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

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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

44.1.1 Global Climate Change

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_2 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 equable 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_2 concentration being higher than at any time during the last 2.6 million years (Lewandowsky et al. 2016). Since pre-industrial times, atmospheric CO_2 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 a anthropogenic CO_2 release rate being 14,000 times faster than the natural net release of CO_2 (Zeebe et al. 2016).

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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_2 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_2 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_2 has been absorbed by the oceans. The rising partial pressure of CO_2 (pCO_2) has major consequences as CO_2 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 (Ω) 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 Ω 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_2 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_2 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 (Ω_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 conveyer 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 saltening 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 μmol kg^{-1} with a high buffering capacity absorbing more CO_2 than the open ocean (CIESM 2008). It is a small to medium sink for CO_2 absorbing ca. 0.24 Gt C year^{-1} (D'Ortenzio et al. 2008) while the reduction of ocean pH is relatively fast with −0.14 to −0.05 pH units year^{-1} (Touratier and Goyet 2009, 2011). Despite this, the Ω 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 Ω_a (Hassoun et al. 2015; Goyet et al. 2016). Present day Ω_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_2 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 (±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_2 used in most of the OA experimental studies ranged between ambient (ca. 400 µatm) and 800–1000 µatm, corresponding to current and future conditions in 2100 using a business-as-usual CO_2 emission scenario. The exception was for two short-term experiments where pCO_2 levels in which pCO_2 values outside this range were used: 280 µatm to represent pre-industrial times (Maier et al. 2012) and 1725 µatm (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_2 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_2 (Form and Riebesell 2012). These two studies show that *L. pertusa* is able to maintain positive calcification rates despite being exposed to undersaturated Ω_a (Maier et al. 2009; Form and Riebesell 2012). Subsequent studies have demonstrated that calcification remains constant for pCO_2 levels corresponding to those between present-day (~400 µatm) and those projected until the end of the century (~800–1000 µatm) (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 Ω_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_2 (800 µatm), 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_2 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_2. For *D. dianthus* it has been shown that genes involved in stress response, metabolism or calcification were upregulated under elevated pCO_2 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_2 and only decrease after a certain threshold has been reached, faster skeletal linear extension under high pCO_2 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*	Dodds et al. (2007)	N-A	+	−	−	−	−	+	−	−	−	−	−	−	+	−	−	−	−	−	+	−	+	−	−	−	+	−	4–6	n	*5*
t1.5	*2*	Maier et al. (2009)	Skag	−	+	−	−	−	+	−	−	−	−	−	+	−	−	−	−	−	+	−	+	−	−	−	+	−	2x8	n	*6*
t1.6	*3*	Form and Riebesell (2012)	N-A	−	+	−	−	−	+	−	−	−	−	−	+	−	−	−	−	−	+	−	+	−	−	−	+	−	4	n	*4*
t1.7																					−	+	+	−	−	−	−	−	5	n	*4*
t1.8	*4*	Maier et al. (2012)	MED	−	+	−	−	−	−	+	−	−	−	−	+	+	−	−	−	−	+	−	+	−	+	+	−	−	15	n	*7*
t1.9	*5*	Maier et al. (2013b)	MED	−	+	−	−	−	+	+	−	−	−	−	+	−	−	−	−	−	+	+	+	+	−	+	+	−	4	n	*7*
t1.10	*6*	Maier et al. (2013a)	MED	+	+	+	−		+	+	−	−	−	−	−	+	−	−	−	−	+	+	+	+	−	+	+	−	4	n	*7*
t1.11	*7*	Brooke et al. (2013)	GoM	+	−	−	−	−	+	−	−	−	−	−	−	−	−	−	−	+	+	−	+	+	−	−	+	−	5	n	*6*
t1.12 t1.13	*8*	Naumann et al. (2013b)	MED	+	−	−	−	−	+	+	−	−	−	−	+	+	−	−	DOC	−	−	+	+	+	−	−	+	−	5	1/n	*5*
t1.14 t1.15	*9*	Naumann et al. (2013a)	MED	+	−	−	−	−	−	−	+	+	−	−	+	−	−	−	−	−	−	+	+	−	−	−	+	−	5	1/n	*4*
t1.16 t1.17	*10*	Carreiro-Silva et al. (2014)	N-A	−	+	−	−	−	−	−	+	−	−	−	+	+	−	+	NUTS GE	−	−	+	+	+	−	−	+	−	6	2/n	*6*
t1.18	*11*	Hennige et al. (2014)	N-A	−	+	−	−	−	+	−	−	−	−	−	+	+	−	−	−	−	+	−	+	+	−	+	+	−	8	1/n	*6*
t1.19	*12*	Lunden et al. (2014)	GoM	+	+	−	−	−	+	−	−	−	−	−	+	−	−	−	−	+	+	−	+	−	+	−	+	−	2x8	2/n	*7*
t1.20	*13*	Movilla et al. (2014a)	MED	−	+	−	−	−	+	+	−	−	−	−	+	−	+	−	−	−	−	+	+	+	−	−	+	−	12–18	3/n	*7*
t1.21	*14*	Movilla et al. (2014b)	MED	−	+	−	−	−	−	−	+	+	−	−	+	−	+	−	OM	−	−	+	+	+	−	+	+	−	9	3/n	*7*
t1.22 t1.23	*15*	Rodolfo-Metalpa et al. (2015)	MED	−	+	−	−	−	−	−	+	+	+	−	+	+	−	−	−	−	−	+	+	−	−	+	+	−	7–23	2/n	*7*
t1.24	*16*	Hennige et al. (2015)	N-A	+	+	+	−	−	+	−	−	−	−	−	+	+	+	−	−	−	−	+	+	+	−	−	+	−	4–8	4/n	*6*
t1.25	*17*	Wall et al. (2015) (#3)	N-A	−	+	−	−	−	+	−	−	−	−	−	−	−	+	−	$d^{11}B$	−	−	+	+	−	−	−	+	−	1–4	n	*n/a*
t1.26	*18*	Gori et al., (2016)	MED	+	+	+	−	−	−	−	+	−	−	−	+	−	+	−	−	−	−	+	+	−	−	−	+	−	3	n	*4*
t1.27 t1.28	*19*	Maier et al. (2016)	MED	−	+	−	+	−	−	+	−	−	−	−	+	+	−	−	TOC; RQ; E	−	+	−	+	+	+	+	−	+	13	n	*9*
t1.29 t1.30	*20*	Georgian et al. (2016a, b)	GoM Skag	−	+	−	+	−	+	−	−	−	−	−	+	+	−	−	Food uptake	−	+	−	+	−	−	−	+	−	8	2/n	*5*
t1.31 t1.32	*21*	Büscher et al. (2017)	N-A	+	+	+	+	−	+	−	−	−	−	−	+	−	+	−	RNA/ DNA	+	−	+	+	−	−	−	+	−	4	n	*4*
t1.33	*22*	Kurman et al. (2017)	GoM	−	+	−	−	−	+	−	−	−	−	−	+	−	−	−	GT	−	+	−	+	−	−	−	+	−	12	1/n	*5*
t1.34															+	−	−	−	CAA	+	−	+	+	+	−	−	+	−	4	1/n	*4*
t1.35	*23*	Burdett et al. (2014)	N-A	−	+	−	−	−	+	−	−	−	−	−	−	−	−	−	DMSP	−	+	−	+	−	−	−	+	−	5	1/n	*4*
t1.36	*24*	Gammon et al. (2018)	SW-P	−	+	−	−	−	−	−	−	−	−	+	+	+	+	−	CS, pH_i	+	−	+	+	+	−	−	+	−	9	*3/n*	*6*
t1.37			MED = 10	8	19	4	2	0	17	6	5	3	1	1	16	9	5	2	8	4	10	11	19	9	3	8	16	1			*5.7*

t1.38 The variables used temperature change (ΔT), 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
t1.39 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*
t1.40 *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
t1.41 (GE), genotypes (GT), polyp mortality (†) and other measurements (OT), like inorganic nutrients (NUTS), dimethylsulfoniopropionate (DMSP), dissolved organic carbon (DOC), organic matter (OM), total
t1.42 organic carbon (TOC), respiratory quotient (RQ), energy requirements (E), boron isotopes (δ11B), carbonic anhydrase activity (CAA), RNA/DNA ratio (RNA/DNA) and loss of coenosarc (CS). Experiments
t1.43 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
t1.44 (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
t1.45 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
t1.46 for >10 replicates. If more than 1 tank per treatment for replicates (tanks/n) was used (>1/n) another point was allocated

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, Ω_a 0.93) and lower pH (7.65, Ω_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 neighbouring 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_2 (Figs. 44.1c and 44.3a; Hennige et al. 2014; Georgian et al. 2016b) no effect on respiration at increased pCO_2 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).

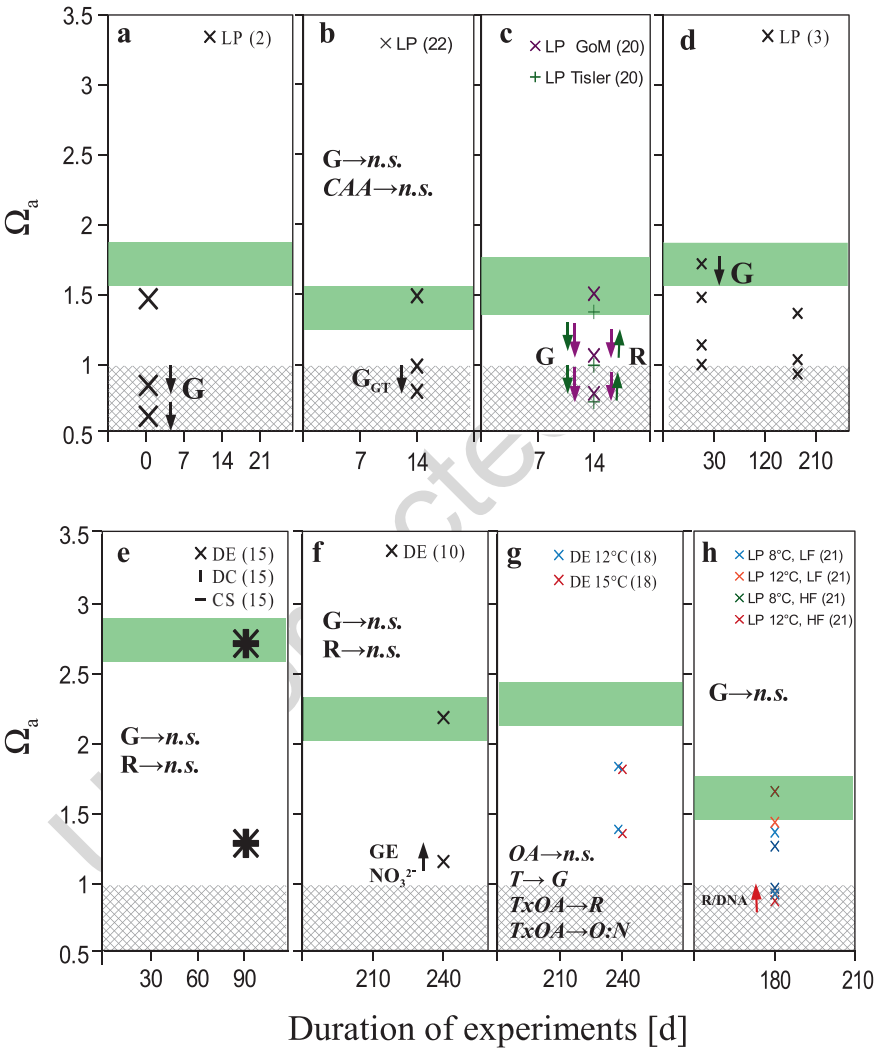

Fig. 44.1 Plot of studies using single-point experimental designs for measurements according to aragonite saturation state (Ω_a) in seawater (y-axis) and acclimation time in days (duration of experiments [d], x axes). The response of physiological functions are shown according to studies (**a–h**) and include calcification (G), calcification of different genotypes (G_{GT}), respiration (R), gene expression (GE), carbonic anhydrase activity (CAA) and nitrate excretion (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 Ω_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)

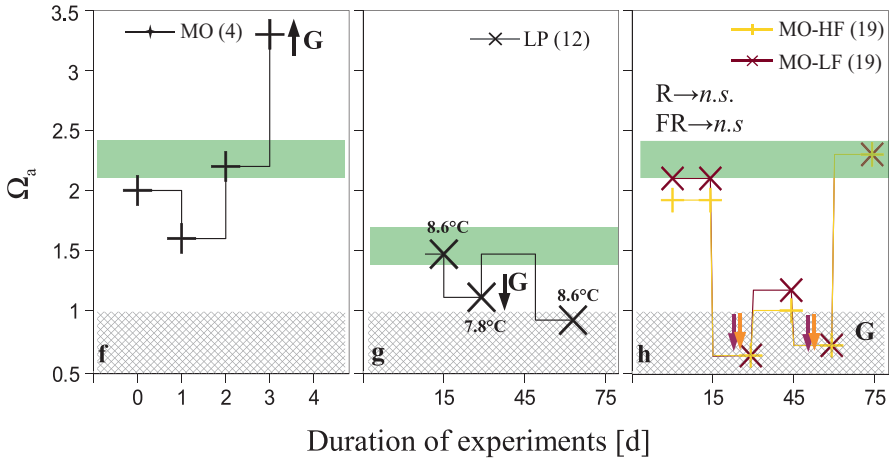

Fig. 44.2 Plot of studies using consecutive experimental designs for measurements according to aragonite saturation state (Ω_a) in seawater (y-axis) and acclimation time in days (duration of experiments [d]; x axes). The symbol lines record changes of Ω_a during experiments with symbols depicting when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

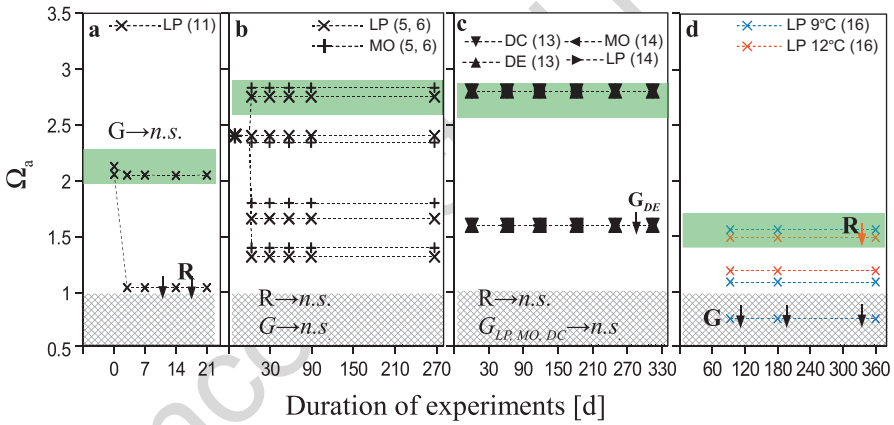

Fig. 44.3 Plot of studies using repeated measurement designs showing measurements points according to aragonite saturation state (Ω_a) in seawater (y-axis) and acclimation time in days (duration of experiments [d]; x-axis). The symbol lines record Ω_a for replicated measurements with symbols depicting 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 Ω_a. Numbers in brackets refer to the publications referenced in Table 44.1. According to the region the ambient Ω_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)

The apparent high resilience of CWCs to OA in both the experimental studies, described here for the Mediterranean and elsewhere, and also observed *in situ* (Thresher et al. 2011; Fillinger and Richter 2013; Jantzen et al. 2013; Bostock et al. 2015; Georgian et al. 2016a; Gammon et al. 2018) has been attributed to pH upregulation of the calicoblastic pH (McCulloch et al. 2012; Wall et al. 2015). The upregulation of calicoblastic pH has been thought to require a high amount of energy and may consequently require high food availability in areas with low Ω_a to maintain calcification constant (McCulloch et al. 2012; Fillinger and Richter 2013; Jantzen et al. 2013). However, a study establishing an energy budget for major physiological functions of Mediterranean *M. oculata* revealed that the energy required for calcification in general and for the upregulation of calicoblastic pH (or Ω_a) in particular only constitutes a minor frac-

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_2 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_2 (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_{10}) 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_2, 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_2 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 (Bashitialshaaer 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_2. There is robust evidence that with the projected Ω_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_2, 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 (Ω_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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