeochemical status of the surface ocean and with the

simultaneous increase of hydrogen and bicarbonate ions and a decrease in carbonate ions the seawater pH will decline by an average 0.3 units by the end of the century (Caldeira and Wickett 2003; Cicerone et al. 2004; Feely et al. 2004; Sabine et al. 2004; Orr et al. 2005b; Gattuso et al. 2015). This change also affects the calcium carbonate saturation state ( $\Omega$ ) in seawater which is the discriminant parameter with respect to the precipitation and solution of calcium carbonates. Solubility increases at higher pressure and lower temperature, which means that  $\Omega$  decreases with increasing water depths and at higher latitudes. OA has been postulated to be of a major concern for various calcifying organisms as they depend on the surrounding seawater to build their shells or in the case of cold-water corals (CWCs), their skeletons (Orr et al. 2005a, b; Kleypas et al. 2006). Over the last decade research on the effects of OA on marine organisms has intensified and new priorities for future research identified. OA impacts have highlighted the urgent need to study keystone species, ecosystem engineers and those ecosystems considered most vulnerable or most resilient to global climate change (Riebesell and Gattuso 2015). Like their tropical counterparts, scleractinian CWCs grow an aragonitic 3-D matrix like exoskeleton, and as such are susceptible to changes in the seawater carbonate chemistry. The surface ocean is currently supersaturated in aragonite and calcite, the two forms of carbonate that marine calcifiers use to form their shells or skeletons. The ongoing absorption of atmospheric CO<sub>2</sub> by the oceans results in a shallowing of the aragonite saturation horizon (ASH), the critical depth between precipitation and dissolution of aragonitic calcium carbonate. Work by Feely et al. (2012) showed that the offset in the ASH in the South Pacific between the 1990s and the 2000s had shifted by 10 m. In the New Zealand region estimates suggest that the ASH may have already shoaled by an order of 50 to 100 m (Bostock et al. 2013, 2015; Law et al. 2016). This places the deep-sea aragonitic scleractinian CWCs, being confined to the deep waters and to colder regions at great risk with 70% of the CWC habitats becoming exposed to undersaturated conditions (Guinotte et al. 2006; Mikaloff-Fletcher et al. 2006; Bostock et al. 2015). Scleractinian CWC ecosystems are thought to be one of the most vulnerable groups that will be impacted by global climate change. This factor and additional anthropogenic stressors such as deep-sea trawling, mineral exploration, mining, and marine pollution (Turley et al. 2007; Roberts et al. 2016), add to the vulnerability of CWCs in a high CO<sub>2</sub> world.

### 44.1.4 Cold-Water Corals

While the biology of shallow-water tropical corals and their response to global change (warming and OA) has been studied for many decades, research on the biology and physi-

ology of deep-sea CWCs such as the abundant scleractinian coral group is still in its infancy (but see Reynaud and Ferrier-Pagès, [this volume](#) and references therein). Until a decade ago knowledge was based on few studies providing some insights on skeletal extension (Bell and Smith 1999; Mortensen 2001), food capture (Mortensen 2001), potential food sources (Kiriakoulakis et al. 2005; Duineveld et al. 2007), the respiratory response to temperature change or hypoxia (Dodds et al. 2007) and reproductive ecology (Waller and Tyler 2005; Waller et al. 2005). However, the knowledge on the abundance and distribution of CWCs has advanced rapidly since the 1990s due to several factors such as an increase in deep-sea biodiversity surveys (e.g. Zibrowius and Gili 1990; Rogers 1999; Roberts et al. 2009; Buhl-Mortensen et al. 2010; Mastrototaro et al. 2010; Tittensor et al. 2010; Gori et al. 2013; Smith and Williams 2015); access to more sophisticated deep-sea technology facilitating surveys in deeper water over larger areas (e.g. Hovland et al. 2002; Sumida et al. 2004; Taviani et al. 2005; Wheeler et al. 2007; Freiwald et al. 2009; Orejas et al. 2009; De Mol et al. 2011; Gori et al. 2013; Savini et al. 2014; Clippele et al. 2016; see also Angeletti et al., [this volume](#); Lo Iacono et al., [this volume](#)), and in several regions, primarily due to fishing activity and fisheries research surveys where the bycatch of deep-sea corals has occurred (e.g. Fosså et al. 2002; Gass and Willison 2005; Hourigan 2009; Tracey et al. 2011; Clark et al. 2015). This growing knowledge of the presence and spatial distribution of CWCs allowed to model and identify the most important parameters supporting or limiting CWC distribution and habitat suitability (Davies et al. 2008; Davies and Guinotte 2011; Tracey et al. 2011; Rowden et al. 2013; Anderson et al. 2016). Among a multitude of environmental and geographic variables taken into consideration depth, temperature, salinity and aragonite saturation state ( $\Omega_a$ ) appear to be some of the most important factors controlling the abundance and distribution of CWCs. Additionally, the knowledge on the physiology and growth of CWCs has rapidly advanced during the last decade (Lartaud et al., [this volume](#); Reynaud and Ferrier-Pagès, [this volume](#)) owing to an increased effort in sampling live CWCs and in establishing aquarium facilities that allow to maintain CWCs for an extended time in the laboratory (see Orejas et al., [this volume](#) and references therein).

#### 44.1.5 Climate Change in the Mediterranean Region

The Mediterranean region has been identified as one among the most important climate change Hot-Spots world-wide as it has become warmer and drier throughout the twenty-first century (Giorgi 2006). The variability in warming during

summer is twice the global standard deviation (Hansen and Sato 2016). With this large increase in variability and a decrease in mean precipitation during the dry, warm seasons the Mediterranean constitutes one of the most responsive and affected regions with respect to global change (Giorgi et al. 2001; Giorgi and Lionello 2008; Mariotti et al. 2008; Alessandri et al. 2014).

The Mediterranean Sea is nearly land-locked, connected to the Atlantic by the shallow (300 m) Strait of Gibraltar. Evaporation greatly exceeds precipitation which drives the thermohaline circulation with deep and intermediate dense water convection in several basins and a unique open upper thermohaline cell that acts in a similar way as the global conveyor belt while it is characterised by a much shorter residence time of ca. 100 years (Malanotte-Rizzoli et al. 2014; Hayes et al., [this volume](#)). Therefore, the waters respond faster and are more sensitive to environmental change and thus can be regarded as a miniature model ocean (Bethoux et al. 1990, 1998; Bethoux and Gentili 1996; Turley 1999). Over the last decades, the trends of long-term warming and salting have been evidenced throughout the Mediterranean Sea (Bethoux et al. 1990; Rixen et al. 2005; Nykjaer 2009; Vargas-Yáñez et al. 2009). Based on model simulations, an increase in sea surface temperature and sea surface salinity (SST and SSS) by 2 to 3 °C and 0.48 to 0.89 are predicted for 2070–2099. This is in comparison to ~30 years of SST and SSS data measured between 1961–1990 (Adloff et al. 2015). The trend has also increased at depth, where a temperature and salinity increase of 0.93–1.35 °C and 0.28 to 0.52 respectively has occurred throughout the water column. At the depths that scleractinian CWCs occur in the Mediterranean (below 200 m), the predicted temperature rise may increase by up to 2 °C and the salinity by ~0.5. Accordingly, Mediterranean CWCs might be exposed to a temperature between 15.5 to 16 °C and a salinity of 39.5 to 40 by the end of the century.

The Mediterranean Sea is characterised by a high total alkalinity ( $A_T$ ) of ca 2600  $\mu\text{mol kg}^{-1}$  with a high buffering capacity absorbing more  $\text{CO}_2$  than the open ocean (CIESM 2008). It is a small to medium sink for  $\text{CO}_2$  absorbing ca. 0.24 Gt C  $\text{year}^{-1}$  (D'Ortenzio et al. 2008) while the reduction of ocean pH is relatively fast with  $-0.14$  to  $-0.05$  pH units  $\text{year}^{-1}$  (Touratier and Goyet 2009, 2011). Despite this, the  $\Omega$  remains higher in the deep Mediterranean waters compared to the deep waters of the North Atlantic (Millero et al. 1979), and even at the deepest water depths the seawater is not likely to become undersaturated with respect to  $\Omega_a$  (Hassoun et al. 2015; Goyet et al. 2016). Present day  $\Omega_a$  reported in the vicinity of Mediterranean CWCs are relatively high ranging between 2.3 and 3.0 (Rodolfo-Metalpa et al. 2015; Maier et al. 2016) but will drastically decrease to ca. 1.5 by the end of the century (Maier et al. 2016).

### 44.1.6 Effect of Climate Change Parameters on Cold-Water Corals

To date 24 experimental studies have been published on the physiological response of scleractinian CWCs to climate change and these studies, from both the Mediterranean and elsewhere, are summarised in Table 44.1. Nineteen of these studies addressed the effect of OA, eight the effect of temperature, four took into account the combined effect of OA and temperature. No studies are available on the effect on CWCs to changes in salinity. Interestingly, 40% of the studies were conducted using CWCs from the Mediterranean Sea region. The studies comprise five scleractinian coral species (*Madrepora oculata*, *Lophelia pertusa*, *Desmophyllum dianthus*, *Dendrophyllia cornigera* and *Caryophyllia smithii*), while most of the non-Mediterranean CWC studies were confined to the species *L. pertusa* (Table 44.1). The studies were distinct with respect to the time allowed for acclimation, replication and the use of single (Fig. 44.1), consecutive (Fig. 44.2) or repeated (Fig. 44.3) measure designs. Most studies were carried out in the laboratory, some short-term experiments were conducted at sea using freshly collected specimens and seawater from the actual sampling site (Maier et al. 2009, 2012; Hennige et al. 2014) and one other Mediterranean study included *in situ* experiments where coral fragments were transplanted to the close vicinity of a natural CO<sub>2</sub> vent site (Rodolfo-Metalpa et al. 2015). To provide an indication on the statistical robustness of the experimental studies a point system was introduced (“SR”; Table 44.1) taking into account criteria such as the number of replication, number of repeated measurements and the type of controls. Theoretically, a minimum point score of 3 and a maximum of 11 was possible, and an average SR of 5.7 points ( $\pm 1.4$  S.D) was typical for the studies (Table 44.1). This point system is not exclusive with respect to other criteria that may be important to evaluate the robustness of a study (e.g. handling stress, sampling and analytical procedures, adequacy of maintenance conditions), however, these criteria are difficult to judge in a scoring system.

## 44.2 Ocean Acidification Studies

The pCO<sub>2</sub> used in most of the OA experimental studies ranged between ambient (ca. 400  $\mu$ atm) and 800–1000  $\mu$ atm, corresponding to current and future conditions in 2100 using a business-as-usual CO<sub>2</sub> emission scenario. The exception was for two short-term experiments where pCO<sub>2</sub> levels in which pCO<sub>2</sub> values outside this range were used: 280  $\mu$ atm to represent pre-industrial times (Maier et al. 2012) and 1725  $\mu$ atm (Maier et al. 2016). The first studies of the effect of OA were performed on *Lophelia pertusa*. They revealed a negative response of calcification to increasing pCO<sub>2</sub> during short-

term exposure (Maier et al. 2009; Form and Riebesell 2012) while no effect was detected when exposed for several months to elevated pCO<sub>2</sub> (Form and Riebesell 2012). These two studies show that *L. pertusa* is able to maintain positive calcification rates despite being exposed to undersaturated  $\Omega_a$  (Maier et al. 2009; Form and Riebesell 2012). Subsequent studies have demonstrated that calcification remains constant for pCO<sub>2</sub> levels corresponding to those between present-day (~400  $\mu$ atm) and those projected until the end of the century (~800–1000  $\mu$ atm) (Figs. 44.1, 44.2, and 44.3). This was found for both short- and long-term exposure and for most CWC species studied, suggesting that no long-term acclimation occurs (Maier et al. 2012, 2013b, 2016; Carreiro-Silva et al. 2014; Hennige et al. 2014; Movilla et al. 2014a, b; Rodolfo-Metalpa et al. 2015). However, some recent literature states that CWCs may exhibit a long-term acclimation response in calcification to OA (Hennige et al. 2015; Roberts et al. 2016). Evidently, calcification is negatively affected in short-term experiments when  $\Omega_a$  is below a certain threshold level (Figs. 44.1a, c and 44.2b, c; Maier et al. 2009; Lunden et al. 2014; Georgian et al. 2016b, Maier et al. 2016) but the same is true in long-term experiments (Fig. 44.3d, Hennige et al. 2015). Furthermore, using a repeated measures experimental design, Movilla et al. (2014b) showed a decline in calcification for the Mediterranean coral *Desmophyllum dianthus* after 314 days of exposure to elevated pCO<sub>2</sub> (800  $\mu$ atm), while no effect at shorter exposure times was observed (Fig. 44.3c; Movilla et al. 2014b). This response might be species-specific, as none of the other three species (*L. pertusa*, *Madrepora oculata* and *Dendrophyllia cornigera*) studied in parallel revealed any significant effect between control and elevated pCO<sub>2</sub> treatments, neither during short- nor long-term exposure (Movilla et al. 2014a,b). It would have been interesting to see, if calcification of *D. dianthus* remains at the lower level it revealed after 314 days, restores calcification to normal rates or in the worst case scenario, further reduces calcification with increasing exposure time. A result such as this could be indicative of an eventual break down in calcification as a consequence of extended and continuous exposure to elevated pCO<sub>2</sub>. For *D. dianthus* it has been shown that genes involved in stress response, metabolism or calcification were upregulated under elevated pCO<sub>2</sub> levels after a 8-month exposure while the rates of calcification and respiration remained stable (Carreiro-Silva et al. 2014). No time-series on gene expression experiments exist for these species to date, and so it is not known whether an up- or down regulation of genes is dependent on the duration of exposure. While calcification rates are relatively constant over a large range of pCO<sub>2</sub> and only decrease after a certain threshold has been reached, faster skeletal linear extension under high pCO<sub>2</sub> has been reported for North Atlantic studies on *L. pertusa* (Hennige et al. 2015). This coincides with thinner and longer corallites and an altered mineral organisation that may impact

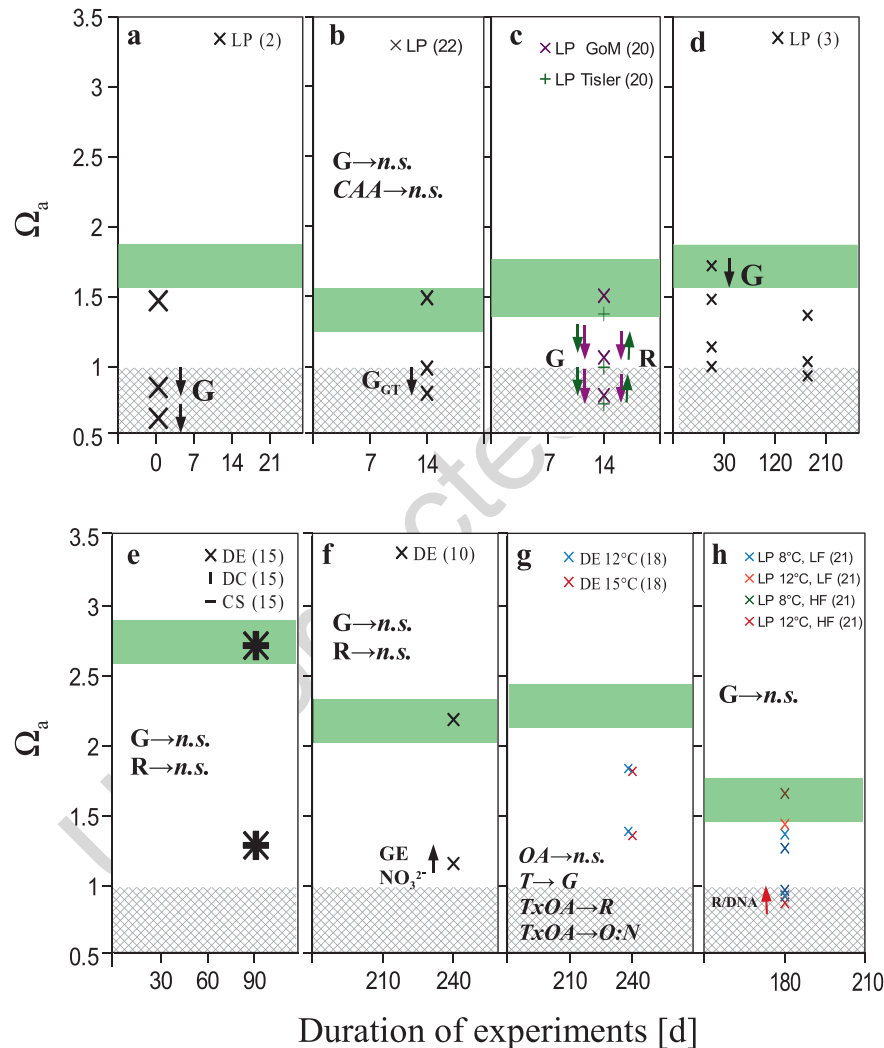
t1.1 **Table 44.1** Summary of experimental studies on the effects of climate change on cold-water corals (CWCs)

| t1.2  | Reference | Region | Factors | Species | Physiol. functions |   |   |    |    |    |    |    |    |   | Experimental design |    |    |                   |   |    |    | Replication |    |    |    |    |    |       |         |     |
|-------|-----------|--------|---------|---------|--------------------|---|---|----|----|----|----|----|----|---|---------------------|----|----|-------------------|---|----|----|-------------|----|----|----|----|----|-------|---------|-----|
| t1.3  | #         |        | T       | OA      | TxOA               | F | S | LP | MO | DE | DC | CS | SV | G | R                   | Sk | GE | OT                | † | ST | LT | SM          | RM | CM | IC | PC | FC | n     | Tanks/n | SR  |
| t1.4  | 1         | N-A    | +       | -       | -                  | - | - | +  | -  | -  | -  | -  | -  | - | +                   | -  | -  | -                 | - | +  | -  | +           | -  | -  | -  | +  | -  | 4-6   | n       | 5   |
| t1.5  | 2         | Skag   | -       | +       | -                  | - | - | +  | -  | -  | -  | -  | -  | + | -                   | -  | -  | -                 | - | -  | -  | +           | -  | -  | -  | +  | -  | 2x8   | n       | 6   |
| t1.6  | 3         | N-A    | -       | +       | -                  | - | - | +  | -  | -  | -  | -  | -  | + | -                   | -  | -  | -                 | - | -  | +  | -           | -  | -  | -  | +  | -  | 4     | n       | 4   |
| t1.7  |           |        |         |         |                    |   |   |    |    |    |    |    |    |   |                     |    |    |                   |   |    |    |             |    |    |    |    |    | 5     | n       | 4   |
| t1.8  | 4         | MED    | -       | +       | -                  | - | - | -  | +  | -  | -  | -  | -  | + | -                   | -  | -  | -                 | - | -  | +  | -           | +  | -  | -  | -  | -  | 15    | n       | 7   |
| t1.9  | 5         | MED    | -       | +       | -                  | - | - | +  | +  | -  | -  | -  | -  | + | -                   | -  | -  | -                 | - | -  | +  | +           | +  | -  | -  | +  | -  | 4     | n       | 7   |
| t1.10 | 6         | MED    | +       | +       | -                  | - | - | +  | +  | -  | -  | -  | -  | - | +                   | -  | -  | -                 | - | -  | +  | +           | +  | -  | -  | +  | -  | 4     | n       | 7   |
| t1.11 | 7         | GoM    | +       | -       | -                  | - | - | +  | -  | -  | -  | -  | -  | - | -                   | -  | -  | DOC               | + | +  | -  | +           | +  | -  | -  | +  | -  | 5     | n       | 6   |
| t1.12 | 8         | MED    | +       | -       | -                  | - | - | +  | +  | -  | -  | -  | -  | + | -                   | -  | -  | -                 | - | -  | +  | +           | +  | -  | -  | +  | -  | 5     | 1/h     | 5   |
| t1.13 |           |        |         |         |                    |   |   |    |    |    |    |    |    |   |                     |    |    |                   |   |    |    |             |    |    |    |    |    |       |         |     |
| t1.14 | 9         | MED    | +       | -       | -                  | - | - | -  | -  | +  | +  | -  | -  | + | -                   | -  | -  | -                 | - | -  | +  | +           | -  | -  | -  | +  | -  | 5     | 1/h     | 4   |
| t1.15 |           |        |         |         |                    |   |   |    |    |    |    |    |    |   |                     |    |    |                   |   |    |    |             |    |    |    |    |    |       |         |     |
| t1.16 | 10        | N-A    | -       | +       | -                  | - | - | -  | -  | +  | -  | -  | -  | + | -                   | -  | +  | NUTS<br>GE        | - | -  | +  | +           | +  | -  | -  | +  | -  | 6     | 2/h     | 6   |
| t1.17 |           |        |         |         |                    |   |   |    |    |    |    |    |    |   |                     |    |    |                   |   |    |    |             |    |    |    |    |    |       |         |     |
| t1.18 | 11        | N-A    | -       | +       | -                  | - | - | +  | -  | -  | -  | -  | -  | + | -                   | -  | -  | -                 | - | -  | +  | +           | +  | -  | -  | +  | -  | 8     | 1/h     | 6   |
| t1.19 | 12        | GoM    | +       | +       | -                  | - | - | +  | -  | -  | -  | -  | -  | + | -                   | -  | -  | -                 | + | +  | -  | +           | -  | -  | -  | +  | -  | 2x8   | 2/h     | 7   |
| t1.20 | 13        | MED    | -       | +       | -                  | - | - | +  | +  | -  | -  | -  | -  | + | -                   | -  | -  | -                 | - | -  | +  | +           | +  | -  | -  | +  | -  | 12-18 | 3/h     | 7   |
| t1.21 | 14        | MED    | -       | +       | -                  | - | - | -  | -  | +  | +  | -  | -  | + | -                   | -  | -  | OM                | - | -  | +  | +           | +  | -  | -  | +  | -  | 9     | 3/h     | 7   |
| t1.22 | 15        | MED    | -       | +       | -                  | - | - | -  | -  | +  | +  | -  | -  | + | -                   | -  | -  | -                 | - | -  | +  | +           | +  | -  | -  | +  | -  | 7-23  | 2/h     | 7   |
| t1.23 |           |        |         |         |                    |   |   |    |    |    |    |    |    |   |                     |    |    |                   |   |    |    |             |    |    |    |    |    |       |         |     |
| t1.24 | 16        | N-A    | +       | +       | +                  | - | - | +  | -  | -  | -  | -  | -  | + | -                   | -  | -  | -                 | - | -  | +  | +           | +  | -  | -  | +  | -  | 4-8   | 4/h     | 6   |
| t1.25 | 17        | N-A    | -       | +       | -                  | - | - | +  | -  | -  | -  | -  | -  | - | -                   | -  | -  | d <sup>11</sup> B | - | -  | +  | +           | -  | -  | -  | +  | -  | 1-4   | n       | n/a |
| t1.26 | 18        | MED    | +       | +       | -                  | - | - | -  | -  | +  | -  | -  | -  | + | -                   | -  | -  | -                 | - | -  | +  | +           | -  | -  | -  | +  | -  | 3     | n       | 4   |
| t1.27 | 19        | MED    | -       | +       | -                  | - | - | -  | +  | -  | -  | -  | -  | + | -                   | -  | -  | -                 | - | -  | +  | +           | +  | -  | -  | +  | -  | 13    | n       | 9   |
| t1.28 |           |        |         |         |                    |   |   |    |    |    |    |    |    |   |                     |    |    |                   |   |    |    |             |    |    |    |    |    |       |         |     |
| t1.29 | 20        | GoM    | -       | +       | -                  | - | - | +  | -  | -  | -  | -  | -  | + | -                   | -  | -  | -                 | - | -  | +  | +           | -  | -  | -  | +  | -  | 8     | 2/h     | 5   |
| t1.30 |           |        |         |         |                    |   |   |    |    |    |    |    |    |   |                     |    |    |                   |   |    |    |             |    |    |    |    |    |       |         |     |
| t1.31 | 21        | N-A    | +       | +       | +                  | - | - | +  | -  | -  | -  | -  | -  | + | -                   | -  | -  | -                 | - | -  | +  | +           | -  | -  | -  | +  | -  | 4     | n       | 4   |
| t1.32 |           |        |         |         |                    |   |   |    |    |    |    |    |    |   |                     |    |    |                   |   |    |    |             |    |    |    |    |    |       |         |     |
| t1.33 | 22        | GoM    | -       | +       | -                  | - | - | +  | -  | -  | -  | -  | -  | + | -                   | -  | -  | GT                | - | -  | +  | +           | -  | -  | -  | +  | -  | 12    | 1/h     | 5   |
| t1.34 |           |        |         |         |                    |   |   |    |    |    |    |    |    |   |                     |    |    |                   |   |    |    |             |    |    |    |    |    |       |         |     |
| t1.35 | 23        | N-A    | -       | +       | -                  | - | - | +  | -  | -  | -  | -  | -  | + | -                   | -  | -  | -                 | - | -  | +  | +           | -  | -  | -  | +  | -  | 4     | 1/h     | 4   |
| t1.36 | 24        | SW-P   | -       | +       | -                  | - | - | -  | -  | -  | -  | -  | -  | + | -                   | -  | -  | -                 | - | -  | +  | +           | -  | -  | -  | +  | -  | 5     | 1/h     | 4   |
| t1.37 |           |        |         |         |                    |   |   |    |    |    |    |    |    |   |                     |    |    |                   |   |    |    |             |    |    |    |    |    | 9     | 3/h     | 6   |
|       |           |        |         |         |                    |   |   |    |    |    |    |    |    |   |                     |    |    |                   |   |    |    |             |    |    |    |    |    | 16    | 1       | 5.7 |

t1.38 The variables used temperature change ( $\Delta T$ ), ocean acidification (OA), combined effects of T and OA (TxOA) and salinity (S). The study regions were the Mediterranean Sea (MED), the focus region of this Chapter, as well the North-Atlantic (N-A), Skagerrak (Skag), Gulf of Mexico (GoM) and South-West Pacific (SW-P). Study species were *Lophelia pertusa* (LP), *Madrepora oculata* (MO), *Desmophyllum dianthus* spp. (DE), *Dendrophyllia cornigera* (DC), *Caryophyllia smithii* (CS) and *Solenosmilia variabilis* (SV). The measures of calcification (G), respiration (R), skeletal structure (Sk), gene expression t1.40 (GE), genotypes (GT), polyp mortality ( $\dagger$ ), polyp requirements (OT), like inorganic nutrients (NUTS), dimethyl/sulfoniopropionate (DMSp), dissolved organic carbon (DOC), organic matter (OM), total t1.41 organic carbon (TOC), respiratory quotient (RQ), energy requirements (E), boron isotopes ( $\delta^{11}B$ ), carbonic anhydrase activity (CAA), RNA/DNA ratio (RNA/DNA) and loss of coenosarc (CS). Experiments t1.42 were evaluated according to their statistical robustness (SR) by using a point-system based on experimental duration short- and/or long-term exposure (ST and/or LT), design with a single (SM), repeated t1.43 (RM) or consecutive (CM) measurements, the type of control(s) used with initial (IC), parallel (PC) and/or final controls (FC). The number of replicates (n), number of tanks per treatment (tanks/n) were t1.44 taken into consideration. The points for statistical robustness (SR) were attributed as follows: each “+” under Experimental Design was counted as 1. For replication 1 point was given for of 5–9 and 2 points t1.45 for >10 replicates. If more than 1 tank per treatment for replicates (tanks/n) was used (>1/n) another point was allocated

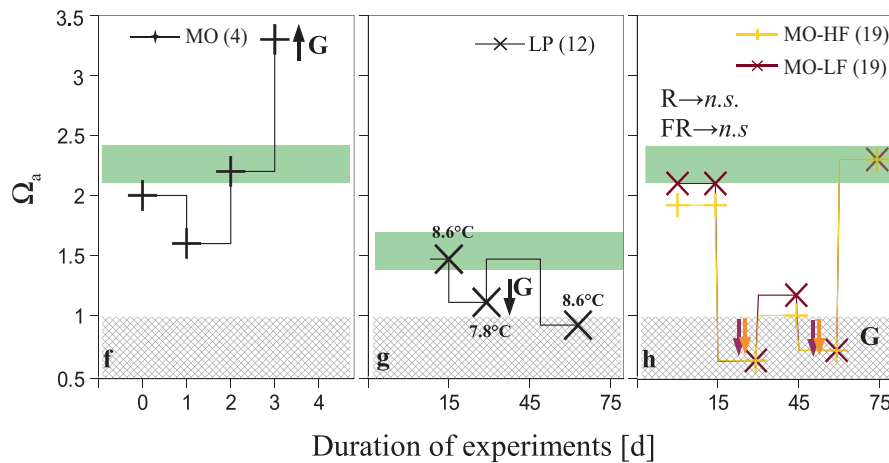
375 the stability and breaking strength of the skeleton and the stability of the CWC framework. Despite this, changes in the micro-density and porosity were not reported under similar conditions, neither for North Atlantic *L. pertusa* (Wall et al. 2015) nor Mediterranean CWC species (Movilla et al. 2014a). In a study on a related species *Solenosmilia variabilis* colonies were grown under ambient pH (7.88,  $\Omega_a$  0.93) and lower pH (7.65,  $\Omega_a$  0.78) for two years (Gammon et al. 2018). Respiration and growth rate were not altered under low pH, although there was a decrease in skeletal colouration attributed to a loss of coenochyme, the tissue connecting neigh-

bouring polyps and covering the outer skeleton, indicating the potential reallocation of energy to other physiological processes such as growth and respiration. While there has been two studies where respiration decreased or increased after two weeks during short-term exposure to higher pCO<sub>2</sub> (Figs. 44.1c and 44.3a; Hennige et al. 2014; Georgian et al. 2016b) no effect on respiration at increased pCO<sub>2</sub> levels has been detected in other studies (Figs. 44.1e–g, 44.2c, and 44.3b, c; Maier et al. 2013a, 2016; Carreiro-Silva et al. 2014; Movilla et al. 2014a, b; Rodolfo-Metalpa et al. 2015; Hennige et al. 2015; Gori et al. 2016; Gammon et al. 2018).



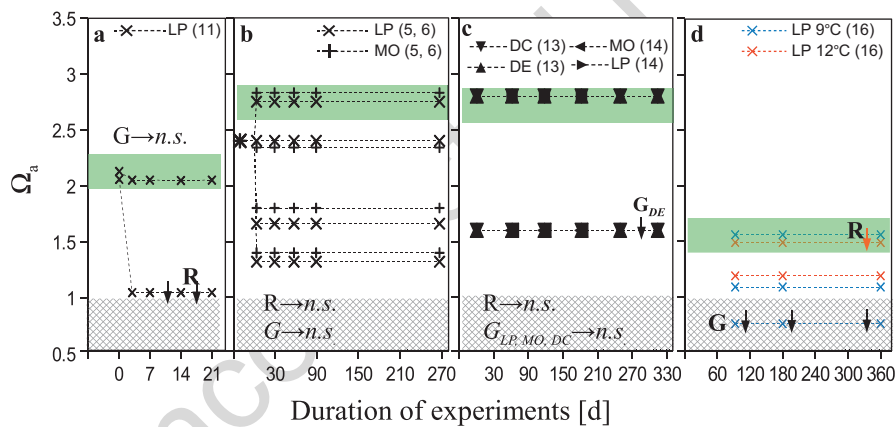
**Fig. 44.1** Plot of studies using single-point experimental designs for measurements according to aragonite saturation state ( $\Omega_a$ ) in seawater (y-axis) and acclimation time in days (duration of experiments [d], x axes). The response of physiological functions are shown according to studies (a–h) and include calcification (G), calcification of different genotypes ( $G_{GT}$ ), respiration (R), gene expression (GE), carbonic anhydrase activity (CAA) and nitrate excretion ( $\text{NO}_3^{2-}$ ) for the species *Lophelia pertusa* (LP), *Madrepora oculata* (MO), *Desmophyllum dianthus* (DE), *Dendrophyllia cornigera* (DC), and *Caryophyllia smithii* (CS). Numbers in brackets refer to the publications referenced in

Table 44.1. For studies addressing combined effects of OA and temperature (g) or OA, temperature and feeding (h) coloured symbols were used. The temperature and high or low food supply (HF and LF) are indicated in the symbol legend. According to the region the ambient  $\Omega_a$  varied and is indicated by the green area. The grey area indicates  $\Omega_a < 1$ . Numbers in brackets refer to the publications referenced in Table 44.1. Size of symbols is indicative of number of replicates (n), vertical arrows depict where a significant positive (↑) or negative (↓) response was revealed, while n.s. indicates that there was no significant effect between treatment levels for the respective variable (© Cornelia Maier)



**Fig. 44.2** Plot of studies using consecutive experimental designs for measurements according to aragonite saturation state ( $\Omega_a$ ) in seawater (y-axis) and acclimation time in days (duration of experiments [d]; x axes). The symbol lines record changes of  $\Omega_a$  during experiments with symbols depicting when calcification (G) or respiration (R) of *Lophelia pertusa* (LP) or *Madrepora oculata* (MO) were assessed during the consecutive changes in  $\Omega_a$ . Numbers in brackets refer to the publications referenced in Table 44.1. Coloured symbols (in h) were used to

depict the high (HF) and low (LF) food regime. According to the region the ambient  $\Omega_a$  varied and is indicated by the green area. The grey area indicates  $\Omega_a < 1$ . Numbers in brackets refer to the publications referenced in Table 44.1. Size of symbols is indicative of number of replicates (n), vertical arrows depict where a significant positive (↑) or negative (↓) response was revealed, while *n.s.* indicates that there was no significant effect between treatment levels or time steps for the respective variable (© Cornelia Maier)



**Fig. 44.3** Plot of studies using repeated measurement designs showing measurements points according to aragonite saturation state ( $\Omega_a$ ) in seawater (y-axis) and acclimation time in days (duration of experiments [d]; x-axis). The symbol lines record  $\Omega_a$  for replicated measurements with symbols depicting when calcification (G) or respiration (R) of *L. pertusa* (LP), *M. oculata* (MO), *D. dianthus* (DE) or *D. cornigera* (DC) were assessed during the consecutive changes in  $\Omega_a$ . Numbers in brackets refer to the publications referenced in Table 44.1. According to the region the ambient  $\Omega_a$  varied

and is indicated by the green area. The grey area indicates  $\Omega_a < 1$ . Numbers in brackets refer to the publications referenced in Table 44.1. Coloured symbols were used for the combined effect of OA and temperature (in d) with the temperature indicated in the symbol legend. Size of symbols is indicative of number of replicates (n), vertical arrows depict where a significant positive (↑) or negative (↓) response was revealed, while *n.s.* indicates that there was no significant effect between treatment levels or time steps for the respective variable (© Cornelia Maier)

397 The apparent high resilience of CWCs to OA in both the  
398 experimental studies, described here for the Mediterranean  
399 and elsewhere, and also observed *in situ* (Thresher et al.  
400 2011; Fillinger and Richter 2013; Jantzen et al. 2013;  
401 Bostock et al. 2015; Georgian et al. 2016a; Gammon et al.  
402 2018) has been attributed to pH upregulation of the calico-  
403 blastic pH (McCulloch et al. 2012; Wall et al. 2015). The  
404 upregulation of calcicoblastic pH has been thought to require

a high amount of energy and may consequently require high  
405 food availability in areas with low  $\Omega_a$  to maintain calcifica-  
406 tion constant (McCulloch et al. 2012; Fillinger and Richter  
407 2013; Jantzen et al. 2013). However, a study establishing an  
408 energy budget for major physiological functions of  
409 Mediterranean *M. oculata* revealed that the energy required  
410 for calcification in general and for the upregulation of calico-  
411 blastic pH (or  $\Omega_a$ ) in particular only constitutes a minor frac-  
412

tion of about 1 to 3% of overall metabolic requirements (Maier et al. 2016). Despite a four-fold food uptake in the high feeding group and the respiratory quotient indicating starvation in the low-food group, no mitigating effect on calcification or respiration at increased pCO<sub>2</sub> levels due to feeding was reported (Maier et al. 2016). Similarly, in a study on North-Atlantic *L. pertusa* no mitigating effect of feeding has been shown despite a tenfold food availability in the high-food group (Büscher et al. 2017).

However, the need to double the energy allocated to calcification at elevated pCO<sub>2</sub> (Maier et al. 2016) might nevertheless constitute a burden over an extended time and permanent exposure to unfavorable conditions. Specifically in an environment where food is permanently scarce, a shift in energy allocation might occur in favor of other physiological functions that may explain the observed decline in calcification of *D. dianthus* (Movilla et al. 2014b). The decrease in skeletal colouration attributed to a loss of coenochyme seen by Tracey et al. may have also reflected a food scarcity response.

#### 44.2.1 Temperature

Of the eight studies assessing the response of CWCs to changes in temperature, two measured the survival of *L. pertusa* from the Gulf of Mexico at a temperature range from 8 (ambient) to 15, 20 and 25 °C and an exposure time of 1 and 8 days (Brooke et al. 2013) or by changing temperature in consecutive steps from 8, 10, 12, 14 to 16°, with an adjustment period of 1 day per 2 °C increment (Lunden et al. 2014). Both studies showed significant mortalities at temperatures ≥15 °C and conclude that the upper temperature limit for the survival of *L. pertusa* would be 15 °C. The projected rise in temperature in the Mediterranean Sea could be as detrimental to the Mediterranean CWCs. However, the experimental design used by Brooke et al. (2013) did not allow for longer term acclimation and was in fact designed to reflect specific conditions prevailing in the Gulf of Mexico, where CWCs can experience occasional flushing by warm-water currents and a rapid and dramatic increase in seawater temperature (Brooke et al. 2013). In the Mediterranean Sea, CWCs are not subject to such an abrupt temperature increase, but they are subject to the high temperatures at the extreme reported for all CWCs. It is for this reason that it has been assumed that the Mediterranean CWCs are already at their upper tolerance limit (ca. 13 °C) and any further increase in temperature might therefore be detrimental. Despite this, there is some evidence that Mediterranean CWCs are well adapted to a relatively constant high temperature. In two experiments without prior acclimation phase, a temperature dependent increase or decrease of respiration has been reported for *L. pertusa* from the North Atlantic (Dodds et al. 2007) and Mediterranean Sea (Maier et al. 2013a, Supplement

SI\_1). At ambient temperature, respiration rates of Mediterranean *L. pertusa* were comparable to those from the North Atlantic region despite the 4 °C temperature difference. The temperature-dependent coefficient of respiration (Q<sub>10</sub>) was lower for Mediterranean *L. pertusa* than for North-Atlantic specimen further indicating that Mediterranean *L. pertusa* as being well adapted to the higher temperature and potentially less sensitive to a further increase in temperature than specimen from colder regions. This is further substantiated by the finding by Naumann et al. (2013a, b) and Hennige et al. (2015) who found that no significant changes in respiration were observed when Mediterranean or North Atlantic *L. pertusa* were acclimated for 3–6 months to lower or higher than ambient temperatures (Naumann et al. 2013a, b; Hennige et al. 2015). However, in the study by Hennige et al. (2015) respiration rates decreased significantly after a total of 9 months exposure to 12 °C. This response is difficult to explain, and with the good replication (n = 8, 4 tanks / n) it is not likely caused by experimental constraints such as tank effects. The authors therefore consider “... that normal’ energetic strategies are no longer applying, possibly due to other processes using energetic reserves. This could be the result of processes that maybe occurring of which we have poor understanding and/or cannot easily measure” (Hennige et al. 2015). In contrast to *L. pertusa*, respiration of Mediterranean *M. oculata* significantly decreased when temperature was lowered from 12 to 9 and then down to 6 °C after a 3-month acclimation (Naumann et al. 2013b). This result led the authors to speculate that *M. oculata* acclimates at a much slower rate to changes in temperature than *L. pertusa*. The results also provide the variable thermal tolerance range for the two species. *M. oculata* is the dominant species in the Mediterranean, while *L. pertusa* prevails in colder regions like the North Atlantic. This preferred distribution for both species could indicate that *L. pertusa* acclimates faster to colder temperature than *M. oculata* and conversely, that *M. oculata* acclimates more easily to increasing temperatures. To date, no longer term study with respect to increasing temperature tolerance exists for these two species and no final conclusion can be made as to: how these two species may acclimate to the ongoing warming in the Mediterranean Sea. For calcification responses, the Mediterranean *D. cornigera* revealed a significant increase in calcification at 17.5 °C while a slight but non-significant reduction to 83% was reported for *D. dianthus* at 17.5 °C (Naumann et al. 2013a). When the temperature was lowered from 12 to 9 to 6 °C, calcification of *M. oculata* and *L. pertusa* was faster at the higher temperature levels in both species. While calcification of *M. oculata* significantly decreased at each temperature step, calcification of *L. pertusa* was only significantly lower at 6°, and between 12 to 9 °C only a slight, non-significant decrease was observed (Naumann et al. 2013b). For North Atlantic *L. pertusa* the response

differed, showing a slight decrease in calcification to 82 and 70% after exposure of 3 and 6 months to higher (12 °C) than ambient (9 °C) temperature, while calcification increased to 1.5 times that at ambient temperature after a total of 9 months (Hennige et al. 2015, Fig. 44.3d). The study on Mediterranean *D. dianthus* by Gori et al. (2016) reported a significant and negative effect on calcification when temperature was increased from 12 to 15 °C. When subjected to both elevated temperature and pCO<sub>2</sub>, however, there was no significant calcification effect and the opposite result was found for respiration (Gori et al. 2016). The experimental approach of the Gori et al. (2016) study was interesting and timely as the authors tackled the question of single and combined effects of temperature and OA impacts with the temperature and pCO<sub>2</sub> levels representative of projected changes in the Mediterranean Sea. However, the statistical robustness of the experiment was limited, due to a low number of sample replicates (n = 3) (Table 44.1). The results are useful as they provide a first indication as to how Mediterranean *D. dianthus* would respond to long-term increasing temperature; however the results require some consolidation.

This can also be said for the general perception that CWCs in the Mediterranean Sea are at their upper tolerance limit with respect to temperature. There is evidence that at least some of the species may be able to cope with increasing temperatures but overall there needs to be some caution before drawing this conclusion. It is important to consider in the first instance experimental design (duration of experiments, sample sizes, replication, and controls), as well as other environmental stressors, before any assumptions can be made when assessing the physiological response of these corals to changes in temperature.

#### 44.2.2 Salinity

As a consequence of global change, the salinity in the Mediterranean Sea will increase by ~0.5 at the depths of CWC occurrence (see Skliris, [this volume](#) and references herein). Despite this fact, and that the current salinity levels are the highest reported for CWC occurrence in any one area, no studies are available on the physiological response of CWCs to increasing salinity. In addition to this and of significance is that climate change models need to take into account the ever growing need of freshwater in this region as consequence of a growing population and a higher consumption per capita. The construction of desalination plants along Mediterranean shorelines has intensified during the last decades several times over to generate fresh water. While 50% of the seawater is converted to drinking water the other 50% is discharged back into the sea as concentrated brine. For the Mediterranean Sea, it has been estimated that the salinity due to brine discharge will increase by an additional

0.81 g / L until 2050 (Bashitialshaer et al. 2011). This situation means that together with the salinity increase due to climate change, the salinity may rise to above levels of around 40, which is comparable to the salinity of the Red Sea. The Red Sea is renowned for its thriving tropical coral reefs and one may therefore speculate that this increase in salinity may not impact Mediterranean CWCs. However, a high sensitivity to small changes in salinity has been reported for the tropical coral *S. pistillata* found in the region and that appeared to acclimate more easily to a decline than to an increase in salinity (Ferrier-Pagès et al. 1999). As with temperature, salinity is the highest reported in the Mediterranean region experienced by CWC habitats to date. It will therefore be important to study the response of Mediterranean CWCs to the added stress of an increase in salinity, particularly in light of the additional climate related impacts due to brine discharge that will potentially accelerate the increase in salinity during the coming decades.

#### 44.3 Conclusions

It has been shown in a number of studies that CWCs exhibit a high resilience to OA and may be able to maintain calcification and respiration rates constant over a large gradient in pCO<sub>2</sub>. There is robust evidence that with the projected  $\Omega_a$  remaining above a level of 1, Mediterranean CWC growth might not be as impacted by OA despite the projected and relatively fast decline in seawater pH. The studies summarised in this chapter indicate that there is potentially some hope for some of Mediterranean CWC study species with some groups able to acclimate to an increase in temperature and withstand ocean acidification. However, upper tolerance limits (thresholds) for single climate change parameters still need to be consolidated for each species. This is particularly so for Mediterranean CWCs that are being exposed to additional stressors such as an increase in salinity or pollution. It will be pivotal to address the effect of the concomitant increase in temperature, pCO<sub>2</sub>, and salinity to ultimately conclude on the potential fate of Mediterranean CWC species in the near future as both calcification and respiration reveal a strong acclimation response to temperature.

It is acknowledged that further work is required to tease out the impacts of multiple stressors on the CWCs. Some species may appear to be able to tolerate temperature and OA impacts but at what expense of other biological processes. The various aspects of human induced salinity changes need to be investigated, particularly as the availability of water to growing populations and agriculture will grow in demand. Also important will be to quantify the saturation state of aragonite ( $\Omega_a$ ) within the calcifying fluid of corals as this is critical for understanding their biomineralisation process and sensitivity to environmental changes including ocean acidification.

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## 621 References

- 622 Adloff F, Somot S, Sevault F, et al (2015) Mediterranean Sea  
 623 response to climate change in an ensemble of twenty first centu-  
 624 ry scenarios. *Clim Dyn* 45:2775–2802. [https://doi.org/10.1007/](https://doi.org/10.1007/s00382-00015-02507-00383)  
 625 [s00382-00015-02507-00383](https://doi.org/10.1007/s00382-00015-02507-00383)
- 626 Alessandri A, Felice MD, Zeng N, et al (2014) Robust assessment of  
 627 the expansion and retreat of Mediterranean climate in the 21st centu-  
 628 ry. *Sci Rep* 4:7211. <https://doi.org/10.1038/srep07211>
- 629 Anderson OF, Guinotte JG, Rowden AA, et al (2016) Habitat suit-  
 630 ability models for predicting the occurrence of vulnerable marine  
 631 ecosystems in the seas around New Zealand. *Deep-Sea Res Part 1*  
 632 *Oceanogr Res Pap* 115:265–292
- 633 Antonov JI, Levitus S, Boyer TP (2002) Steric Sea level variations dur-  
 634 ing 1957–1994: importance of salinity. *J Geophys Res* 107:8013.  
 635 <https://doi.org/10.1029/2001JC000964>
- 636 Arrhenius S (1896) On the influence of carbonic acid in the air upon the  
 637 temperature of the ground. *Philos Mag Ser* 41:237–276
- 638 Arrhenius S (1908) *Worlds in the making. The evolution of the Universe*,  
 639 vol. Harper & Brothers Publishers, New York, London, 264 p
- 640 Bashitialshaaer RAI, Persson KM, Aljaradin M (2011) Estimated future  
 641 salinity in the Arabian Gulf, the Mediterranean Sea and the Red Sea.  
 642 Consequences of brine discharge from desalination. *Int J Acad Res*  
 643 *3*:133–140
- 644 Bell N, Smith J (1999) Coral growing on North Sea oil rigs. *Nature*  
 645 402:601
- 646 Bethoux JP, Gentili B (1996) The Mediterranean Sea, coastal and deep-  
 647 sea signatures of climatic and environmental changes. *J Mar Syst*  
 648 *7*:383–394
- 649 Bethoux JP, Gentili B, Raunet J, et al (1990) Warming trend in the west-  
 650 ern Mediterranean deep water. *Nature* 347:660–662
- 651 Béthoux J-P, Gentili B, Tailliez D (1998) Warming and freshwater bud-  
 652 get changes in the Mediterranean since the 1940s: their possible  
 653 relation to the greenhouse effect. *Geophys Res Lett* 25:1023
- 654 Bostock HC, Mikaloff-Fletcher SE, Williams MJM (2013) Estimating  
 655 carbonate parameters from hydrographic data for the intermediate  
 656 and deep waters of the Southern Hemisphere oceans. *Biogeosciences*  
 657 *10*:6199–6213
- 658 Bostock HC, Tracey DM, Currie KI, et al (2015) The carbonate mineralogy  
 659 and distribution of habitat-forming deep-sea corals in the Southwest  
 660 Pacific region. *Deep-Sea Res Part 1 Oceanogr Res Pap* 100:88–104
- 661 Bova SC, Herbert TD, Fox-Kemper B (2016) Rapid variations in deep  
 662 ocean temperature detected in the Holocene. *Geophys Res Lett*  
 663 *43*:12190–12198. <https://doi.org/10.1002/2016GL071450>
- 664 Brooke S, Ross SW, Bane JM, et al (2013) Temperature tolerance of  
 665 the deep-sea coral *Lophelia pertusa* from the southeastern United  
 666 States. *Deep-Sea Res Part 2 Top Stud Oceanogr* 92:240–248
- 667 Buhl-Mortensen L, Vanreusel A, Gooday AJ, et al (2010) Biological  
 668 structures as a source of habitat heterogeneity and biodiversity  
 669 on the open ocean margins. *Mar Ecol* 31:21–50. [https://doi.](https://doi.org/10.1111/j.1439-0485.2010.00359.x)  
 670 [org/10.1111/j.1439-0485.2010.00359.x](https://doi.org/10.1111/j.1439-0485.2010.00359.x)
- 671 Burdett HL, Carruthers M, Donohue P, et al (2014) Effects of high  
 672 temperature and CO<sub>2</sub> on intracellular DMSP in the cold-water coral  
 673 *Lophelia pertusa*. *Mar Biol* 161:1499–1506
- 674 Büscher JV, Form AU, Riebesell U (2017) Interactive effects of ocean  
 675 acidification and warming on growth, fitness and survival of the  
 cold-water coral *Lophelia pertusa* under different food availabili-  
 ties. *Front Mar Sci* 4. <https://doi.org/10.3389/fmars.2017.00101>
- Caldeira K, Wickett ME (2003) Anthropogenic carbon and ocean  
 pH. *Nature* 425:365–365. <https://doi.org/10.1038/425365a>
- Carreiro-Silva M, Cerqueira T, Godinho A, et al (2014) Molecular  
 mechanisms underlying the physiological responses of the  
 cold-water coral *Desmophyllum dianthus* to ocean acidifi-  
 cation. *Coral Reefs* 33:465–476. [https://doi.org/10.1007/](https://doi.org/10.1007/s00338-00014-01129-00332)  
 s00338-00014-01129-00332
- Chen X, Tung K-K (2014) Varying planetary heat sink led to global-  
 warming slowdown and acceleration. *Science* 345:897–903. [https://](https://doi.org/10.1126/science.1254937)  
 doi.org/10.1126/science.1254937
- Cheng L, Zheng F, Zhu K (2015) Distinctive Ocean interior changes  
 during the recent warming slowdown. *Sci Rep* 5:14346. [https://doi.](https://doi.org/10.11038/srep14346)  
 org/10.11038/srep14346
- Church JA, White NJ, Konikow LF, et al (2011) Revisiting the Earth's  
 sea-level and energy budgets from 1961 to 2008n.d.. *Geophys Res*  
 Lett 38:L18601. <https://doi.org/10.11029/12011GL048794>
- Cicerone R, Orr J, Brewer P, et al (2004) The ocean in a high-CO<sub>2</sub>  
 world. *Oceanography* 17:72–78
- CIESM (2008) Impacts of ocean acidification on biological, chemi-  
 cal and physical systems in the Mediterranean and black seas. In:  
 Briand F (ed) CIESM workshop monographs, Monaco, p 124
- Clark MR, Althaus F, Schlacher TA, et al (2015) The impacts of deep-  
 sea fisheries on benthic communities: a review. *ICES J Mar Sci*  
 73:i59–i69. <https://doi.org/10.1093/icesjms/fsv1123>
- Clippele LHD, Gafeira J, Robert K, et al (2016) Using novel acoustic  
 and visual mapping tools to predict the small-scale spatial distribu-  
 tion of live biogenic reef framework in cold-water coral habitats.  
*Coral Reefs* 36:255–268
- D'Ortenzio F, Antoine D, Marullo S (2008) Satellite-driven model-  
 ing of the upper ocean mixed layer and air-sea CO<sub>2</sub> flux in the  
 Mediterranean Sea. *Deep-Sea Res Part 1 Oceanogr Res Pap*  
 55:405–434
- Davies AJ, Guinotte JM (2011) Global habitat suitability for  
 framework-forming cold-water corals. *PLoS One* 6:e18483. [https://](https://doi.org/10.11371/journal.pone.0018483)  
 doi.org/10.11371/journal.pone.0018483
- Davies AJ, Wisshak M, Orr JC, et al (2008) Predicting suitable habitat  
 for the cold-water coral *Lophelia pertusa* (Scleractinia). *Deep-Sea*  
*Res Part 1 Oceanogr Res Pap* 55:1048–1062
- De Mol L, van Rooij D, Pirlet H, et al (2011) Cold-water coral habitats  
 in the Penmarch and Guilvinec Canyons (Bay of Biscay): Deep-  
 water versus shallow-water settings. *Mar Geol* 282:40–52
- Desbruyères DG, Purkey SG, McDonagh EL, et al (2016) Deep and  
 abyssal ocean warming from 35 years of repeat hydrography.  
*Geophys Res Lett* 43. <https://doi.org/10.1002/2016GL070413>
- Dodds LA, Roberts JM, Taylor AC, et al (2007) Metabolic tolerance of  
 the cold-water coral *Lophelia pertusa* (Scleractinia) to temperature  
 and dissolved oxygen change. *J Exp Mar Biol Ecol* 349:205–214
- Duineveld GCA, Lavaley MSS, Bergman MJN, et al (2007) Trophic  
 structure of a cold-water coral mound community (Rockall Bank,  
 NE Atlantic) in relation to the near-bottom particle supply and cur-  
 rent regime. *Bull Mar Sci* 81:449–457
- England MH, McGregor S, Spence P, et al (2014) Recent intensification  
 of wind-driven circulation in the Pacific and the ongoing warming  
 hiatus. *Nat Clim Chang* 4:222–227
- Feely RA, Sabine CL, Lee K, et al (2004) Impact of anthropogenic CO<sub>2</sub>  
 on the CaCO<sub>3</sub> system in the oceans. *Science* 305:362–366
- Feely RA, Sabine CL, Byrne RH, et al (2012) Decadal changes in the  
 aragonite and calcite saturation state of the Pacific Ocean. *Glob*  
*Biogeochem Cycles* 26:GB3001
- Ferrier-Pagès C, Gattuso J-P, Jaubert J (1999) Effect of small varia-  
 tions in salinity on the rates of photosynthesis and respiration of  
 the zooxanthellate coral *Stylophora pistillata*. *Mar Ecol Progr Ser*  
 181:309–314

- 741 Fillinger L, Richter C (2013) Vertical and horizontal distribution of  
742 *Desmophyllum dianthus* in Comau Fjord, Chile: a cold-water coral  
743 thriving at low pH. PeerJ 1:e194. <https://doi.org/10.7717/peerj.7194>
- 744 Form AU, Riebesell U (2012) Acclimation to ocean acidifica-  
745 tion during long-term CO<sub>2</sub> exposure in the cold-water coral  
746 *Lophelia pertusa*. Glob Change Biol 18:843–853. <https://doi.org/10.1111/j.1365-2486.2011.02583.x>
- 747 Fosså JH, Mortensen PB, Furevik DM (2002) The deep-water coral  
748 *Lophelia pertusa* in Norwegian waters: distribution and fishery  
749 impacts. Hydrobiologia 471:1–12
- 750 Freiwald A, Beuck L, Rüggeberg A, et al (2009) The white coral com-  
751 munity in the Central Mediterranean Sea revealed by ROV surveys.  
752 Oceanography 22:36–52
- 753 Fyfe JC, Meehl GA, England MH, et al (2016) Making sense of the  
754 early-2000s warming slowdown. Nat Clim Chang 6:224–228.  
755 <https://doi.org/10.1038/nclimate2938>
- 756 Gammon MJ, Tracey DM, Marriott PM, et al (2018) The physiologi-  
757 cal response of the deep-sea coral *Solenosmilia variabilis* to ocean  
758 acidification, e5236. PeerJ 6. <https://doi.org/10.7717/peerj.5236>
- 759 Gass SE, Willison JHM (2005) An assessment of the distribution of  
760 deep-sea corals in Atlantic Canada by using both scientific and local  
761 forms of knowledge. In: Freiwald A, Roberts JM (eds). Cold-water  
762 corals and ecosystems. Springer, Berlin, Heidelberg, pp 223–245
- 763 Gattuso J-P, Magnan A, Billé R, et al (2015) Contrasting futures for  
764 ocean and society from different anthropogenic CO<sub>2</sub> emissions  
765 scenarios. Science 349:aac4722. <https://doi.org/10.1126/science.aac4722>
- 766 Georgian SE, DeLeo D, Durkin A, et al (2016a) Oceanographic pat-  
767 terns and carbonate chemistry in the vicinity of cold-water coral  
768 reefs in the Gulf of Mexico: implications for resilience in a chang-  
769 ing ocean. Limnol Oceanogr 61:648–665
- 770 Georgian SE, Dupont S, Kurman M, et al (2016b) Biogeographic  
771 variability in the physiological response of the cold-water coral  
772 *Lophelia pertusato* ocean acidification. Mar Ecol 37:1345–1359
- 773 Giorgi F (2006) Climate change hot-spots. Geophys Res Lett  
774 33:L08707. <https://doi.org/10.01029/02006GL025734>
- 775 Giorgi F, Lionello P (2008) Climate change projections for the  
776 Mediterranean region. Glob Planet Chang 63:90–104
- 777 Giorgi F, Whetton PH, Jones RG, et al (2001) Emerging patterns of  
778 simulated regional climatic changes for the 21st century due to  
779 anthropogenic forcings. Geophys Res Lett 28:3317–3320
- 780 Gori A, Orejas C, Madurell T, Bramanti L, et al (2013) Bathymetrical  
781 distribution and size structure of cold-water coral populations in  
782 the Cap de Creus and Lacaze-Duthiers canyons (northwestern  
783 Mediterranean). Bigeosciences 10:2049–2060
- 784 Gori A, Ferrier-Pagès C, Hennige SJ, et al (2016) Physiological  
785 response of the cold-water coral *Desmophyllum dianthus* to ther-  
786 mal stress and ocean acidification. PeerJ 4:e1606. <https://doi.org/10.7717/peerj.1606>
- 787 Goyet C, Hassoun AER, Gemayel E, et al (2016) Thermodynamic  
788 forecasts of the Mediterranean Sea acidification. Mediterr Mar Sci  
789 17:508–518
- 790 Guinotte JM, Orr J, Cairns S, et al (2006) Will human-induced changes  
791 in seawater chemistry alter the distribution of deep-sea scleractinian  
792 corals? Front Ecol Environ 4:141–146
- 793 Hansen J, Sato M (2016) Regional climate change and national respon-  
794 sibilities. Environ Res Lett 11:034009
- 795 Hansen J, Sato M, Kharecha P, et al (2011) Earth's energy imbalance  
796 and implications. Atmos Chem Phys 11:13421–13449
- 797 Hassoun AER, Gemayel E, Krasakopoulou E, et al (2015) Acidification  
798 of the Mediterranean Sea from anthropogenic carbon penetration.  
799 Deep-Sea Res Part 2 Top Stud Oceanogr 102:1–15
- 800 Hausfather Z, Cowtan K, Clarke DC, et al (2017) Assessing recent  
801 warming using instrumentally homogeneous sea surface tempera-  
802 ture records. Sci Adv 3:e1601201
- 803 Hennige SJ, Wicks LC, Kamenos NA, et al (2014) Short-term meta-  
804 bolic and growth responses of the cold-water coral *Lophelia per-  
805 tusa* to ocean acidification. Deep-Sea Res Part 2 Top Stud Oceanogr  
806 99:27–35. <https://doi.org/10.1016/j.dsr.2013.1007.1005>
- 807 Hennige SJ, Wicks LC, Kamenos NA, et al (2015) Hidden impacts of  
808 ocean acidification to live and dead coral framework. Proc R Soc B  
809 282:20150990
- 810 Hourigan TF (2009) Managing fishery impacts on deep-water coral  
811 ecosystems of the USA: emerging best practices. Mar Ecol Progr  
812 Ser 397:333–340
- 813 Hovland M, Vasshus S, Indreeide A, et al (2002) Mapping and imag-  
814 ing deep-sea coral reefs off Norway, 1982–2000. Hydrobiologia  
815 471:13–17
- 816 IPCC (2013) Climate change 2013: the physical science basis.  
817 Contribution of Working Group I to the Fifth Assessment Report  
818 of the Intergovernmental Panel on Climate Change. In: Stocker  
819 TF, Qin D, Plattner G-K, et al (eds) Cambridge University Press,  
820 Cambridge
- 821 Jantzen C, Häussermann V, Försterra G, et al (2013) Occurrence  
822 of a cold-water coral along natural pH gradients (Patagonia,  
823 Chile). Mar Biol 160:2597–2607. <https://doi.org/10.1007/s00227-00013-02254-00220>
- 824 Karl TR, Arguez A, Huang B, et al (2015) Possible artifacts of data  
825 biases in the recent global surface warming hiatus. Science  
826 348:1469–1472
- 827 Kiriakoulakis K, Fisher E, Wolff GA, et al (2005) Lipids and nitro-  
828 gen isotopes of two deep-water corals from the North-East Atlantic:  
829 initial results and implications for their nutrition. In: Freiwald A,  
830 Roberts JM (eds) Cold-water corals and ecosystems. Springer,  
831 Berlin, Heidelberg, pp 715–729
- 832 Kleypas JA, Feely RA, Fabry VJ, et al (2006) Impacts of ocean acidi-  
833 fication on coral reefs and other marine calcifiers: a guide to future  
834 research. Report of a workshop sponsored by the National Science  
835 Foundation, the National Oceanographic and atmospheric admin-  
836 istration, And the US geological survey 96 p. Available at: [www.isseucaredu/Florida/](http://www.isseucaredu/Florida/)
- 837 Kosaka Y, Xie S-P (2013) Recent global-warming hiatus tied to equa-  
838 torial Pacific surface cooling. Nature 501:403–407. <https://doi.org/10.1038/nature12534>
- 839 Kurman MD, Gómez CE, Georgian SE, et al (2017) Intra-specific  
840 variation reveals potential for qdaptation to ocean acidification in  
841 a cold-water coral from the Gulf of Mexico. Front Mar Sci 4:111.  
842 <https://doi.org/10.3389/fmars.2017.00111>
- 843 Landschützer P, Gruber N, Bakker DCE (2016) Decadal variations and  
844 trends of the global ocean carbon sink. Global Biogeochem Cycles  
845 30:1396. <https://doi.org/10.1002/2015GB005359>
- 846 Law CS, Rickard GJ, Mikaloff-Fletcher SE, et al (2016) The New  
847 Zealand EEZ and south West Pacific. Synthesis report RA2, marine  
848 case study. Climate Changes, Impacts and Implications (CCII) for  
849 New Zealand to 2100. MBIE contract C01X1225, 41pp
- 850 Levermann A, Clark PU, Marzeion B, et al (2013) The multimillen-  
851 nial sea-level commitment of global warming. Proc Natl Acad Sci  
852 110:13745–13750
- 853 Levitus S, Antonov JI, Boyer RP, et al (2012) World ocean heat content  
854 and thermosteric sea level change (0–2000 m), 1955–2010, 1955–  
855 2010. Geophys Res Lett 39:L10603 <https://doi.org/10.11029/12012GL051106>
- 856 Lewandowsky S, Cook J, Lloyd E (2016) The ‘Alice in Wonderland’  
857 mechanics of the rejection of (climate) science: simulating  
858 coherence by consiracism. Synthese 195:175–196. <https://doi.org/10.1007/s11229-11016-11198-11226>
- 859 Lovel W, Willis K, Landerer FW, et al (2014) Deep-ocean contribu-  
860 tion to sea level and energy budget not detectable over the past  
861 decade. Nat Clim Chang 4:1031–1035. <https://doi.org/10.1038/nclimate2387>

- 871 Lunden JJ, Nicholl CGM, Sears CR, et al (2014) Acute survivorship of  
872 the deep-sea coral *Lophelia pertusa* from the Gulf of Mexico under  
873 acidification, warming, and deoxygenation. *Fron Mar Sci* 1:78.  
874 <https://doi.org/10.3389/fmars.2014.00078>
- 875 Maier C, Hegeman J, Weinbauer MG, et al (2009) Calcification of  
876 the cold-water coral *Lophelia pertusa* under ambient and reduced  
877 pH. *Biogeosciences* 6:1671–1680
- 878 Maier C, Watremez P, Taviani M, et al (2012) Calcification rates and  
879 the effect of ocean acidification on Mediterranean cold-water corals.  
880 *Proc R Soc Lond* 279:1713–1723. [https://doi.org/10.1098/](https://doi.org/10.1098/rspb.2011.1763)  
881 [rspb.2011.1763](https://doi.org/10.1098/rspb.2011.1763)
- 882 Maier C, Bills F, Weinbauer M, Watremez P, et al (2013a) Respiration  
883 of Mediterranean cold-water corals is not affected by ocean acidifi-  
884 cation as projected for the end of the century. *Biogeosciences*  
885 10:5671–5680. <https://doi.org/10.5194/bg-5610-5671-2013>
- 886 Maier C, Schubert A, Berzunza Sánchez MM, et al (2013b) End of the  
887 century pCO<sub>2</sub> levels do not impact calcification in Mediterranean  
888 cold-water corals. *PLoS One* 8:e2655. [https://doi.org/10.1371/jour-](https://doi.org/10.1371/journal.pone.0062655)  
889 [nal.pone.0062655](https://doi.org/10.1371/journal.pone.0062655)
- 890 Maier C, Popp P, Sollfrank N, et al (2016) Effects of elevated pCO<sub>2</sub> and  
891 feeding on net calcification and energy budget of the Mediterranean  
892 cold-water coral *Madrepora oculata*. *J Exp Biol* 219:3208
- 893 Malanotte-Rizzoli P, Font J, García-Ladona E, et al (2014) Physical  
894 forcing and physical/biochemical variability of the Mediterranean  
895 Sea: a review of unresolved issues and directions for future research.  
896 *Ocean Sci* 10:281–322
- 897 Mariotti A, Zeng N, Yoon J-H, et al (2008) Mediterranean water  
898 cycle changes: transition to drier 21st century conditions in obser-  
899 vations and CMIP3 simulations. *Environ Res Lett* 3:044001  
900 10.041088/041748-049326/044003/044004/044001
- 901 Mastrototaro F, D'Onghia G, Corriero G, et al (2010) Biodiversity of  
902 the white coral bank off Cape Santa Maria di Leuca (Mediterranean  
903 Sea): an update. *Deep-Sea Res Part 2 Top Stud Oceanogr* 57:412–430
- 904 McCulloch M, Trotter J, Montagna P, et al (2012) Resilience of  
905 cold-water scleractinian corals to ocean acidification: boron  
906 isotopic systematics of pH and saturation state up-regulation.  
907 *Geochim Cosmochim Acta* 87:21–34. [https://doi.org/10.1016/j.](https://doi.org/10.1016/j.gca.2012.1003.1027)  
908 [gca.2012.1003.1027](https://doi.org/10.1016/j.gca.2012.1003.1027)
- 909 McGregor S, Timmermann A, Stuecker MF, et al (2014) Recent Walker  
910 circulation strengthening and Pacific cooling amplified by Atlantic  
911 warming. *Nat Clim Chang* 4:888–892. [https://doi.org/10.1038/](https://doi.org/10.1038/nclimate2330)  
912 [nclimate2330](https://doi.org/10.1038/nclimate2330)
- 913 Meehl GA, Arblaster JM, Fasullo JT, et al (2011) Model-based evi-  
914 dence of deep-ocean heat uptake during surface-temperature hia-  
915 tus periods. *Nat Clim Chang* 1:360–364. [https://doi.org/10.1038/](https://doi.org/10.1038/nclimate1229)  
916 [nclimate1229](https://doi.org/10.1038/nclimate1229)
- 917 Mikaloff-Fletcher SE, Gruber N, Jacobson AR, et al (2006) Inverse  
918 estimates of anthropogenic CO<sub>2</sub> uptake, transport, and stor-  
919 age by the ocean. *Global Biogeochem Cycles* 20. [https://doi.](https://doi.org/10.1029/2005GB002530)  
920 [org/10.1029/2005GB002530](https://doi.org/10.1029/2005GB002530)
- 921 Millero FJ, Morse J, Chen CT (1979) The carbonate system in the  
922 western Mediterranean Sea. *Deep-Sea Res Part 1 Oceanogr Res Pap*  
923 26A:1395–1404
- 924 Mortensen PB (2001) Aquarium observations on the deep-water coral  
925 *Lophelia pertusa* (L., 1758) (Scleractinia) and selected associated  
926 invertebrates. *Ophelia* 54:83–104
- 927 Movilla J, Gori A, Calvo E, et al (2014a) Resistance of two Mediterranean  
928 cold-water coral species to low-pH conditions. *Water* 5:59–67
- 929 Movilla J, Orejas C, Calvo E, et al (2014b) Differential response of two  
930 Mediterranean cold-water coral species to ocean acidification. *Coral*  
931 *Reefs* 33:675–686
- 932 Naumann MS, Orejas C, Ferrier-Pagès C (2013a) High thermal tol-  
933 erance of two Mediterranean cold-water coral species main-  
934 tained in aquaria. *Coral Reefs* 32:749. [https://doi.org/10.1007/](https://doi.org/10.1007/s00338-00013-01011-00337)  
935 [s00338-00013-01011-00337](https://doi.org/10.1007/s00338-00013-01011-00337)
- Naumann MS, Orejas C, Ferrier-Pagès C (2013b) Species-specific  
physiological response by the cold-water corals *Lophelia pertusa*  
and *Madrepora oculata* to variations within their natural tempera-  
ture range. *Deep-Sea Res Part 2 Top Stud Oceanogr* 99:36–41
- Nykjaer L (2009) Mediterranean Sea surface warming 1985–2006.  
*Clim Res* 39:11–17
- Orejas C, Gori A, Lo Iacono C, et al (2009) Cold-water corals in the Cap  
de Creus canyon, northwestern Mediterranean: spatial distribution,  
density and anthropogenic impact. *Mar Ecol Progr Ser* 397:37–51
- Orr JC, Maier-Reimer E, Mikolajewicz U, et al (2001) Estimates of  
anthropogenic carbon uptake from four three-dimensional global  
ocean models. *Global Biogeochem Cycles* 15:43–60
- Orr JC, Fabry VJ, Aumont O, et al (2005a) Anthropogenic Ocean acidi-  
fication over the twenty-first century and its impact on calcifying  
organisms. *Nature* 437:681–686
- Orr JC, Pantoja S, Pörtner HO (2005b) Introduction to special section:  
the ocean in a high-CO<sub>2</sub> world. *J Geophys Res* 110:C09S01. [https://](https://doi.org/10.1029/2005JC003086)  
952 [doi.org/10.1029/2005JC003086](https://doi.org/10.1029/2005JC003086)
- Pierce DS, Gleckler PJ, Barnett TP, et al (2012) The fingerprint of  
human-induced changes in the ocean's salinity and temperature  
fields. *Geophys Res Lett* 39:L21704. [https://doi.org/10.21029/220](https://doi.org/10.21029/22012GL053389)  
956 [12GL053389](https://doi.org/10.21029/22012GL053389)
- Purkey SG, Johnson GC (2010) Warming of global abyssal and deep  
Southern Ocean waters between the 1990s and 2000s: contributions  
to global heat and sea level rise budgets. *J Clim* 23:6336–6351.  
<https://doi.org/10.1175/2010JCLI3682.6331>
- Revelle R, Suess HE (1957) Carbon dioxide exchange between  
atmosphere and ocean and the question of an increase of atmo-  
spheric CO<sub>2</sub> during the past decades. *Tellus* 9:18–27. [https://doi.](https://doi.org/10.3402/tellusa.v9i1.9075)  
962 [org/10.3402/tellusa.v9i1.9075](https://doi.org/10.3402/tellusa.v9i1.9075)
- Rhein M, Rintoul SR, Aoki S, et al (2013) Observations: ocean. In:  
Stocker TF, Qin D, Plattner G-K, et al (eds) *Climate change 2013:*  
the physical science basis contribution of working group I to the  
fifth assessment report of the Intergovernmental Panel on Climate  
Change. Cambridge University Press, Cambridge, New York
- Riebesell U, Gattuso JP (2015) Lessons learned from ocean acidifica-  
tion research. *Nat Clim Chang* 5:12–14
- Rixen M, Beckers JM, Levitus S, et al (2005) The western Mediterranean  
deep water: a proxy for climate change. *Geophys Res Lett* 32:L12608
- Roberts JM, Davies AJ, Henry LA, et al (2009) Mingulay reef complex:  
an interdisciplinary study of cold-water coral habitat, hydrography  
and biodiversity. *Mar Ecol Progr Ser* 397:139–151
- Roberts JM, Murray F, Anagnostou E, et al (2016) Cold-water corals  
in an era of rapid global change: are these the deep ocean's most  
vulnerable ecosystems? In: Goffredo S, Dubinsky Z (eds) *The*  
*Cnidaria, past, present and future*. Springer, Cham, pp 593–606
- Rodolfo-Metalpa R, Montagna P, Aliani S, et al (2015) Calcification is  
not the Achilles' heel of cold-water corals in an acidifying ocean.  
*Glob Chang Biol* 21:2238–2248
- Rogers AD (1999) The biology of *Lophelia pertusa* (Linnaeus 1758)  
and other deep-water reef-forming corals and impacts from human  
activities. *Int Rev Hydrobiol* 84:315–406
- Rowden AA, Guinotte JM, Baird SJ, et al (2013) Developing predictive  
models for the distribution of vulnerable marine ecosystems in the  
South Pacific region. *New Zealand aquatic environment and biodi-*  
990 *versity report* 120:70p
- Sabine CL, Feely RA, Gruber N, et al (2004) The oceanic sink for  
anthropogenic CO<sub>2</sub>. *Science* 305:367–371
- Savini A, Vertino A, Marchese F, et al (2014) Mapping cold-water coral  
habitats at different scales within the Northern Ionian Sea (Central  
Mediterranean): an assessment of coral coverage and associated  
vulnerability. *PLoS One* 9:e87108
- Smith AM, Williams MJM (2015) The carbonate mineralogy and dis-  
tribution of habitat-forming deep-sea corals in the southwest pacific  
region. *Deep-Sea Res Part 1 Oceanogr Res Pap* 100:88–104

- 1001 Song J, Wang Y, Tang J (2016) A hiatus of the greenhouse effect. *Sci Rep* 6:33315 1041
- 1002
- 1003 Sumida PYG, Yoshinaga MY, Madureira LASP, et al (2004) Seabed 1042
- 1004 pockmarks associated with Deepwater corals off SE Brazilian con- 1043
- 1005 tinental slope, Santos Basin. *Mar Geol* 207:159–167 1044
- 1006 Taviani M, Freiwald A, Zibrowius H (2005) Deep coral growth in the 1045
- 1007 Mediterranean Sea: an overview. In: Freiwald A, Roberts JM (eds) 1046
- 1008 Cold-water corals and ecosystems. Springer, Berlin, Heidelberg, 1047
- 1009 pp 137–156 1048
- 1010 Thresher RE, Tilbrook B, Fallon S, et al (2011) Effects of chronic low 1049
- 1011 carbonate saturation levels on the distribution, growth and skeletal 1050
- 1012 chemistry of deep-sea corals and other seamount megabenthos. *Mar 1051*
- 1013 *Ecol Progr Ser* 442:87–99 1052
- 1014 Tittensor DP, Baco AR, Hall-Spencer JM, et al (2010) Seamounts as 1053
- 1015 refugia from ocean acidification for cold-water stony corals. *Mar 1054*
- 1016 *Ecol* 31:212–225 1055
- 1017 Touratier F, Goyet C (2009) Decadal evolution of anthropogenic 1056
- 1018 CO<sub>2</sub> in the northwestern Mediterranean Sea from the mid- 1057
- 1019 1990s to the mid-2000s. *Deep-Sea Res Part 1 Oceanogr Res Pap* 1058
- 1020 56:1708–1716
- 1021 Touratier F, Goyet C (2011) Impact of the Eastern Mediterranean 1059
- 1022 Transient on the distribution of anthropogenic CO<sub>2</sub> and first esti- 1060
- 1023 mate of acidification for the Mediterranean Sea. *Deep-Sea Res Part 1061*
- 1024 *1 Oceanogr Res Pap* 58:1–15 1062
- 1025 Tracey DM, Rowden AA, Mackay KA, et al (2011) Habitat-forming 1063
- 1026 cold-water corals show affinity for seamounts in the New Zealand 1064
- 1027 region. *Mar Ecol Progr Ser* 430:1–22 1065
- 1028 Turley CM (1999) The changing Mediterranean Sea – a sensitive eco- 1066
- 1029 system? *Progr Oceanogr* 44:387–400 1067
- 1030 Turley CM, Roberts JM, Guinotte JM (2007) Corals in deep-water: will 1068
- 1031 the unseen hand of ocean acidification destroy cold-water ecosys- 1069
- 1032 tems? *Coral Reefs* 26:445–448 1070
- 1033 Vargas-Yáñez M, Moya F, Tel E, et al (2009) Warming and salting in the 1071
- 1034 western Mediterranean during the second half of the 20th century: 1072
- 1035 inconsistencies, unknown and the effect of data processing. *Sci Mar* 1073
- 1036 73:7–28 1074
- 1037 Wall M, Ragozzola F, Foster LC, et al (2015) pH up-regulation as 1075
- 1038 a potential mechanism for the cold-water coral *Lophelia per-*
- 1039 *tusa* to sustain growth in aragonite undersaturated conditions. 1076
- 1040 *Biogeosciences* 12:6869–6880 1077
- Waller RG, Tyler PA (2005) The reproductive biology of two deep- 1041
- water, reef-building scleractinians from the NE Atlantic Ocean. 1042
- Coral Reefs* 24:514–522 1043
- Waller RG, Tyler PA, Gage JD (2005) Sexual reproduction in three her- 1044
- maphroditic deep-sea Caryophyllia species (Anthozoa: Scleractinia) 1045
- from the NE Atlantic Ocean. *Coral Reefs* 24:594–602 1046
- Wheeler AJ, Beyer A, Freiwald A, et al (2007) Morphology and envi- 1047
- ronment of cold-water coral carbonate mounds on the NW European 1048
- margin. *Int J Earth Sci* 96:37–56 1049
- Yan X-H, Boyer T, Trenberth K, et al (2016) The global warming hia- 1050
- tus: slowdown or redistribution. *Earth's Future* 4:472–482. <https://doi.org/10.1002/2016EF000417> 1051
- Zeebe RE, Ridgwell A, Zachos JC (2016) Anthropogenic carbon 1052
- release rate unprecedented during the past 66 million years. *Nat Geosci* 9:325–329 1053
- Zibrowius H, Gili J-M (1990) Deep-water Scleractinia (Cnidaria: 1054
- Anthozoa) from Namibia, South Africa, and Walvis ridge, south- 1055
- eastern Atlantic. *Sci Mar* 54:19–46 1056

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## Cross References

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