How marine organisms cope with changing climate

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Cover image: *Pseudaphritis urvillii*, and *Favonigobius lateralis* (left to right). Photo credit: Almendra Rodriguez Dominguez

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ABSTRACT

As anthropogenic CO_2 levels continue to rise, the oceans are becoming warmer and more acidic. Organisms need to adjust to such environmental changes and display a variety of mechanisms to maintain their fitness in novel conditions. These adjustments can operate at various levels of biological organisation: from cellular levels to organismal physiology and behaviour. Such adaptive responses of species will determine their persistence under future ocean warming and acidification conditions. If organisms are capable of maintaining fitness after long-term exposure to a stressor this can be indicative of acclimation potential. However, their sensitivity to stressors is linked to life stage. Early life phases are considered to be the most vulnerable to fluctuations in the environment. If detrimental effects occur during an organism's early life this could modify its capability to handle stress at later life stages. The physiological and behavioural adjustments that are triggered in response to changing conditions can lead to modifications in the phenotypic distributions of traits within a population. Analysing the variation of phenotypical traits offers an insight into the capacity of populations to persist by acclimating to their environment. In this thesis I evaluated the sensitivity of marine organisms to ocean warming and acidification and their various coping mechanisms. I reveal that ocean acidification and warming can alter the behaviour of fish species by increasing their anxiety (chapter 2), boldness (chapter 3 and 5), or feeding rates (chapter 2). Modifications in feeding behaviour were linked to physiological and to changing environmental conditions, creating a feedback mechanism between their cellular and behavioural responses that helped organisms maintain their fitness (chapter 3). However, altered behaviours in a population are not always accompanied by physiological changes, as in chapter 5 I also found changes in risk taking behaviours that did not alter the body condition of temperate or tropical fishes. The direction of responses (negative, positive or neutral) exhibited by a species in response to changing conditions will depend on their specific physiological requirements that determine their sensitivity to stressors. Using a meta-analysis in chapter 4 I showed that when facing climatic stressors, the growth and survival of diverse marine species vary according to their species-specific physiological requirements. For example, negative responses in growth were observed in calcifying organisms and positive responses were found for primary

producers. Life stage was key in determining survival, as eggs and larvae showed to be more vulnerable to stressors than older juvenile and adult stages. The sensitivity of early life stages was also found in laboratory experiments performed in this thesis (chapter 2). A mouthbrooder species was used to test early stage sensitivity, and I showed that the parental environment of the mouthbrooder fish did not provide protection to embryos from acidified conditions. Enriched CO_2 conditions exerted negative effects on the behaviour of their juvenile stage by increasing their anxiety. The distinct species-specific responses in physiology and behaviour have the potential to modify the distribution of phenotypical traits. I revealed that ocean acidification and warming can alter the phenotype distribution of risk taking behaviours (chapter 5). The redistribution of phenotypical traits has the potential to re-shape populations interactions as more dominant species are selected for under future conditions. Additionally, under naturally acidified and warming conditions I found that some species experience a loss of risk-taking phenotypes, as their phenotypic variability was reduced compared to the control conditions. This behavioural homogenisation puts populations of animals at risk to increasing global environmental change. The coping strategies that species use by adjusting their physiology and behaviour can enable them to maintain their fitness under climate change. If species maintain fitness during their entire life span and in future generations, then species will have a greater chance to persist under climatic disturbances. Understanding species sensitivity and their potential to acclimate to environmental change will help improve how we anticipate the future of adaptive capacity of organisms to warming and acidifying oceans.

Key words: Ocean acidification, ocean warming, fitness indicators, fish behaviour, marine organisms sensitivity

Chapter I: General introduction

General Introduction

Carbon dioxide (CO_2) emissions result from natural processes (i.e. weathering and volcanic activity) and anthropogenic activities, notably fossil fuel burning, cement making and changes in land use (Brierly and Kingsford, 2009; Tresguerres and Hamilton, 2017). Since preindustrial times, the atmospheric levels of CO_2 have risen profoundly (from ~280 parts per millions (ppm) to current levels of ~407 ppm; Dunn et al., 2019). Under a business as usual scenario, it is projected that atmospheric CO_2 levels will double again (~936 ppm by the year 2100; Riahi et al. 2011; Nazarenko et al., 2015). These emissions have caused an increase in atmospheric and oceanic temperatures (Rhein et al., 2013). In addition to warming, about 30% of the anthropogenic CO_2 has been absorbed by the ocean (Feely et al., 2004), causing a process known as ocean acidification, where the ocean's surface pH decreases by the dissolution of atmospheric CO_2 (Caldeira and Wickett, 2003; Doney et al., 2009). It is expected that with the continuous emission of anthropogenic CO_2 into the atmosphere, the ocean's surface waters will reach a pH of 7.8 by the year 2100 (Branch et al., 2013), as opposed to the current average of 8.1 (Feely et al., 2009).

The rate at which CO_2 levels are increasing has never been so rapid. Knowledge of organisms' mechanisms to cope with environmental changes is crucial for planning conservation strategies. Fluctuations in the abiotic environment, such as elevated levels of CO_2 and temperature can drive biological responses and alter species geographic ranges, productivity, and interactions (Caldeira and Wickett, 2003; Murray et al., 2014; Bozinovic and Pörtner, 2015; Vargas et al., 2017). The tolerance threshold to stressors can vary between species, or even during the different life stages experienced by an organism (Munday et al., 2009; Munday et al., 2012). The strategies that will allow species to persist with environmental change include range shifts towards more suitable environments, genetic adaptation, or adjust through phenotypic plasticity (Nunney, 2016; Franks et al., 2014). These strategies can occur simultaneously to allow the persistence of populations (Franks et al., 2014).

Climate change effect on marine organisms

Marine ecosystems are currently experiencing profound physical, chemical, and biological disturbances generated by human activities; mainly as a consequence of rising temperatures and acidity in the oceans (Doney et al., 2012). The physico-chemical changes in the ocean can alter directly or indirectly several biological responses in marine organisms. Extreme temperatures can restrain the optimal function of molecular, cellular, and systemic processes in an organism, as they all operate within a restricted window of environmental tolerance (Pörtner and Farrel, 2008; Bozinovic and Naya, 2014). The alteration of important biochemical processes in an organism, such as metabolic rate, will directly alter the growth, reproduction, foraging, and behaviour of individuals (Hoegh-Guldberg and Bruno, 2010; Pörtner and Farrel 2008; O'Connor et al., 2007).

In calcifying organisms negative effects have been observed with ocean warming and acidification. Warming has caused extensive bleaching events on coral reefs with subsequent increased mortality (Hughes et al., 2017; Hughes et al., 2018). Acidification can affect calcifying organisms by impairing their capacity to build their calcified structures (Marubini et al., 2003), where some can adjust (Leung et al., 2019) and others decline (Doney et al., 2009). This can occur at different life stages. Indeed, life stages of organisms differ in their sensitivity to climate change. Early life stages are known to be more vulnerable than adults due to their poor developed physiological functions (Brierly and Kingsford, 2008; Gagliano and McCormick, 2007). In addition, the duration and survival of embryonic and larval phases can be altered by temperature (Pankhurst and Munday, 2011). Survival decreases if there are mismatches between eggs hatching times and food availability (Brierly and Kingsford, 2008) for which zooplankton and phytoplankton are essential food sources for larvae. However, the seasonal cycle, timing and duration of this primary producer (i.e. phytoplankton) can be differentially affected by climate change (Henson et al., 2016), and can pose phenological mismatches between plankton production and larval spawning (Asch, 2015; Cushing, 1990).

As warming takes place in the ocean there is an increase in the oxygen and energy demands of organisms, additionally, the basal metabolic rate of heterotrophic organisms increases and reduces their developmental time (Hoegh-Guldberg and Bruno, 2010). The different sensitivities to rising temperatures can disrupt interactions between species and

eventually have indirect consequences at community levels and for ecosystem processes (Hoegh-Guldberg and Bruno, 2010; Brierly and Kingsford, 2008).

Ocean acidification effects on marine organisms

Organisms may also be affected by acidification of the ocean, but mixed responses have been found across marine biota. Primary producers have an advantage from increased CO_2 availability as it can propagate photosynthesis. Some macroalgae and phytoplankton species will benefit from rising CO_2 (Gao et al., 2019). By contrast, negative effects on different fitness traits such as growth, reproduction, calcifying rates, and survival have been found for several species (Kroeker et al., 2010).

Calcifying species are among the most affected organisms from rising levels of CO_2, as the concentration of carbonate ions necessary for the building of their shells and outer structures is reduced by acidification (Marubini et al., 2003). Calcifying macroalgae and coccolithopores can be negatively affected as their calcification levels decrease (Gao et al., 2019). The negative effects on calcifying organisms will also have repercussions for organisms that depend on them for food or shelter (Guinotte and Fabry, 2008; Doney et al., 2012). For instance, Sunday et al. (2017) forecast a reduction in species diversity that rely on habitat formers such as coral reefs, mussel beds, and calcifying algae due to the detrimental effects of ocean acidification on the structure of such organisms. Yet, some calcifying herbivores can benefit indirectly from carbon emissions (Connell et al. 2017) that boost the nutritional value of their food (Leung et al. 2019).

Early life stages tend to be more vulnerable than adults to ocean acidification. Many invertebrates start their calcification processes during the early life stages, and the larvae and juveniles of such organisms can present a delayed development and reduced survival rates when exposed to acidify conditions (Dupont et al., 2008; Koeker et al. 2010). In fish, juveniles and adults have an acid-base and osmoregulatory capacity that enables some species to tolerate elevated levels of CO_2, while their embryos and larvae continue to develop these physiological controls making them more sensitive to physico-chemical variability (Ishimatsu et al., 2005; Murray et al., 2014). The sensory system of juveniles of some fish species can be insensitive to ocean acidification (Clark et al., 2020), yet for fish

larvae the rising CO_2 levels can impair their olfactory capacity (Munday et al., 2009), vision (Chung et al., 2014), and predator cue recognition (Munday et al., 2016). However, for some organisms their developmental mode may improve their probability of survival in stressful environments.

Brooding (eggs guarded in the protected parental environment) or direct developmental (offspring does not go through a larval stage after hatching) strategies could enable organisms with greater chances of resistance and survival to climate change (Foggo et al., 2007; Lucey et al., 2015). Eggs and larvae that have direct development are not as exposed to the harsh conditions such as spawned eggs or pelagic larvae (Lucey et al., 2015). Additionally, the physiological system of the hatchlings that develop directly will be more developed and confer them greater resistance to climate change (Lucey et al., 2015). Brooding effects have been tested on polychaetes, where they showed to be more successful under acidified conditions than pelagic developing species (Lucey et al., 2015). Whether developmental strategies can help other organism to adjust o changing environments is still largely unknown.

Combined effects of elevated temperature and ocean acidification

The effects of one stressor on organisms could significantly differ from the effects of several stressors interacting. At least three types of responses exist when organisms are exposed to multi-stressor conditions: additive (multi-stressors interaction effects represent the sum of the effect of each stressor), antagonistic (effects of multi-stressors in combination is less than the sum of their effects in isolation), or synergistic (effects of interacting multi-stressors is greater than the expected sum of their effect in isolation) (Gunderson et al., 2016).

Some studies have documented that the effects of combined temperature and ocean acidification in fish yield different results from studies that evaluate them separately. The interaction of climatic stressors have been found to pose antagonistic and synergistic effects, than when evaluated alone, on predator selectivity, mortality, fish lateralization and foraging behaviour (Domenici et al., 2014; Ferrari et al., 2015; Munday et al., 2009; Nowicki et al., 2012). The physico-chemical variations in the environment can alter multiple processes and in different ways among marine environments (Kroeker et al., 2010;

Kübler and Dudgeon, 2015). It is important to include evaluations that test the interaction between stressors as this could allow us to determine which populations will be more vulnerable or which could benefit from environmental change. Ultimately, species responses will depend on their acclimation and adaptation capacities when facing novel conditions.

Resilience and adaptive capacity of marine organisms to climate change

Organisms can respond to changes in the environment from the cellular level to organismal and behaviour levels. Ocean acidification and warming trigger the production of reactive oxygen species (ROS) due to the increase in metabolic rates (Pimentel et al., 2015; Sampaio et al., 2018). When there is an excess of ROS production oxidative stress occurs, and organisms behaviours can be modified (Lesser, 2006). To prevent oxidative stress, a set of cellular antioxidant defences are activated (Pimentel et al., 2015). The defence mechanisms against cellular oxidative stress require the use of energetic resources that are offset against functions key to fitness, such as growth and reproduction (Beaulieu et al., 2014; Birnie-Gauvin et al., 2017). Insufficient endogenous resources may alter the overall condition of an individual, as ROS production will overcome antioxidant defences causing oxidative stress and cellular damage, unless additional energy sources such as food are available (Hochachka and Somero, 2002; Pimentel et al., 2015). Additionally, oxidative stress will lead to damage in organisms' biomolecules, such as DNA (Lesser, 2006), and can alter their behavioural responses.

The first response of many organisms to altered conditions is a change in behaviour (Tuomainen and Candolin, 2011; Wong and Candolin, 2015). For instance, elevated CO_2 has the potential to modify the behaviour and sensory systems of some organisms (Pankhurst and Munday, 2011). Fish can regulate their bicarbonate and chloride ions to maintain stable pH levels in blood and tissues (Ishimatsu et al., 2005; Chung et al., 2014). But these physiological regulations lead to the disruption on the $GABA_A$ receptor in the brains of fishes (Nilsson et al., 2012), which has been related to alterations of fish sensory systems, swimming, foraging, and risk-taking behaviours (Nilsson et al., 2012; Schunter et al., 2016). Behavioural responses are regulated by physiological functions and biochemical processes, and can buffer the negative effects of environmental stressor and maintain

fitness in organisms (Wong and Candolin, 2015; Matis et al., 2017; Davis et al., 2018). Adaptive responses to ocean acidification and warming have not been widely studied, in particular their physiological and behavioural responses after long term exposure to stressors (Pimentel et al., 2016; Davis et al., 2018). Most experiments only encompass a short exposure time to climatic stressor and limit the capacity to evaluate the potential of species to acclimate.

Acclimation can take place over a shorter timescale compared to adaptation, since the latter requires genetic modifications over more than two generations (Munday, 2014). Acclimation refers to an organism capacity to modify phenotypical traits that alter its physiology, behaviour or morphology in order to maintain fitness in novel environments (Donelson et al., 2011; Munday, 2014). For some species, acclimation can result in a cost, where the maintenance of the new phenotypical trait can take energy from other activities (Harney et al., 2016; Sunday et al., 2014; Leung et al. 2019), or may not fully compensate for fitness loss under stressful conditions (Leung and McAfee, 2020). In fish, some parental and transgenerational studies have documented behavioural traits that can only be restored partially, or not at all, from the negative effects of environmental change (Allan et al., 2014; Welch et al., 2014). Additionally, if the environmental conditions of the parents differs from the one experience by their offspring's there can be an associated energetic cost for them (Donelan and Trussell, 2015). In spite of the cost that acclimation may have on some species, when organisms experience prolonged exposure to stressful conditions, their response can be altered as a result of acclimation, and provide time for adaptation to occur if the new phenotype has a favourable selection (Crozier and Hutchings, 2014; Sunday et al., 2014).

Acclimation can be considered a form of adaptive phenotypic plasticity (Gerken et al., 2015) which is defined as the expression of variation in phenotype, from a single genotype, in response to variations in the environment (Scheiner, 1993; Pigliucci, 2005; Souza et al., 2018). Plasticity can impact population fitness in different manners; it can be adaptive when it improves fitness in a population and allows its persistence when facing environmental stressors (Schmid and Guillaume, 2017; Bonamour et al., 2019). Otherwise, it will be maladaptive when fitness is reduced, or neutral if fitness is not affected (Ghalambor et al., 2007).

Most studies evaluating the effects of climate change on marine populations usually describe the mean or average response of traits (Gibert and Brassil, 2014). However, plastic responses can be found across morphological, behavioural, and physiological species traits within populations and represent an important source of variation, where a range of phenotypic responses will be available in a population (Henn et al., 2018; Gibert and Brassil, 2014; Matesanz et al., 2012; Sultan and Spencer, 2002). Traits phenotypic plasticity and variation will favour populations' persistence under changing environments, because a larger range of phenotypic responses within a population increase the probability that some pre-adapted phenotypes will be selected for under natural selection and provide optimal fitness under altered climate conditions (Reed et al., 2011). Despite the important role that plastic and adaptive responses have for population persistence, their long-term responses to climate change and ocean acidification are poorly understood in marine systems.

Thesis aims and approach

Species adjustments to environmental change are diverse. Their capacity to persist under future climatic conditions will depend on their buffering strategies, sensitivity, and acclimation and adaptation capacities. Few studies have evaluated the responses of marine species, in terms of behaviour and fitness, to long term exposure to future climate conditions, and their potential to acclimate to novel conditions. In this thesis, I addressed these gaps using a range of techniques, including enclosed laboratory set-ups, large outdoor mesocoms, natural systems, and a meta-analysis. This thesis aims to assess the sensitivity of marine species, in particular fish species, and their potential to acclimate to the effects of ocean acidification and ocean warming in terms of behaviour, physiology and life history traits.

The specific aims of the thesis are:

- To test the sensitivity during the early life stages of a mouthbrooder fish to long term exposure to ocean acidification in terms of behaviour.

- To evaluate how long term exposure to ocean acidification and warming will affect two temperate fish species across various cellular and physiological processes, and how this will shape their behavioural responses.

- To investigate how marine species are affected in their growth and survival by ocean acidification and warming, and test if these responses are driven by life history factors through a meta-analysis.

- To assess the potential of temperate and tropical fish species to persist under future ocean acidification and warming conditions, by analysing their behavioural and physiological plastic responses to these climatic stressors in natural and laboratory conditions.

Thesis outline of data chapters

Chapter 2

Ocean acidification is known to alter the behaviour of multiple species. The extent to which this stressor will influence species responses will depend on their sensitivity during their different life stages. However, responses of fish during their early life stages tend to be overlooked. This chapter investigated the direct effects of ocean acidification on the behaviour of a mouth-brooding fish species, comparing its sensitivity when exposed to elevated CO_2 levels and control conditions during its embryonic and juvenile stages. Also, the aim was to test if the parental environment (mouth) provided any protection to the embryos against ocean acidification.

Chapter 3

Ocean acidification and warming drive change in the behaviour and physiology of marine organisms. How fish will respond in terms of fitness to long term exposure to environmental stressors is not clear. In this chapter, I examine how two temperate fish species respond to ocean acidification and ocean warming after a 5 month period of exposure in mesocosm and aquarium conditions. I tested for their behavioural and physiological adaptive responses to climatic stressors.

Chapter 4

The exposure of marine organisms to ocean acidification and ocean warming are having an effect on important fitness traits. How different marine species will respond and their potential to persist under changing environments is poorly understood. In chapter 4, I performed a meta-analysis to determine the effects of ocean acidification and ocean warming on the fitness (growth and survival) of different marine species.

Chapter 5

Alterations in the environment modify the behaviour and physiology of fish species. Most studies use the mean values of species traits, disregarding phenotypic distribution and variability. In this chapter, I examine the response of different fish species in natural and laboratory systems to ocean acidification and ocean warming. Various behavioural and physiological traits are analysed to test whether climatic stressor induce a shift in the phenotypic distribution of populations traits.

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Chapter II - Irreversible behavioural impairment or fish starts early: embryonic exposure to ocean acidification

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Abstract

Long-term species responses to ocean acidification depend on their sensitivity during different life stages. We tested for sensitivity of juvenile fish behaviour to ocean acidification by exposing eggs to control and elevated CO_2 levels, and translocating offspring between treatments in a reciprocal design. After 12 weeks of exposure, activity, inactivity and anxiety levels of juveniles from control eggs were similar, whether juveniles had experienced elevated CO_2 conditions or not, and this pattern was consistent over time. However, juveniles raised as eggs under elevated CO_2 showed increased anxiety levels compared to those from control eggs. This response was not reversed when CO_2-exposed juveniles were translocated to control conditions. Our findings highlight the value of evaluating fish sensitivities to global change pollutants across different life stages, and indicate that sensitivity during the often-overlooked egg stage can be critical with long-lasting impairment of behaviours that are coupled to individual fitness and population persistence.

Key words: embryonic stage, fish sensitivity, activity levels, anxiety levels, long-lasting impairment

1. Introduction

Increasing atmospheric CO_2 levels due to human greenhouse gas emissions are projected to reach ~ 936 ppm by the year 2100 (Hoegh- Guldberg et al., 2014) and warm and acidify the world's oceans (Caldeira and Wickett, 2003; IPCC, 2013). Marine life is expected to be affected by these changing physico-chemical conditions in their environment (Lefort et al., 2014; Nagelkerken and Connell, 2015). Understanding how organisms respond across their alternate life stages is fundamental (Russell et al., 2012) as physiological, phenological, and behavioural alterations are often life-stage specific (Rijnsdorp et al., 2009; Hollowed et al., 2013; Bozinovic and Portner, 2015) and leave a legacy on older stages. Furthermore, differential sensitivity to environmental stressors across life stages can create bottlenecks for population growth and persistence (Munday et al., 2009b; Lucey et al., 2015; Marshall et al., 2016). As such, the capacity of each life

stage to acclimate or adapt represents a critical component of how populations might respond to future climates (Munday et al., 2009a; Munday et al., 2012).

Whilst environmental change can alter the performance of marine organisms at distinct life stages, it is the early life stages that tend to be more sensitive to stressors than adults (Pineda et al., 2012; Marshall et al., 2016). The larvae and adults of a species not only differ in morphology and function, but also in the habitat they occupy and their habitat-specific environmental conditions (Marshall et al., 2016). The large surface to volume ratio of small larvae not only increase their exposure to environmental stressors (Baumann et al., 2012; Marshall et al., 2016), but also their less developed anatomy hampers their capacity to buffer these stressors (Marshall et al., 2016). Marine invertebrates are often tolerant to ocean warming during their gamete phase and during fertilization, while their embryos tend to exhibit high rates of mortality (Byrne, 2011). Likewise, for some fish species their eggs and larvae have narrower thermal windows than adults (Pörtner and Farrell, 2008; Rijnsdorp et al., 2009).

Early stages of marine organisms are disproportionately sensitive to enriched CO_2 because their acid-base mechanisms have not yet developed fully (Ishimatsu et al., 2005; Murray et al., 2014; Przeslawski et al., 2015; Munday et al., 2016). Most studies on early life stages, however, have focussed on calcifying organisms due to the perceived fragility of their skeleton during early development (Byrne, 2011; Kroeker et al., 2013). By contrast, fish have been considered to be more tolerant to ocean acidification because of their physiological capacity for acid-base regulation (Munday et al., 2016). Yet recent work suggests that fish are vulnerable during their embryonic and larval stages (Wittmann and Pörtner, 2013) and that there is potential for their harmful effects to carry over onto older life stages, many of which mediate population persistence. In fish, only a few studies have evaluated their potential to acclimate over longer-term periods and they are mainly based on tropical species (Welch et al. 2014).

In this study, we evaluated how ocean acidification can affect the behaviour of a temperate fish when exposed at two different life stages – embryonic and juvenile – and whether they show any degree of acclimation with increasing length of exposure (4, 8 and 12 weeks). Fertilized eggs of a mouth-brooding fish, *Vincentia badia*, were exposed to near-future levels of elevated CO_2. Because their larvae undergo direct development

(personal observation from the field and laboratory), juvenile hatchlings may be more resistant to stressful conditions as their physiological machinery is more developed relative to those broadcast as spawned eggs and pelagic larvae (Lucey et al., 2015). Insight into the potential influence of ocean acidification on early developmental stages, particularly the impairment of essential behavioural traits (e.g. such as activity and anxiety levels) provides clues about future recruitment and population persistence.

2. Materials and methods

2.1 Study site and fish collection

The benthic Scarlet cardinalfish, *Vincentia badia*, inhabit shallow subtidal seagrasses and nearshore reefs of Western and Southern Australia (Baker et al. 2010). We used a seine net to collect fish from November 2016 to January 2017 at Port Vincent (34°46'30.7" S, 137°51'36.7" E). Six adult scarlet cardinalfish with fertilized eggs in their mouth were placed at ambient or elevated CO_2 levels in 40 l nally bins with two pieces of PVC pipe per fish that acted as shelter. Adult fish were kept in two tanks under ocean acidification (OA) conditions: tank 1 housed two parents, and tank 2 one parent. The three parents with eggs inside the two tanks were exposed to elevated CO_2 conditions for 13 and 26 days, respectively. Exposure time of parents with eggs was determined by the time from capture until the egg hatched. For the control treatment one tank housed two parents that were kept under ambient conditions for 7–13 days. Additionally, there was a second control group were one parent spat out the eggs/hatchlings when it was captured, but the juveniles could still be used for the experiment. Upon hatching, juvenile fish from the ambient and elevated CO_2 treatments were transplanted reciprocally to an ambient (Control) or elevated CO_2 (OA) treatment using 20 l nally bins. This configuration resulted in four treatments that incorporate an embryonic phase followed by the juvenile phase: Control–>Control (n = 5, 5, and 4, for week 4, 8, and 12, respectively), Control–>OA (n = 4, 4, 2), OA–>Control (n = 5, 5, 2), and OA–>OA (n = 5, 5, 3). Cardinalfish offspring were fed with Artemia (*Artemia salina*) twice a day *ad libitum* during the 12 week period of the experiment.

2.2 Water chemistry

The 20 l tanks that housed the fish were placed inside temperature-controlled water baths of 300 l. Water temperature was kept at an average of 18.2°C (approximate seawater temperature at the time of fish collection) using submersible titanium heaters with an automated temperature controller (Weipro 500W). Each tank was provided with two air stones, one supplying ambient air and the other supplying either ambient air or a mix of air and CO_2 (average pH: 7.9; pCO_2: 1,068 µatm) using a Pegas 4000 MF gas mixer. Temperature and pH were measured every day using a 913 Metrohm pH meter and salinity was measured using a StarterPen conductivity meter (IC-ST10C-C). Total alkalinity values were estimated by Gran titration from 40 ml water samples at before the beginning of behavioural experiments, and after one month samples were taken three more times weekly. Samples were processed on the same day of collection. Mean pCO_2 water values were calculated using CO2SYS (Pierrot et al. 2006) for Excel with constants from Mehrbach et al. (1973) refit by Dickson and Millero (1987) (see Table 1 for a summary of water parameters).

2.3. Behavioural experiments

The effects of ocean acidification on activity levels were assessed by quantifying the behaviour of juveniles after four, eight and twelve weeks. Each fish was removed from its tank and placed individually at the end of a rectangular 20 l bin, with the same water chemistry conditions as their treatment. Due to the small number of juvenile fish the same individuals were used at weeks 4, 8 and 12. A weighted mesh was positioned in front of the fish to prevent the fish from swimming to a different position of the bin, maintaining the same start position for each fish (with an area of 30 cm long×10 cm wide). After an acclimation time of 3 min. (Huijbers et al., 2012; Jutfelt et al., 2013), a PVCpipe (4 cm diameter×9 cm long) was provided as shelter and the mesh removed. To avoid observer's bias and effects of observer presence on fish behaviour, juvenile fish behaviour was remotely recorded for3 min. From the top of the bin, using either a Canon Legria HF-R406 or a Canon Legria HFM52 camera attached to a metal frame. Three behaviours were considered for this study. 1) swimming: defined as the forward movement of the juvenile fish through the water column as realised by caudal fin action (Vollset et al., 2011). 2) floating: defined as the lack of movement by the fish or movements no greater than the fish

body length. 3) hiding: fish entering the PVC pipe or positioning itself within the shadow of the pipe. Recordings were recorded using VLC media player 2.1.3. Swimming, floating and hiding behaviours were quantified in each video as the proportion of time they spent performing each activity. Experiments were performed under The University of Adelaide Animal Ethics Committee approval # S-2016-165.

2.4. Statistical analyses

Generalized linear mixed models were used to compare the proportion of time the juveniles spent swimming, hiding, and floating among embryonic treatment, juvenile treatment, and time (fixed effects).One model was performed for each behaviour. Embryonic acclimation time in their respective treatment (control or elevated CO_2) was included in the models as a random effect. Assumptions were tested with fitted residual and normality plots. The response variables were treated with a beta distribution, and the models were fitted with a log-it link function. Likelihood ratio tests were used to evaluate differences among treatments.

Table 1. Average (± S.E.) of water chemistry parameters (temperature, salinity, pH, total alkalinity, pH, and pCO_2). pCO_2 values were estimated using CO2SYS. SW = seawater

Treatment		Temperature (°C)	Salinity	pH	Total alkalinity (mmol/kgSW)	pCO_2 (µatm)
Embryonic	Juvenile					
Control	Control	18.2 (±0.1)	37.4 (±0.4)	8.09 (±0.001)	2641.1 (±52.2)	600 (±1.8)
	OA	18.2 (±0.3)	38.1 (±0.1)	7.89 (±0.03)	2640.3 (±35.8)	969 (±139.8)
OA	Control	18.3 (±0.1)	37.1 (±0.3)	8.08 (±0.01)	2590.5 (±32.3)	582 (±5.9)
	OA	18.2 (±0.1)	37.7 (±0.3)	7.83 (±0.02)	2628.3 (±46)	1167 (±44.2)

3. Results

Juveniles raised under ambient CO_2 as eggs and transferred to enriched CO_2 at hatching did not differ in their swimming activity, inactivity(floating) or hiding behaviour compared to juveniles that were raised both as eggs and hatchlings under control conditions (Table 2,Fig. 1a, b, c). Similarly, behaviours of juveniles exposed as embryos to enriched CO2 did not differ when they were raised after hatching in control vs. elevated CO_2conditions (Table 2). Activity and inactivity levels of juveniles which experienced embryonic CO2 enrichment were similar to those that experienced control embryonic conditions (Table 2, Fig. 1b,c). However, the percentage of time that fish spent hiding was

higher for all juveniles that had experienced elevated CO_2 embryonic exposure compared to ambient CO_2 embryonic exposure (Table 2, Fig. 1a).Returning juveniles that had experienced CO_2 enrichment during the embryonic stage to control conditions did not reverse the opposing effects of elevated CO_2 on anxiety levels (Table 2, Fig. 1a). The observed responses for all four embryonic/juvenile treatments were maintained during the 12 week exposure (Fig. 1a, b, c), and showed no significant effect of time (Table 2).Different embryonic acclimation times to treatments had no effect on the variability of fish responses, as random effect variation was close to 0 for all the models (Sup. Table 1).

Table 2. Likelihood ratio test results for swimming, hiding and floating behaviours.

	Swim				Hide				Float			
	Df	AIC	LRT	Pr(>Chi)	Df	AIC	LRT	Pr(>Chi)	Df	AIC	LRT	Pr(>Chi)
EmbrT	1	-11.014	1.9386	0.1638	1	-89.398	4.0774	**0.04346 ***	1	-40.962	0.001	0.9748
JuvT	1	-12.931	0.0216	0.8832	1	-92.277	1.198	0.27372	1	-40.859	0.1036	0.7476
time	2	-10.437	4.5156	0.1046	2	-92.192	3.283	0.19369	2	-40.486	2.4768	0.2898
EmbrT:JuvT	1	-3.9214	2.3198	0.14695	1	-85.802	0.5268	0.468	1	-32.296	2.82	0.0931
EmbrT:time	2	-7.702	0.5392	0.7988	2	-86.972	1.356	0.5067	2	-36.076	1.0394	0.5947
JuvT:time	2	-7.502	0.7392	0.7847	2	-86.84	1.4886	0.4751	2	-36.866	0.02494	0.8828
EmbrT:JuvT:time	2	-4.2412	5.1138	0.07754	2	-84.328	0.9026	0.6368	2	-33.116	3.4452	0.1786

Df = Degrees of freedom, AIC = Akaike Information Criterion, LRT = Likelihood ratio test. EmbrT= Embryonic treatment, JuvT= Juvenile treatment. Asterisks and bold numbers indicate significant ($p < 0.05$) differences.

4. Discussion

Ocean acidification did not affect juvenile cardinalfish that spent their embryonic period in ambient CO_2 concentrations; their activity and inactivity levels, and hiding behaviours remained unchanged. This result contrasts studies that exposed larvae or juvenile fish to ocean acidification after hatching, often observing declines in boldness and swimming speed and increases in anxiety levels (Hamilton et al., 2014; Rossi et al., 2015). A most plausible reason for this resistance to ocean acidification centres on the life-history of cardinalfish; they are direct developers whose young do not go through a larval phase after hatching. This trait could account for their resistance because their acid-base and osmoregulatory capacities are more developed than embryonic or larval stages, enabling them to tolerate higher levels of CO_2 than earlier life phases (Ishimatsu et al., 2005, Murray et al., 2014). Similarly, activity and boldness of juvenile fish is unaffected by ocean acidification in some other species (Melzner et al., 2009; Nowicki et al., 2012; Nagelkerken et al., 2017). Direct development involves the latent development of physiological

machinery and may therefore act as an adaptive mechanism that enables resistance to oceanic enrichment of anthropogenic CO_2.

In contrast, we show that when embryos were exposed to elevated CO_2, the subsequent juvenile life stage responded negatively. Increased anxiety (more hiding) levels occurred in fish hatchlings that had been exposed to elevated CO_2 during their embryonic staged and raised under the same conditions during their juvenile stage. Importantly, when we switched hatchlings from the elevated CO_2 treatment into ambient conditions the detrimental effects were not reversible. This has also been observed for non-behavioural traits, where detrimental effects on growth and survival were only evident if larvae had been exposed to elevated CO_2 during the egg stage, and no CO_2 effects were discernible when larvae were exposed only after hatching (Baumann et al., 2012). Disproportionate sensitivity during early life can be a response of the undeveloped acid-base mechanisms that would otherwise help them regulate changes in pCO_2 (Baumann et al., 2012; Munday et al., 2016). Fish sensory behavioural responses appear sensitive to elevated CO_2 due to the impairment of neurotransmitter receptors (Nilsson et al., 2012; Munday et al., 2012; Forsgren et al., 2013). Early disruption of physiological functions can therefore impede restoration of critical behaviours such as hiding even if fish were to be exposed to lower CO_2 environments in older life stages.

We show that the detrimental effects of ocean acidification on fish behaviour were not only irreversible, but also showed lack of acclimation after a three month exposure. Aside from direct embryonic effects (as discussed above), non-genetic inheritance and parent condition (ultimately altering parental care) are other mechanisms that could explain altered performance by offspring that experienced environmental change during early development. Even though parents had not been exposed to ocean acidification prior to reproduction, they did experience exposure to this stressor while brooding their eggs and non-genetic inheritance can therefore not be ruled out. While our results contrast a few studies that found parental and transgenerational acclimation effects to restore growth and metabolism through non genetic inheritance (Donelson et al., 2012; Miller et al., 2012), they align with behavioural studies that find no acclimation in fish when their parents were expose to elevated CO_2 (Allan et al., 2014; Welch et al., 2014). Poor parental condition during egg brooding (Green, 2008) can also affect the parental care of the eggs. In

sticklebacks, poor parenting results in more anxious offspring (McGhee and Bell 2014). Adult cardinalfish could be particularly affected by elevated CO_2 because they are mouthbrooders that do not consume food during this parental phase. Most studies to date that have evaluated responses under embryonic or parental exposure to elevated CO_2 have been unable to discriminate between the above three mechanisms. These mechanisms could all act together and drive carry over effects into older life stages, and in such instances where species fail to acclimate the persistence of their populations could be at risk (Nagelkerken and Munday, 2016).

Larger fish samples and longer embryonic and parental exposure times before fertilization could give a better explanation of juvenile behavioural performance. The exposure period of embryos inside parents' mouth to ambient and elevated CO_2 was not the same for all fish. Different exposure time in parents has been report to affect morphometric traits in sea urchins, having longer periods to acclimate to this stressor with longer exposure times (Suckling et al., 2014). However, our results showed that the differences in exposure times of embryos had no effect on the variability observed.

In conclusion, the environmental imprint on early development can carry over to adult life, so that embryonic exposure to enriched CO_2 can have irreversible carry over effects onto juvenile stages and subsequently on adult life stages. We provide evidence that CO_2 enrichment has the potential to increase anxiety levels in fish which can affect functions governing population persistence – effects that are only expressed when exposure to CO_2 takes place during the embryonic stage. This sensitivity of fish during their early life makes them particularly vulnerable, yet this early stage of life history is seldom examined. Predictions of the future influence of acidifying oceans will be improved when researchers include responses across an organism's life stages, especially their most vulnerable stages of early development.

Supplementary data to this article can be found online at https://doi.org/10.1016/j.marpolbul.2018.06.004.

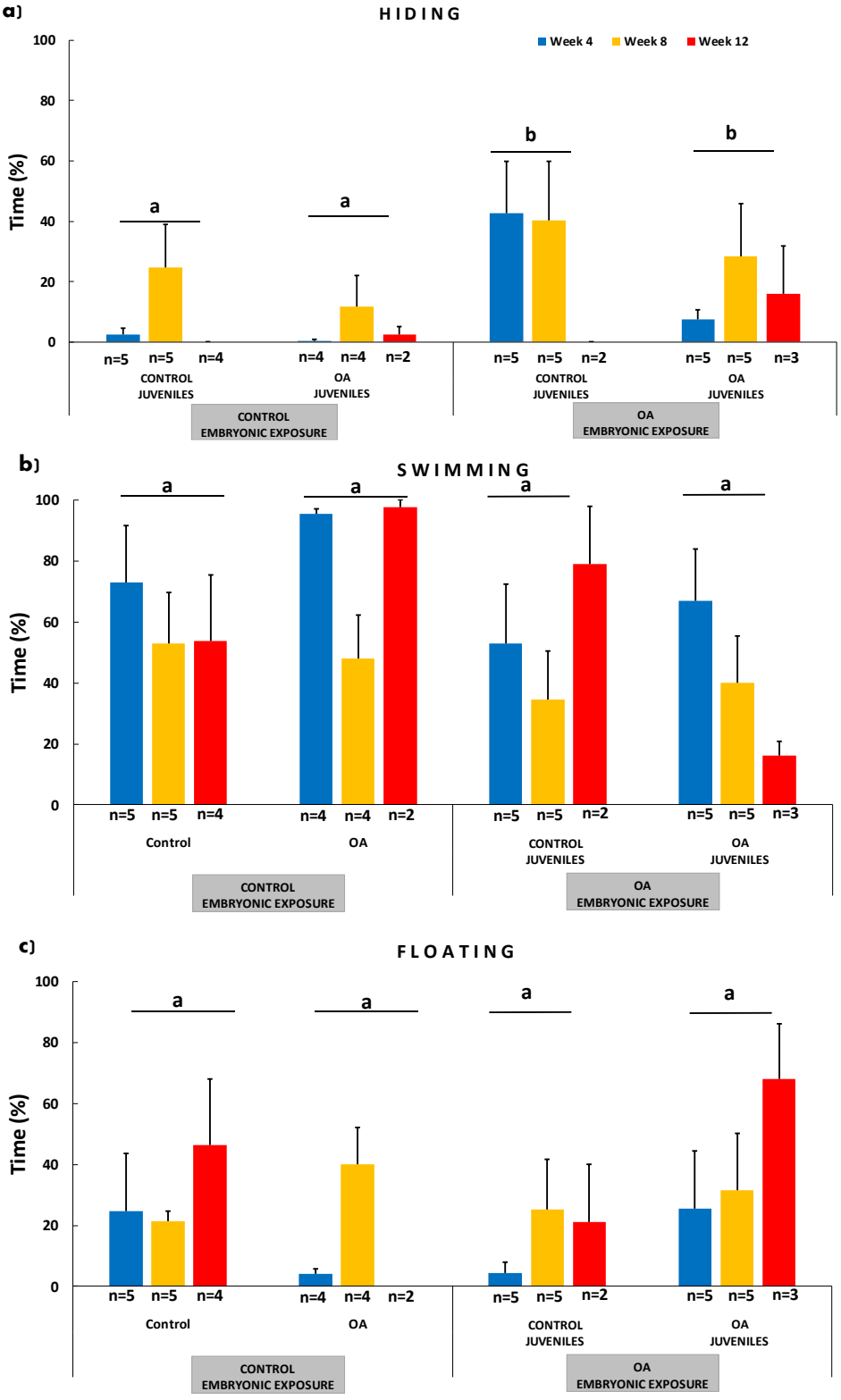

Figure 1. Percentage of time spent by juvenile scarlet cardinalfish hiding (a), swimming (b), and floating (c), under four different treatments: juveniles from control embryonic exposure that have subsequently been

exposed to control vs elevated CO_2 (OA) conditions after hatching, and juveniles from elevated CO_2 embryonic exposure that have subsequently been exposed to control vs elevated CO_2 conditions after hatching. Results are shown for weeks 4, 8, and 12 after hatching. Different letters represent significant differences among the four treatments; time had no significant effect. Error bars represent standard errors. n = number of replicate fish tested.

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Supplementary Results

Supplementary table 1. Generalized Linear Mixed Models output for swimming, hiding, and floating behaviours. All model used a beta distribution with a log-it link.

	Swim				Hide				Float			
Coefficients:												
	Estimate	Std. Error	z value	Pr(>|z|)	Estimate	Std. Error	z value	Pr(>|z|)	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	0.848	0.630	1.35	0.179	-1.870	0.504	-3.71	0.00021 ***	-0.845	0.526	-1.61	0.11
EmbrTOA	-0.962	0.864	-1.11	0.265	1.631	0.697	2.34	0.01927 *	-0.697	0.725	-0.96	0.34
JuvTOA	0.639	0.756	0.85	0.398	-0.104	0.722	-0.14	0.88551	-0.603	0.769	-0.78	0.43
timeWB8	-0.868	0.725	-1.20	0.231	0.623	0.687	0.91	0.36452	0.166	0.738	0.23	0.82
timeWC12	-0.771	0.743	-1.04	0.299	-0.136	0.721	-0.19	0.85068	0.773	0.791	0.98	0.33
EmbrTOA:JuvTOA	-0.579	1.002	-0.58	0.563	-1.191	1.002	-1.19	0.23461	1.334	1.059	1.26	0.21
EmbrTOA:timeWB8	0.373	0.990	0.38	0.706	-0.946	0.975	-0.97	0.33190	0.474	1.033	0.46	0.65
EmbrTOA:timeWC12	2.341	1.301	1.80	0.072	-1.631	1.162	-1.40	0.16028	-0.227	1.242	-0.18	0.86
JuvTOA:timeWB8	-0.754	1.068	-0.71	0.480	-0.209	1.026	-0.20	0.83848	1.020	1.104	0.92	0.36
JuvTOA:timeWC12	0.792	1.215	0.65	0.515	0.328	1.180	0.28	0.78073	-1.078	1.250	-0.86	0.39
EmbrTOA:JuvTOA:timeWB8	0.432	1.431	0.30	0.763	1.077	1.418	0.76	0.44762	-1.497	1.514	-0.99	0.32
EmbrTOA:JuvTOA:timeWC12	-3.603	1.845	-1.95	0.051	1.413	1.687	0.84	0.40222	1.882	1.800	1.05	0.30

Signif. codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Number of observations: total=49, fEbrExp=4
Random effect variance(Group=fEbrExp

	Variance	StdDev
(Intercept)	0.2618	0.5117

Number of observations: total=49, fEbrExp=4
Random effect variance(Group=fEbrExp

	Variance	StdDev
(Intercept)	3.45e-06	0.001857

Number of observations: total=49, fEbrExp=4
Random effect variance(Group=fEbrExp

	Variance	StdDev
(Intercept)	6.242e-07	0.0007901

Chapter III - Adaptive responses of fishes to climate change: feedback between physiology and behaviour

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i. the candidate's stated contribution to the publication is accurate (as detailed above);

ii. permission is granted for the candidate in include the publication in the thesis; and

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Abstract

The adaptive capacity of individuals, from their cells to their overall performance, allows species to adjust to environmental change. We assess a hierarchy of responses (from cells to organismal growth and behaviour) to understand the flexibility of adaptive responses to future ocean conditions (warming and acidification) in two species of fish with short lifespans by conducting a long-term mesocosm/aquarium experiment. Fishes were exposed to elevated CO_2 and temperature in a factorial design for a five-month period. We found a feedback mechanism between cellular defence and behavioural responses. In circumstances where their antioxidant defence mechanism was activated (i.e. warming or acidification), increased feeding rates prevented oxidative damage (i.e. during warming Sp. 1). However, when feeding rates failed to increase to provide additional energy needed for antioxidant defence, oxidative damage could not be prevented (warming + acidification Sp. 1). In contrast, when the activation of antioxidant defence was not required, energy intake from increased feeding was redirected to increased fish growth (acidification Sp. 2, warming + acidification Sp. 2), whilst no gain in growth rate was observed where feeding remained unchanged (acidification Sp. 1 or warming Sp. 2). This adaptive strategy seems to rely on the inherent behavioural response of fishes to their environment and such adjustability shows the kind of responses that organisms may express to prevail in future ocean climate. Indeed, assessing the link between responses from cellular to organismal levels, using a diversity of fitness indicators and behaviour, provides a fundamental understanding of how organisms as a whole may adjust to prevail in a future world.

Key words: Ocean acidification; Ocean warming; Fitness indicators; Long-term exposure

Highlights

• We studied long-term effects of climate change on fish physiology and behaviour.

• Fish responses were tested from cellular to organismal levels in mesocosms/aquaria.

• Fish altered their growth and behaviour as an adaptive response to climate change.

• Fish showed feedbacks between cellular defences and behaviour.

• Adaptive responses show species strategies to prevail under future climate change.

1. Introduction

With ongoing anthropogenic CO_2 emissions, it is projected that atmospheric CO_2 concentrations will reach ~936 ppm by the year 2100 (Riahi et al., 2011; Nazarenko et al., 2015), thereby increasing the acidity and temperature of the world's oceans (Caldeira and Wickett, 2003; IPCC, 2013). The combination of ocean acidification and warming will pose significant challenges for marine organisms (Pimentel et al., 2015) to maintain their fitness and survival because their acid-base balance, metabolism, growth, reproduction, and behaviour can be adversely affected (Pimentel et al., 2016; Wittman and Pörtner, 2013; Leung et al., 2018). Marine organisms are constantly subject to a fluctuating environment and their initial response usually involves behavioural alterations, regulated by physiological and biochemical processes (Tuomainen and Candolin, 2011; Matis et al., 2017; Davis et al., 2018). For instance, metabolic or neural processes in fish associated with abiotic stressors can have direct effects on their activity level, boldness, and foraging behaviour (Nagelkerken and Munday, 2016).

The ability of organisms to counteract, resist, or avoid the detrimental effects of environmental stress is known as adaptive response (Crawford and Davies, 1994; Cabej, 2012). To minimize the impacts of environmental perturbations, including ocean acidification and warming, organisms can activate a set of biochemical reactions at cellular level, fuelled by an increased metabolism (Pimentel et al., 2015; Sampaio et al., 2018). However, an unavoidable elevated production of reactive oxygen species (ROS) ensues due to the increased metabolism. Excess production of ROS leads to oxidative stress, which in turn causes damage to biomolecules (e.g. lipids and DNA) (Lesser, 2006) and an associated change in behaviour. For example, Patki et al. (2013) found learning and memory impairment, and increased anxiety in laboratory rats after experiencing social defeat stress and oxidative stress.

To cope with oxidative stress, many organisms rely on antioxidant defence mechanisms (Pimentel et al., 2015) so that they can modulate their physiological pathways and allocate energy to self-maintenance (Chainy et al., 2016; Birnie-Gauvin et al., 2017). However, the activation of antioxidant defence requires the use of endogenous resources (Beaulieu et al., 2014), which inevitably diverges resources away from key functions, such as growth, reproduction, and survival (Birnie-Gauvin et al., 2017). Without additional

external energy sources (i.e. food), energy allocated to antioxidant defence might not be adequate to counter the oxidative stress, resulting in cellular damage and a reduced energy budget (Hochachka and Somero, 2002; Pimentel et al., 2015). To date, only a few studies have investigated the effects of ocean acidification and warming on both the physiology and behaviour of marine organisms (Pimentel et al., 2016; Davis et al., 2018). It is still unclear how fitness is altered or retained after long-term exposure to these climate change stressors as most studies focus on short-term exposure, which only indicates immediate stress responses but not potential acclimation mechanisms.

By conducting a mesocosm/aquarium experiment, the longer-term effects of ocean acidification and warming on the physiology and behaviour of two coastal fish species were evaluated by a hierarchy of responses (from cells to organismal growth and behaviour) to assess the flexibility of adaptive responses to future ocean conditions (warming and acidification). Fishes with a short life span (1–2 years) were selected so that the experimental exposure to future climate covered a relatively long proportion of their life span. We tested a suite of cellular stress and defence indicators, growth, physiological traits, and behavioural responses that are associated with the stress and body condition of fishes. Total antioxidant capacity and malondialdehyde production were measured to reflect antioxidant defence and cellular stress, respectively. RNA/DNA ratio of muscle tissues was used as an indicator of energy allocation towards short-term somatic growth, based on the concept that DNA cellular content remains constant while that of RNA involved in protein synthesis varies with environmental fluctuations, age, life stage, organismal size, and disease-state (Bulow, 1970; Chícharo and Chícharo, 2008). Somatic growth, fish body condition, energy reserves, and reproductive investment were included as fitness indicators of physiological traits, while behavioural traits included fish activity levels and foraging rates. Fish physiological and behavioural responses to elevated CO_2 and temperature are considered to be species-specific (Clements and Hunt, 2015; Vargas et al., 2017; Davis et al., 2018). Long-term exposure to climate change stressors can either exacerbate or buffer the direction of stressor effects on fish physiological and behavioural traits. In the presence of unlimited food, additional energetic intake could be sufficient to help compensate the negative effects of ocean acidification and ocean warming (Thomsen et al., 2013; Gobler et al., 2018). Hence, we hypothesise that in a future climate, maintenance of individual fitness

depends heavily on the presence of non-limiting food sources and an associated increase in foraging behaviour. For species whose behaviours are not impaired (e.g. activity and feeding), larger buffering capacity will be present to regulate physiological processes and sustain homeostasis. Assessing the link between responses at cellular and organismal levels (through indicators of fitness and behaviour) sheds light on how organisms as a whole are affected by climate change and on their adaptive responses to future environments.

2. Materials and methods

2.1. Study species

The small-mouthed hardyhead (*Atherinosoma microstoma*) is an endemic fish of South Australia that can inhabit shallow estuaries, marine embayments, and hypermarine lagoons (Ye et al., 2015), and are considered a pelagic-neritic species (Riede, 2004). Their lifespan encompasses one year, reaching a maximum length of 100 mm (Ye et al., 2015). They are considered to be an important part of their ecosystem as they function as prey for different fish and birds (Ye et al., 2015).

The southern longfin goby (*Favonigobius lateralis*) is distributed throughout southern and western Australia and Tasmania (Hutchins and Thompson, 1983; Hoese and Larson, 2008). They are usually found in shallow waters with sandy substratum of estuaries and bays, as well as seagrass beds (Hoese et al., 2006; Gomon et al., 2008). Their lifespan has not been reported; however, it has been estimated that some temperate gobies can live two years or more, reaching their sexual maturity after their first year of life (Kornis et al., 2017).

2.2. Mesocosm experimental design

Juveniles of small-mouthed hardyhead and southern longfin goby were collected using a seine net in the northern part of the Spencer Gulf and the eastern coast of the Gulf St. Vincent, South Australia from September to October 2016. After collection, the fish were immediately transferred to 73 l bins, where they were acclimated under ambient temperature and pH levels to tank condition for three weeks, and subsequently transferred to large outdoors mesocosms. After one week of acclimation in the mesocosms, future

climate conditions were simulated in a factorial design. A total of 12 mesocosms (1800 l capacity) were maintained for four treatments (control, ocean acidification, elevated temperature, and combined ocean acidification and elevated temperature), each with three replicates.

Temperatures in mesocosms fluctuated with outdoor air temperatures, but they were adjusted to represent a 1.2 °C increase in future climate change compared to the control mesocosm conditions. Temperature was controlled using submersible titanium heaters with a programmed temperature controller (Weipro 500 W). Heaters were placed inside each elevated-temperature mesocosm as well as in the header tank that distributed warmed seawater to all elevated-temperature mesocosms. Seawater pCO_2 was maintained at an average of 370 ppm for control treatments and 500 ppm for ocean acidification mesocosms, with a mean difference of 0.13 pH units between control and OA treatments (Table 1). A header tank where pure CO_2 was bubbled into the seawater provided pre-treated seawater to the ocean acidification mesocosms. Additionally, each ocean acidification mesocosm was provided with enriched CO_2 levels using a Pegas 4000 MF gas mixer. Temperature and pH were measured 2–3 times a day in each mesocosm using a 913 Metrohm pH meter and a Mettler Toledo SG2 SevenGo meter. Total alkalinity was measured weekly using potentiometric titrator (888 Titrando, Metrohm, Switzerland). CO2SYS (Pierrot et al., 2006) for Excel with constants from Mehrbach et al. (1973) refit by Dickson and Millero (1987) (see Table 1 for a summary of water parameters) was used to calculate pCO_2 (μatm). Each mesocosm had a seawater inflow rate of $2\,l\,min^{-1}$, corresponding to a full replenishment every 15 h.

Seven southern longfin gobies and 14 small-mouthed hardyheads were added into each mesocosm. Fishes were fed ad libitum on a daily basis with a mixture of blended sardines, shrimps and squids. After a 2-month period of climate treatment exposure, the mesocosm project was terminated, and fish were transferred into an indoor temperature-controlled aquarium.

Table 1. Mean (± SE) values of seawater chemistry parameters in the 1,800 L outdoor mesocosm tanks (temperature, salinity, pH, total alkalinity, pH, and pCO_2). pCO_2 values were estimated using CO2SYS. SW = seawater. OA = Ocean acidification; W = warming; OAW = combination of ocean acidification and warming.

Treatment	Temperature (°C)	Salinity	pH	Total alkalinity (mmol/kgSW)	pCO2 (µatm)
Control	19.6 (±0.53)	36	8.2 (±0.02)	2431.7 (±4.5)	352 (±19.0)
OA	19.7 (±0.51)	36	8.1 (±0.01)	2415.7 (±5.2)	505 (±19.5)
W	20.7 (±0.45)	36	8.2 (±0.02)	2431.5 (±5.2)	377 (±22.4)
OAW	21.0 (±0.45)	36	8.1 (±0.02)	2429.5 (±5.2)	519 (±22.4)

2.3. Aquarium experimental design

Fish transferred to the aquarium room were held in 40 l tanks for an additional 3.2 months. Because biomarkers, RNA/DNA ratios, and behaviour respond almost immediately to treatment effects, and because fish were held in aquaria for 3.2 months before tissue sampling, these measurements relate to the effects of the aquarium treatment conditions rather than those of the mesocosm. Only for somatic growth, the effects of mesocosm and aquaria are integrated. Water quality was maintained to replicate the conditions of the mesocosms; however, fish were kept separated by species. Seawater temperature in the tanks was kept at an average of 20.5 °C under present-day conditions and an average of 21.8 °C (+1.3 °C difference) under future climate conditions (Table 2). Temperature was controlled by placing the 40 l tanks inside 300 l water baths, which held submersible titanium heaters with programmed temperature controllers (Weipro 500 W). Elevated seawater pCO_2 was maintained by placing two air stones in each tank: one air stone supplied ambient air (average pCO_2: 529 µatm; pH: 7.95) and one air stone supplied CO_2-enriched air (average pCO_2: 825 μatm; pH: 7.76; 0.2 pH units difference compared to controls) using a Pegas 4000 MF gas mixer. Ambient pCO_2 conditions were maintained by only supplying ambient air to the respective tanks. Daily measurements of temperature and pH were performed using a 913 Metrohm pH meter, while salinity was measured using a StarterPen conductivity meter (IC-ST10C-C). Seawater total alkalinity was measured after one week of transfer to the aquarium; after one month, samples were taken weekly during three consecutive weeks. Seawater alkalinity samples were processed on the same day of collection by Gran titration from 40 ml samples. Mean pCO_2 of seawater were calculated using CO2SYS (Pierrot et al., 2006) for Excel with constants from (Mehrbach et al., 1973)

refit by (Dickson and Millero, 1987). Seawater changes were performed daily (after feeding the fish) to remove food waste, with pre-treated seawater from their respective treatment.

Control (C) and warming (W) treatments for southern longfin gobies each had two replicate tanks, while ocean acidification (OA) and the combined ocean acidification and warming (OAW) each had three replicate tanks. All tanks harbouring southern longfin gobies were supplemented with sand on the bottom and harboured PVC pipes as shelter. Each tank contained seven southern longfin gobies. Hardyheads had two replicate tanks for each treatment, with 14 fish per tank, and all tanks harboured PVC pipes for shelter. Both southern longfin gobies and hardyheads were fed daily ad libitum with the same diet as in the mesocosms. Individual fish weight and total length were measured at the start of the mesocosm experiment, and at the end of the aquarium experiment. Fish were euthanized with the *iki jime* technique after a total 5.2 months of treatment exposure (mesocosm + indoor aquaria) and immediately frozen in liquid nitrogen and then stored at −80 °C until further analyses.

Table 2. Mean (± SE) values of seawater chemistry parameters in the 40 l laboratory tanks (temperature, salinity, pH, total alkalinity, pH, and pCO_2) for both fish species. pCO_2 values were estimated using CO2SYS. SW = seawater. OA = Ocean acidification; W = warming; OAW = combination of ocean acidification and warming.

Species	Treatment	Temperature (°C)	Salinity	pH	Total alkalinity (mmol/kgSW)	pCO2 (µatm)
Goby	Control	20.6 (±0.06)	35.4 (±0.07)	7.9 (±0.01)	2099.4 (±110.4)	515 (±38.1)
	OA	20.6 (±0.04)	35.5 (±0.05)	7.7 (±0.01)	2012.6 (±55.0)	842 (±64.8)
	W	21.8 (±0.04)	36.1 (±0.08)	8.0 (±0.01)	2188.2 (±120.2)	554 (±35.2)
	OAW	21.9 (±0.03)	38.7 (±1.80)	7.7 (±0.01)	2066.8 (±42.1)	926 (±70.7)
Hardy head	Control	20.4 (±0.04)	37.0 (±0.10)	8.0 (±0.01)	2194.7 (±30.7)	536 (±45.5)
	OA	20.3 (±0.04)	37.2 (±0.08)	7.8 (±0.01)	2178.8 (±41.4)	798 (±63.9)
	W	21.8 (±0.05)	36.5 (±0.09)	8.0 (±0.01)	2191.7 (±75.8)	510 (±46.2)
	OAW	21.7 (±0.05)	37.0 (±0.10)	7.8 (±0.01)	2214.5 (±67.8)	734 (±54.0)

2.4. Behavioural experiments

Fish activity levels and bite rates were assessed inside the 40 l aquarium tanks after 3.7 months of exposure to treatments (combined mesocosm and aquarium conditions). A 50 mL transparent vial with apertures on the sides and covered with mesh was placed in the middle of the tank. The vial contained 25 live adult brine shrimps (*Artemia salina*) as visual cues, and a mixture of food (3 g of blood worms and 1.5 g of blended sardines, shrimp and squid) as olfactory cues. Fish behaviour was recorded remotely from the top of the tank for

7 min, using either a Canon Legria HF-R406 or a Canon Legria HFM52 camera attached to a metal frame. Behaviour was then analysed from the videos on a computer screen with a grid of eight squares overlapping the tank arena. Activity level was assessed as the number of lines crossed by the fish per minute (Munday et al., 2013), while bite rate was quantified as the number of bites that the fish took at the food vial per minute. Due to some blurriness of some videos, we only evaluated 6 min of the recordings for southern longfin gobies and 5 min for hardyheads. Experiments were performed under The University of Adelaide Animal Ethics Committee approval # S-2016-165.

2.5. Physiological proxies

Stress responses and condition of the fishes were evaluated by assessing different indicators: RNA/DNA ratio, total antioxidant capacity (TAC), lipid peroxidation or oxidative damage (MDA), gonadosomatic index (GSI), hepatosomatic index (HSI), Fulton's condition index, and somatic growth (see Table 3 for a summary of the indicators used).

Table 3. Fish behavioural and physiological indicators.

Indicator	Description
Behaviour	
Activity level	Number of lines crossed by the fish per minute
Bite rates	Number of bites by the fish at a food vial per minute
Physiology	
RNA/DNA	Indicator of short term somatic growth
TAC	Indicator of total antioxidant capacity
MDA	Indicator of oxidative stress
GSI	Indicator of reproductive investment of the fish
HSI	Indicator of the fish energy reserves
K-factor	Indicator of fish body condition
Somatic growth	Indicator of long term somatic growth

TAC = total antioxidant capacity; MDA = malondialdehyde; GSI = gonadosomatic index; HSI = hepatosomatic index.

Fish muscle tissue (~25 mg) was used for the RNA/DNA ratio analyses. The *D7001 ZR-Duet™ DNA/RNA MiniPrep Kit* was used for DNA and RNA extraction. RNA samples were also treated with the *E1010 DNase I Set (250 U) w/DNA Digestion Buffer* to prevent

contamination from DNA into RNA samples. A Quantus Fluorometer was used for quantification of the DNA and RNA samples. In order to adjust the quantified value to the weight of the sample, we obtained the total weight of DNA or RNA sample and divided this by the weight of the tissue sample:

$$\frac{RNA}{DNA} = \frac{\left\{\left[\text{Quantus value}\left(\frac{\text{ng}}{\mu\text{l}}\right) / \text{Volume}\ (\mu\text{l})\right] * \text{Weight of sample (mg)}\right\}}{\left\{\left[\text{Quantus value}\left(\frac{\text{ng}}{\mu\text{l}}\right) / \text{Volume}\ (\mu\text{l})\right] * \text{Weight of sample (mg)}\right\}}$$

Muscle (~100 mg) tissue was also used to prepare a 10% tissue homogenate in an ice bath, which was subsequently used to assess total antioxidant capacity (TAC) and malondialdehyde concentration (MDA, indicative of oxidative damage). Coomassie blue staining method was used to measure the protein concentration in the 10% tissue homogenate. Assay kits purchased from Nanjing Jiancheng Bioengineering Institute, China, were used to evaluate TAC (CAT no: A015–1) and MDA concentration (CAT no: A003–1), following the manufacturer's manuals.

The reproductive investment of the fish was calculated based on the gonadosomatic index (GSI). GSI was measured based on the wet weight of the gonads and of the entire fish:

GSI = (wet gonad weight/total body wet weight) × 100

The energy reserves of the fish were calculated based on the hepatosomatic index (HSI). The HSI was calculated based on the wet weight of the liver and of the entire fish:

HSI = (wet liver weight/total body wet weight) × 100

Fish body condition was calculated for each individual using the Fulton's condition factor (K-factor):

$K = 100 \times \text{wet weight}/\text{standard length}^3$

Fish somatic growth was calculated based on the difference between mean initial weight of all fish in each mesocosm (start of the mesocosm experiment) and final mean fish weight per tank (end of the aquarium experiment). Mean tank fish weight was used as individual fishes were not tagged and hence their individual growth could not be followed over time.

2.6. Statistical analyses

Activity levels, bite rates, RNA/DNA ratios, TAC, MDA, GSI and HSI indexes, and Fulton's condition factor were each compared separately for the two species among the four treatments using two-way ANOVAs, with elevated temperature and ocean acidification as fixed factors, and with two treatment levels: present and future. To compare short-term growth (RNA/DNA ratio) and long-term growth (somatic growth) with the two treatment levels (present and future), we ran a 2-way MANOVA with temperature and ocean acidification as fixed factors using $\log_{10}$ transformed values for somatic growth.

3. Results

3.1. Total antioxidant capacity (TAC)

TAC did not differ among treatments ($F_{1,20} = 3.89$; $p = 0.062$) for southern longfin gobies (Fig. 1a). For hardyheads, however, TAC was higher in elevated temperature treatments than ambient temperature treatments (W and OAW; $F_{1,20} = 4.77$; $p = 0.039$; Fig. 2a).

3.2. Oxidative damage

Oxidative damage levels did not differ among treatments ($F_{1,16} = 0.57$; $p = 0.536$) for southern longfin gobies (Fig. 1b), while hardyheads had higher MDA levels under the combined temperature/acidification treatment ($F_{1,20} = 5.07$; $p = 0.034$; Fig. 2b).

3.3. Feeding behaviour and activity levels

The bite rates ($F_{1,39} = 4.31$; $p = 0.044$; Fig. 1d) and activity levels ($F_{1,39} = 6.84$; $p = 0.016$; Fig. 1c) of southern longfin gobies were higher under both OA and OAW treatments than under the C and W treatments. The bite rates of hardyheads were only higher under W ($F_{1,70} = 8.92$; $p = 0.002$; Fig. 2d), whilst activity levels were greater in

all three climate treatments compared to the control treatment ($F_{1,70} = 4.41$; $p = 0.039$; Fig. 2c).

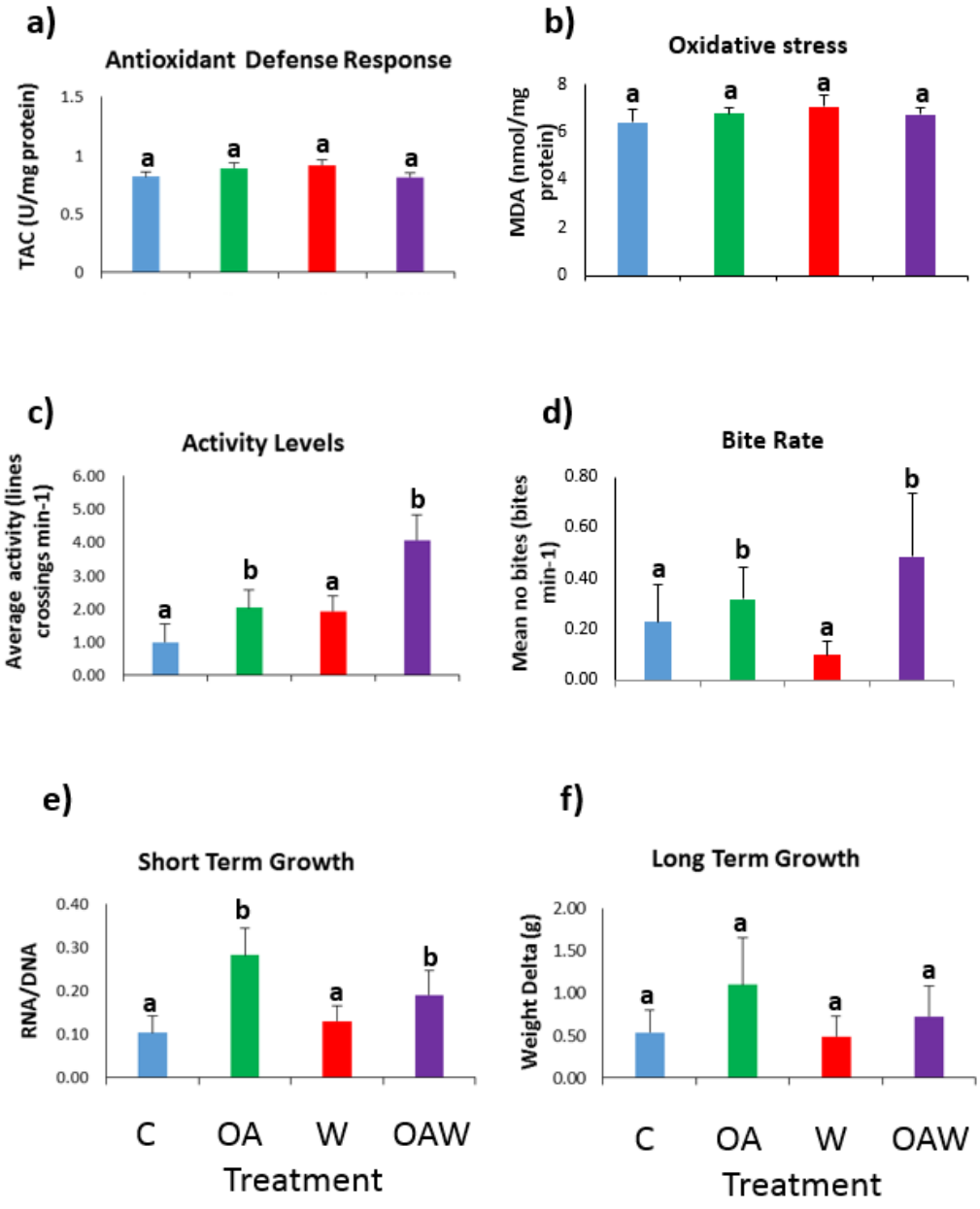

Figure 1. Effects of climate treatments on southern longfin gobies for: total antioxidant capacity (a), oxidative stress (b), activity levels (c), bite rate (d), RNA/DNA ratio (e), and the weight increase from the start of the experiment until the end (f). If letters above bars are different from one another, they represent significant differences ($p < 0.05$) between those treatments. C = control, OA = ocean acidification, W = warming, OAW = combination of ocean acidification and warming. Error bars represent standard error.

3.4. Growth

RNA/DNA ratio ($F_{1,20} = 5.81$; $p = 0.027$; Fig. 1e) in southern longfin gobies and the multivariate analysis of RNA/DNA ratio and somatic growth combined ($F_{1,7} = 3.42$; $p = 0.037$) showed greater values under ocean acidification treatments (OA and

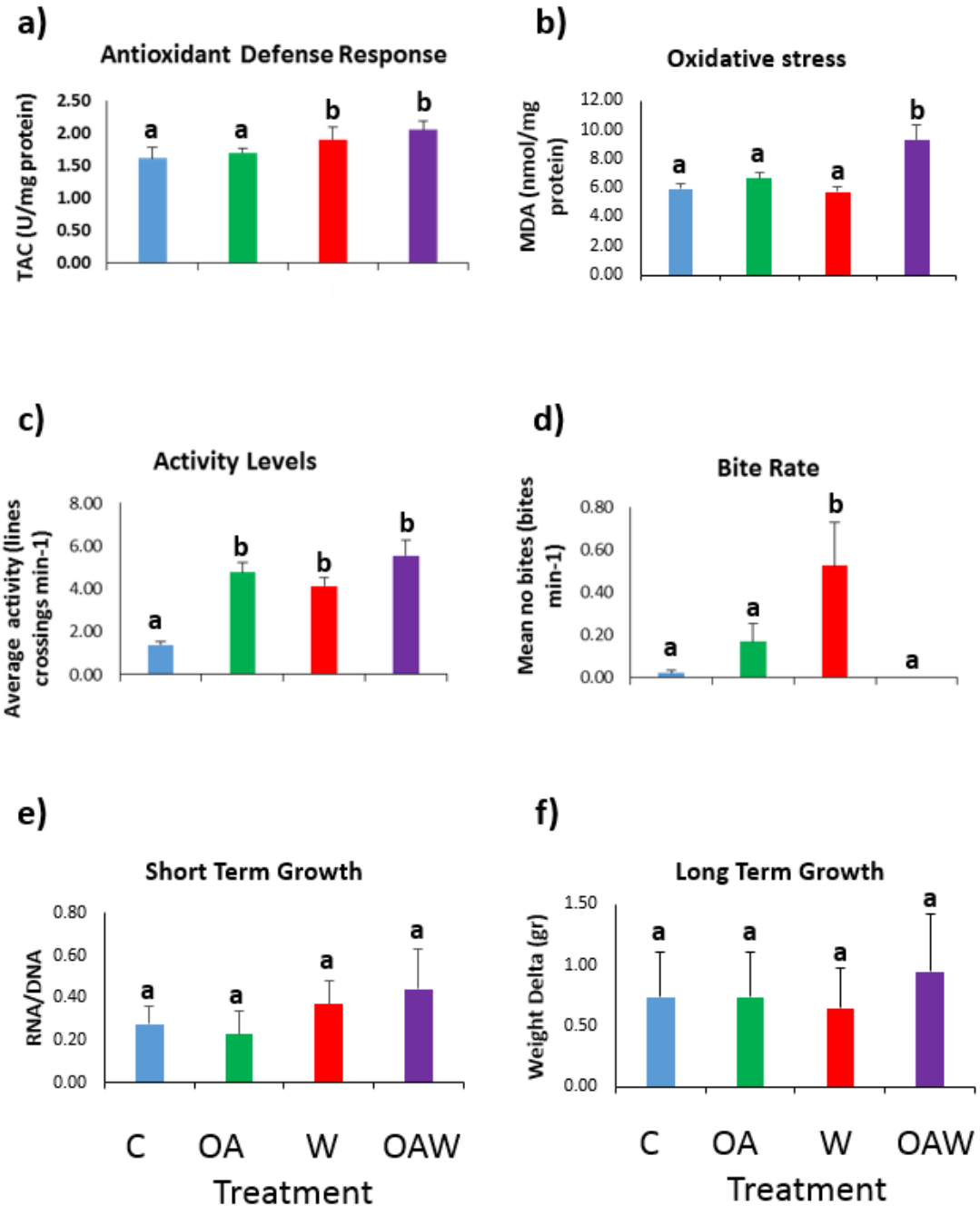

Figure 2. Effects of climate treatments on small-mouthed hardyheads for: total antioxidant capacity (a), oxidative stress (b), activity levels(c), bite rate (d), RNA/DNA ratio (e), and the weight increase from the start of the experiment until the end (f). If letters above bars are different from one another they represent

significant differences between those treatments ($p < 0.05$). C = control, OA = ocean acidification, W = warming, OAW = combination of ocean acidification and warming. Error bars represent standard error.

OAW) than the ambient CO_2 treatments. Treatment effects were neither found in hardyheads for RNA/DNA ratio ($F_{1,20} = 0.009$, $p = 0.922$, OA; $F_{1,20} = 1.47$, $p = 0.242$, T; $F_{1,20} = 0.214$, $p = 0.660$, OAW; Fig. 2e) nor RNA/DNA ratio and somatic growth combined ($F_{1,4} = 0.1.42$, $p = 0.378$, OA; $F_{1,4} = 0.94$, $p = 0.423$, T; $F_{1,4} = 0.29$, $p = 0.768$, OAW; Table S2).

3.5. Other physiological traits

The gonadosomatic index (GSI), hepatosomatic index (HSI), and Fulton's condition factor did not differ among treatments for either species (Table S1, S2), except the HSI in hardyheads which was lower in the ocean acidification treatment than the other treatments ($F_{1,21} = 4.11$; $p = 0.040$; Table S2).

3.6. Physiological and behavioural pathways

Based on the results of the two fish species combined, we observed a strong link between environmental stress, physiological defence mechanisms, adaptive behaviour, and ultimately fitness (Fig. 3). Where the antioxidant defences increased to counteract oxidative stress, increased feeding allowed extra energy intake to be allocated towards negating oxidative damage rather than an increase in somatic growth (hardyheads–W). Under the same conditions, but where fish did not increase feeding rate (and hence lack of energetic supplement), the outcome was oxidative damage (hardyheads–OAW). Following the same logic, in cases where there was no need to activate antioxidant defence, energetic supplements through increased feeding (southern longfin gobies–OA and OAW) resulted in increased growth, and likewise, lack of increased feeding (southern longfin gobies–OA; hardyheads–W) resulted in a lack of increased growth.

4. Discussion

We reveal the adaptive responses of fishes to climate change via adjustments to their growth and behaviour. Increased feeding behaviour of hardyheads was driven by elevated temperature in isolation, whilst that of southern longfin gobies by increased CO_2 levels

irrespective of temperature. In the latter case, CO_2 had a boosting effect on both feeding activity and growth. In contrast, southern longfin gobies under elevated temperature alone or hardyheads in any of the treatments showed no boosting effect in any of their fitness traits (i.e., growth, reproductive and energetic investment). Elevated temperature (in isolation or in combination with increased CO_2) led to an increase in antioxidant defence of hardyheads, which indicates the capacity of hardyheads to cope with oxidative stress. As a result, oxidative damage was averted (i.e. no elevated MDA concentration) under elevated temperature in isolation. Despite the benefit of antioxidant defence, this results in a high energetic demand (Poljsak et al., 2011) and therefore hardyheads in the temperature alone treatment increased their feeding behaviour to compensate for the energy required for antioxidant defence. Such a response is adaptive because the energetic cost of repairing cellular damage is even higher, and with increased feeding, somatic growth and other fitness traits (reproductive investment and energy reserves) can be maintained.

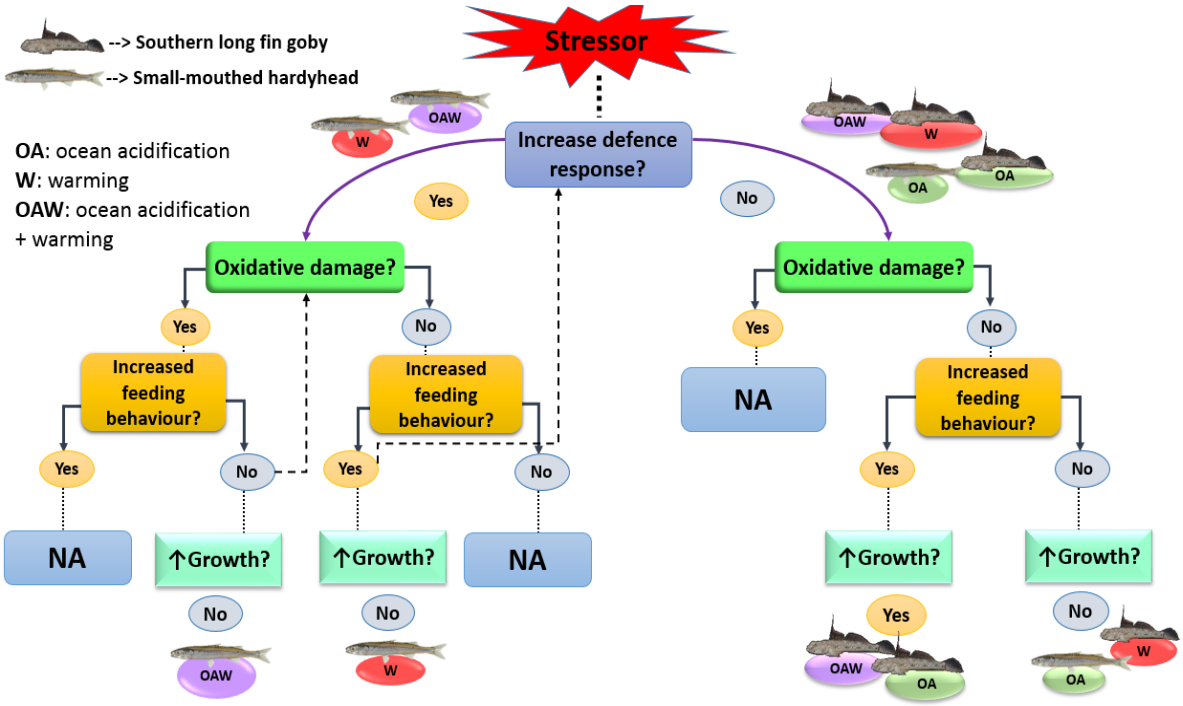

Figure 3. Summary of the effects of climate stressors on fish physiology and behaviour under *ad libitum* food supply based on the results from our experimental study. OA = ocean acidification, W = warming, OAW = combination of ocean acidification and warming, NA = Not applicable.

Where elevated temperature and CO_2 were combined, however, the antioxidant defence of hardyheads was insufficient to prevent cellular damage caused by oxidative stress (i.e. elevated MDA concentration), as also observed in other marine organisms (Feidantsis et al., 2015). The cellular damage incurred in such stressful environments may explain why the foraging behaviour of hardyheads was compromised (Bernier, 2006; Almeida et al., 2009; Bernier and Peter, 2001). For example, oxidative damage in fish exposed to cadmium was observed to reduce their food consumption and growth rate (Almeida et al., 2009). In our study, the lack of increased foraging behaviour impeded a higher production of antioxidants to prevent oxidative damage. Giordano et al. (2015) found evidence for decreased levels of oxidative damage in birds when food was provided, even when antioxidant levels were maintained. This suggests food may enable some organisms to downregulate their oxidative levels, if the conditions of their environment do not impair their rate of food intake.

Elevated CO_2 in isolation did not cause cellular damage in either species, and this was also the case for its combination with temperature or temperature alone in southern longfin gobies. No increase in antioxidant defence was observed and no oxidative damage incurred for these species-treatment combinations. Where feeding rates were maintained (hardyheads in elevated CO_2 and southern longfin gobies in elevated temperature), somatic growth was also maintained because the lack of energy expenditure for antioxidant defence allowed for the maintenance of their fitness traits. In contrast, where feeding rates increased (southern longfin gobies under elevated CO_2 with or without warming), somatic growth also increased. Bolder behaviour and increased activity in fish are some of the changes triggered by elevated CO_2 (Nilsson et al., 2012; Nagelkerken and Munday, 2016), which may be related to the increased feeding rates of southern longfin gobies exposed to ocean acidification. In vent ecosystems where CO_2 is naturally elevated, a boosting effect on primary and secondary production was found, which increased resources for benthic fish species that were able to take advantage of greater quantities of food (Nagelkerken et al., 2017; Doubleday et al., 2019). In natural systems, where resources are boosted (indirect effect) or where feeding rates increase (direct effect), species that are resilient to damage at cellular level can transform enhanced food intake into higher growth. Such adjustments may allow individuals to prevail in future oceans.

Our research did not cover physiological or behavioural responses of fish under food limitation or starvation. Studies have shown that deprivation of food can significantly increase the oxidative status of fish (Pascual et al., 2003; Zheng et al., 2016) and alter behavioural responses (Wang et al., 2019). However, the present study only considered a scenario where food resources were available without limitation, as has also been observed in some naturally CO_2–enriched environments where prey abundances are boosted (Nagelkerken et al., 2017; Doubleday et al., 2019).

By linking physiological indicators at a cellular and organismal level, we were able to describe multiple pathways of adaptive responses in fishes that adjust to environmental stress. These adaptive responses provide insight into possible feedback mechanisms at different levels or biological organisation, and an appreciation of species adaptability to future climate change conditions. Where such responses confer a competitive advantage on a species that can resist environmental change, they may alter the structure of communities (Nagelkerken et al., 2018). Indeed, those species that adapt at cellular and organismal levels or even take advantage of environmental change have a greater chance of becoming competitive dominants that displace their competitors.

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Author contributions

ARD, SC, and IN conceptualized the study. ARD and IN designed the mesocosm and aquarium experiments. ARD and JL performed some of the laboratory analyses. ARD

analysed the data and performed the statistical analyses. IN and SC supervised the project. ARD, JL, SC, and IN wrote the manuscript.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2019.07.226.

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Supplementary Material

Table S1. Results of the ANOVAs and MANOVAs for the physiological, fitness, and behavioural indicators of the southern longfin gobies.

	df	Mean square	F	*p*	Pairwise comparisons
TAC					
OA	1	1.53×10^{-3}	0.130	0.714	
Warming	1	6.28×10^{-4}	5.33×10^{-2}	0.819	
OA x Warming	1	4.59×10^{-2}	3.89	0.067	
Residuals	20	1.18×10^{-2}			
MDA					
OA	1	1.44×10^{-3}	1.44×10^{-3}	0.971	
Warming	1	0.59	0.590	0.465	
OA x Warming	1	0.76	0.767	0.405	
Residuals	20	19.93			
Feeding behaviour					
OA	1	0.76	4.309	**0.044**	
Warming	1	1.65×10^{-2}	9.40×10^{-2}	0.763	
OA x Warming	1	7.28×10^{-2}	0.416	0.513	
Residuals	39	0.18			
Activity levels					
OA	1	26.35	6.836	**0.012**	
Warming	1	23.18	6.014	**0.016**	
OA x Warming	1	3.18	0.825	0.374	
Residuals	39	3.85			
RNA/DNA					
OA	1	8.54×10^{-2}	5.815	**0.027**	
Warming	1	6.37×10^{-3}	0.434	0.511	
OA x Warming	1	2.10×10^{-2}	1.431	0.246	
Residuals	20	1.47×10^{-2}			
Delta weight					
OA	1	0.32	2.831	0.154	
Warming	1	0.13	1.116	0.327	

OA x Warming	1	5.31×10^{-2}	0.463	0.503
Residuals	6	0.115		
Multivariate (RNA/DNA - Delta Weight)				
OA	1	2220.9	3.096	0.057
Warming	1	891.08	1.242	0.293
OA x Warming	1	247.14	0.345	0.804
Residuals	6	717.3		
OA	1	2220.9	3.416	**0.037**
Warming	1	983.45	1.513	0.202
Pooled Res + OA x Warming	7	650.13		
GSI				
OA	1	8.04×10^{-2}	0.37	0.557
Warming	1	5.81×10^{-2}	0.267	0.620
OA x Warming	1	0.222	1.022	0.326
Residuals	37	0.217		
HSI				
OA	1	1.32×10^{-5}	4.64×10^{-3}	0.949
Warming	1	3.39×10^{-3}	1.194	0.284
OA x Warming	1	5.82×10^{-3}	2.046	0.156
Residuals	36	2.84×10^{-3}		
Fulton's condition factor				
OA	1	0.182	2.306	0.145
Warming	1	0.11	1.416	0.249
OA x Warming	1	4.53×10^{-2}	0.576	0.465
Residuals	20	7.88×10^{-2}		

df = degrees of freedom; C = control; OA = ocean acidification; W = warming; OAW = combination of ocean acidification and warming. TAC = total antioxidant capacity; MDA = malondialdehyde; GSI = gonadosomatic index; HSI = hepatosomatic index. Bold numbers indicate significant ($p<0.05$) differences.

Table S2. Results of the ANOVAs and MANOVAs for the physiological, fitness, and behavioural indicators of the small-mouthed hardyheads.

	df	Mean square	F	*p*	Pairwise comparisons
TAC					
OA	1	7.67×10^{-2}	0.6	0.443	
Warming	1	0.61	4.77	**0.036**	
OA x Warming	1	5.83×10^{-3}	4.58×10^{-2}	0.83	
Residuals	20	0.13			
MDA					
OA	1	26.54	11.13	**0.003**	
Warming	1	8.59	3.6	0.072	
OA x Warming	1	12.08	5.07	**0.033**	C - N.S.- W OAW > OA C - N.S.- OA OAW > W
Residuals	20 23	47.7			
Feeding behaviour					
OA	1	0.663	2.823	0.097	
Warming	1	0.52	2.231	0.133	
OA x Warming	1	2.09	8.923	**0.002**	W > C OA - N.S.- OAW OA - N.S.- C W > OAW
Residuals	70	0.235			
Activity levels					
OA	1	106.97	26.531	**0.0001**	
Warming	1	57.52	14.233	**0.0002**	
OA x Warming	1	17.8	4.415	**0.0389**	W > C OA - N.S.- OAW OA > C W - N.S.- OAW
Residuals	70	4.03			
RNA/DNA					
OA	1	9.22×10^{-4}	9.49×10^{-3}	0.922	

Warming	1	0.143	1.47	0.242	
OA x Warming	1	2.08×10^{-2}	0.214	0.660	
Residuals	20				
Delta weight					
OA	1	5.31×10^{-2}	2.393	0.251	
Warming	1	1.01×10^{-2}	0.456	0.574	
OA x Warming	1	3.48×10^{-2}	1.569	0.293	
Residuals	4	2.22×10^{-2}			
Multivariate (RNA/DNA - Delta Weight)					
OA	1	7.25×10^{-2}	1.412	0.378	
Warming	1	4.78×10^{-2}	0.937	0.423	
OA x Warming	1	1.49×10^{-2}	0.292	0.768	
Residuals	4	5.10×10^{-2}			
GSI					
OA	1	8.19×10^{-3}	8.58×10^{-2}	0.765	
Warming	1	1.02×10^{-3}	1.07×10^{-2}	0.920	
OA x Warming	1	0.188	1.965	0.169	
Residuals	48	9.55×10^{-2}			
HSI					
OA	1	2.02×10^{-6}	1.61×10^{-2}	0.971	
Warming	1	4.77×10^{-3}	3.797	**0.046**	
OA x Warming	1	5.17×10^{-3}	4.115	**0.040**	C - N.S.- W OAW > OA C > OA OAW - N.S.- W
Residuals	21	2.64×10^{-2}			
Fulton's condition factor					
OA	1	0.623	1.158	0.354	
Warming	1	0.68	1.256	0.308	
OA x Warming	1	0.61	1.134	0.352	
Residuals	21	0.538			

df = degrees of freedom; C = control; OA = ocean acidification; W = warming; OAW = combination of ocean acidification and warming. TAC = total antioxidant capacity; MDA = malondialdehyde; GSI = gonadosomatic index; HSI = hepatosomatic index. Bold numbers indicate significant ($p<0.05$) differences. N.S. = No significant differences.

Chapter IV- Testing inter-specific response to ocean warming and ocean acidification – a meta-analysis

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Co-Author Contributions

By signing the Statement of Authorship, each author certifies that:

i. the candidate's stated contribution to the publication is accurate (as detailed above);

ii. permission is granted for the candidate in include the publication in the thesis; and

iii. the sum of all co-author contributions is equal to 100% less the candidate's stated contribution.

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Abstract

The continuous exposure of marine organisms to increasing temperatures and acidify conditions in the ocean are having an impact on important fitness traits. The distinct responses display by species in responses to environmental changes will depend on their specific sensitivity to stressors. We perform a meta-analysis to determine the effects of ocean acidification and ocean warming on the growth and survival of marine organisms and test if those effects are driven by life history factors. The results revealed negative responses in growth for calcifying heterotroph organisms and positive responses for non-calcifying autotrophs. We also found a negative effect of ocean acidification, warming, and their combination on the survival of egg and larva stages. These responses found for growth and survival only explain a small amount of the heterogeneity across studies. The large variety of species and taxonomic groups included in the analysis can be responsible for the great amount of unexplained variability. Organisms' responses to climate changes will not be uniform across taxa as each has specific physiological requirements. Assessing the role that different variables will play on species responses to future climate changes will help making more accurate predictions on community responses.

Introduction

The current rate of increase in atmospheric CO_2 concentrations is driving environmental change at an unprecedented rate, modifying the ocean temperature and acidity. Ocean warming and ocean acidification are anticipated to pose stressful environmental conditions for a variety of marine organisms (Byrne, 2011; Pörtner et al., 2014). Such physico-chemical change can influence an organisms' metabolism, growth, productivity, reproduction, and ultimately survival (Pimentel et al., 2016; Wittman and Pörtner, 2013). Yet, variable responses are anticipated among species. Every species presents a unique body plan with functional specialization that provides varying capacity (physiological and ecological traits) to adjust to environmental change (Pörtner, 2010; Harvey et al., 2013; Wittman and Pörtner, 2013). As a result, the magnitude and direction of species responses tend to differ in response to climatic stressors (Harvey et al., 2013) and understanding these differences is important to predicting future population and community dynamics.

Primary producers, in particular, show a wide range of responses to warming and acidification. Some are positively affected by warming within certain parts of their seasonal cycle (Henson et al., 2016), and whilst others are negatively affected (Richardson and Schoeman, 2004; Peter and Sommer, 2012; Osman et al., 2019). The effects of elevated CO_2 can favour primary productivity by stimulating photoshynthesis (Gao et al., 2019), but negatively affect calcifying macroalgae and coccolithophores (calcareous phytoplankton) as their calcite production is reduced by acidity (Riebesell et al., 200; Gao et al., 2019). Where temperature and ocean acidification combine, they can interact to promote growth of non-calcifying primary producers (Fu et al., 2007, Kremp et al., 2012, Gao et al., 2019), but reduce the growth rate and calcification of coccolithophores (Schluter et al., 2014; Gao et al., 2019).

Both ocean warming and acidification can exert heavy costs and negative influences on the growth and survival of calcifying organisms. Excessive warming has caused extensive coral bleaching events that result in increased mortality of coral species (Hughes et al., 2017; Hughes et al., 2018). Yet, such negative effects are not universal for calcifiers. Short-lived coralline algae can be resilient to warming, as their short generation time increases their ability to acclimatize (Cornwall et al., 2019, whilst longer life spans are less resilient (Cornwall et al., 2019). Many calcifiers maybe more vulnerable to the effects of elevated CO_2 levels compared to non-calcifying groups, as their capacity to produce their calcified structures is impaired (Marubini, et al., 2003; Doney et al., 2009), but some are able to adjust their shell-building to adapt to acidity with stronger and tougher shells (Leung et al. 2019).

Species responses to environmental changes also differ among their life stages. Early life stages are considered to be more vulnerable to variability in ocean temperatures and pH levels (Byrne, 2011; Harvey et al., 2013). The smaller size of eggs and larvae confines them with a larger surface to volume ratio, and their organs are less developed than adults, which adds to their vulnerability to abiotic stressors (Byrne, 2011; Przeslawski et al., 2015; Marshall et al., 2016).

Species with different nutrition modes (autotrophs and heterotrophs) also show differences in their responses to multi-stressors. For instance, Crain et al. (2008) found antagonistic effects of climatic stressors in autotrophs, and synergistic effects in heterotrophs. Life span

will also determine how species react to changes in the environment as species with shorter life span have greater potential to acclimate than long-lived species. Species with short life span present fast generation time and usually large populations, which can enable faster genetically responses and improve their scope for micro-evolution (Balanya et al., 2006; Hetem et al., 2014). Finally, is also important to consider the time organisms are exposed to a stressor, as they can acclimate to environmental changes with longer exposure times (Harvey et al., 2013).

We currently lack in knowledge of which life history traits shape the species responses when undergoing ocean acidification and warming, and the direction of their response (positive, neutral, or negative). Such responses to climatic stressors can indicate if a taxonomic or functional group is more resistant or vulnerable than other groups. We analysed peer-review articles to assess how taxa vary in key fitness responses to ocean warming and acidification. The effect of distinct categories link to species life history were included (treatment, taxa, trophic level, life stage, life span, and treatment exposure time) and analysed to determine which variable had a greater influence on the growth and survival of marine species.

Materials and methods

Study selection and data criteria

We searched for peer-reviewed publications investigating the effect of global change stressors on growth and survival of marine species, focussing on ocean acidification, temperature and the combination of both stressors. We conducted a literature search using Clarivate Analytics Web of Science using the key words: Ocean acidification; AND temperature or warming; AND survival or mortality or grow*. Given that unicellular organisms such as phytoplankton and bacteria growth can also be measured in terms of abundance a second search was made. The key words for the second search were: Ocean acidification; AND temperature or warming; AND phytoplankton or bacteri*; AND abundance or densit*.

The search was based on studies published through to 14th of February 2019 (search for growth and survival), and 18th of February 2019 (search for abundance of unicellular organisms). Only studies that included a control group treatment and a factorial design with

ocean acidification and temperature were included for the analysis. When additional environmental stressors where included in the publications (i.e. salinity, nutrients), only the ambient levels where considered for the analysis. Studies also needed to include the sample size of each treatment, and some measure of variance that could be transformed to a standard deviation if not already provided.

Growth and survival were chosen as the response variables for the analysis. Growth was included whether this was presented as the increase in weight or length of the organism(s); following previous meta-analyses procedures if both measures were included in a study, then only biomass measurements were selected, as it was consider the most inclusive metric for growth (Kroeker et al., 2010; Kroeker et al., 2013). Calcification studies where only selected if they were measured as buoyant weight increases. However if calcification was measured as calcifying rate the studies were not considered for the analysis to reduce the risk of including measurements of net calcification. In addition, studies for phytoplankton and bacteria also were considered when abundance or density had been measured. Survival studies were usually presented as proportions, mortality studies were also included in the analysis and converted to survival.

When data for more than one species or experiment were presented in the same study they were all included in the analysis if they met the above selection criteria. This addition could reduce the independence of some data points, but it allowed analysing a wider range of species responses (Kroeker et al., 2010). Where multiple time points where included we selected the last one with greater exposure time for the analyses. The data from the selected studies was taken from the published values or it was extracted from the figures using WEBPLOTDIGITIZER software (https://apps.automeris.io/wpd/).

During data extraction, we recorded the life stage of the species (egg, larvae, juvenile, adult), the nutrition mode (autotrophs vs heterotrophs), taxon, calcification (calcifying vs. non calcifying), their life span, and treatment exposure time. These variables were included in the analyses as moderators.

Meta-analyses

Before the data from the selected studies could be analysed we calculated their effect sizes so that the data were standardized to a uniform scale. For growth, the effect size was

calculated using the standardized mean difference (SMD), based on Hedges g statistic (Hedges, 1981). SMD allows testing the effect size for the difference between two means (control vs. experimental treatment)

$$SMD = \frac{M1 - M2}{SD * pooled}$$

Where:

M1 – M2 = difference in means;

SD^*_{pooled} = pooled and weighted standard deviation.

For survival, the effect size was estimated using the transformed standardized mean difference into log odds ratio (Borenstein et al., 2009) which allowed us to work with proportion values.

$$LogOddsRatio = SMD\frac{\pi}{\sqrt{3}}$$

Where:

π = 3.1416

SMD = Standardized mean difference.

Separate analyses for growth and survival were carried out using R-Studio v.3.6.0, using the rma.mv function within the "Metafor" package (Viechtbauer, 2010).

We fitted a three-level random-effects meta-analysis, where three components of variance are considered: variance between effect sizes from the same study, variance between studies, and sampling variance (Cheung, 2014; Assink and Wibbelink, 2016). We adopted a three-level approach because the use of effect sizes from within the same study provides greater statistical power (Assink and Wibbelink, 2016). A likelihood ratio test was used to assess between-study and within-study heterogeneity (Raudenbush, 2009). If there was significant variation between effect sizes from the same study or between studies, then moderator analyses were conducted to test for additional explanatory variables. We applied the Knapp and Hartung's (2003) adjustment to control for Type I error, where the *t*-distribution was used to test individual coefficients (no explanatory variables). For moderator analyses the omnibus test was performed, with the Knapp and Hartung's (2003) adjustment which uses an F-distribution.

The explanatory variables included in the moderator analyses were: treatment, life stage, nutrition mode, taxa, and calcification as categorical factors, and life span and treatment exposure time as continuous variables. We performed a random-effects metaregression to test which of the explanatory variables were more important for the observed changes in growth and survival. Before analysing the metaregression model we minimized the number of investigated predictors to select the most parsimonious model. We used an automated model selection (MuMIN-R package), where the best model was the one that with the lowest corrected Akaike Information Criteria (AICc) and had the highest AICc weights. When several metaregression models presented similar probabilities we proceeded with a multimodel inference. The inference of various explanatory variables takes into account the weight of all possible models, and then ranks the importance of each variable. We chose a variable importance threshold of 80%, where a score smaller than the threshold value represented an unimportant predictive variable (Calcagno and de Mazancourt, 2010).

We tested the possible effects of publication bias in the analysis by estimating Rosenthal and Rosenberg unweighted fail-safe numbers (Rosenthal 1979, Orwin 1983, Rosenberg 2005). These analyses indicate the number of non-significant effect sizes that are necessary to make significant patterns non-significant (Rosenthal 1979, Orwin 1983). Larger values of fail-safe numbers indicate more robust results. Fail-safe numbers greater than 5*N + 10 (Rosenthal, 1979, N = sample size), were considered to be robust against publication bias.

Results

We included a total of 187 studies in the meta-analysis, from which 53 studies were used for the survival analysis and 172 studies were used for the growth analysis. Growth and survival analyses presented fail-safe numbers (Rosenthal and Rosenberg) larger than the 5*N + 10 threshold, which indicates robustness against sampling bias (Table S2).

We found that the effect sizes differed significantly within ($p<0.01$) and between ($p<0.01$) studies for growth and survival. Thus, we proceeded with the moderator analyses and AICc tests.

The meta-analysis of growth revealed that the most parsimonious meta-regression model (AICc test) included calcification and nutrition mode. When examining the meta-

regression model we found that autotrophs had an overall positive response, but it was only significant for non-calcifying autotrophs ($p<0.001$, Fig. 1a, b). However, seven additional meta-regression models were also selected to be as parsimonious as the first model, as they presented AIC values within 2 delta units (Table 1). Only a small percentage of the heterogeneity (R^2= 2.1%, for most parsimonious meta-regression model) across studies was explained by the models (Table 1). We proceeded with a multimodel inference, where we rank the importance of each variable, and found that calcification had the highest weight as an explanatory variable, but with an importance score of 71%, and taxa had the lowest score <10% (Fig. 3). None of the variables reached the 80% threshold for their importance scores. The averaged model showed no significant responses for either of the explanatory variables (Table S3).

The meta-analysis of survival revealed that the most parsimonious metaregression model (AICc test) included treatment and life stage. This model showed that egg and larvae stages presented a negative and significant ($p<0.04$) response to ocean acidification, temperature, and their combination (Fig. 2a, b, c). However, four additional models were within 2 delta units and were considered just as parsimonious as the first model. The models for survival also explained only a small percentage of the heterogeneity across studies (Table 2). The multimodel inference ranked treatment as the most important explanatory variable, and it had an importance value of 81% (Fig. 4). The averaged model showed a significant negative effect for the egg and larva life stages ($p<0.04$), and for ocean acidification ($p<0.01$) and the combination of ocean acidification and temperature treatments ($p<0.5$; Table S4).

Table 1. Most parsimonious meta-regression models for the effects of ocean warming and acidification on growth in marine species.

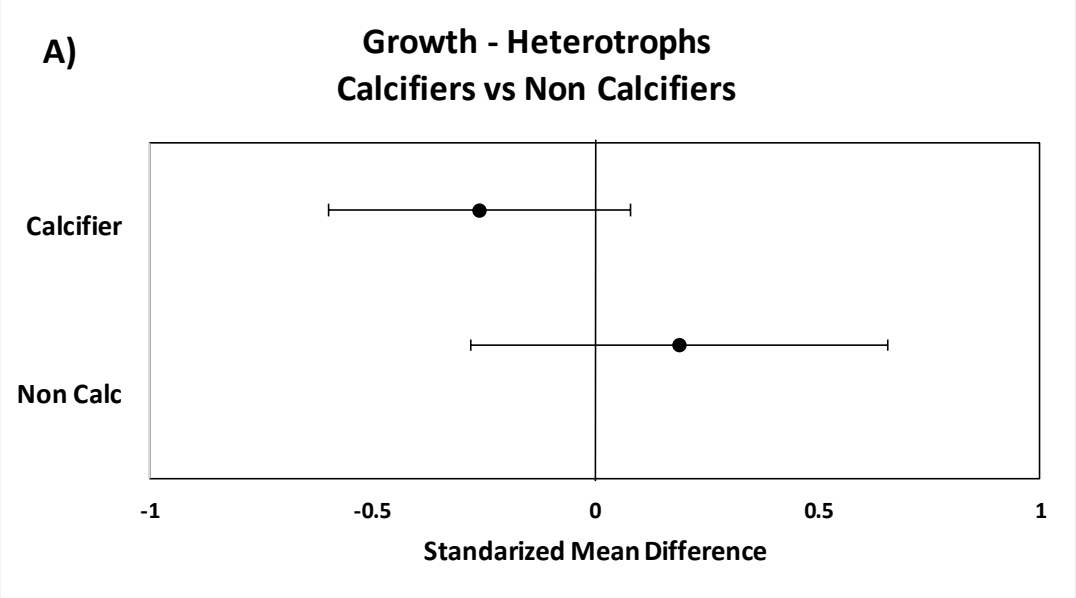
	Model			AICc	Delta	Weights	R^2
1	yi ~ 1 + Calcifier + NutritionMode	4071.073	9.954163e-02	4071.1	0.00	0.102	2.1
2	yi ~ 1 + Calcifier + log(L.span)	4071.219	9.251090e-02	4071.2	0.15	0.095	1.6
3	yi ~ 1 + Calcifier	4072.045	6.120444e-02	4072.0	0.97	0.063	1.5
4	yi ~ 1 + Calcifier + NutritionMode + log(L.span)	4072.138	5.843741e-02	4072.1	1.07	0.060	2
5	yi ~ 1 + NutritionMode	4072.274	5.458175e-02	4072.3	1.2	0.050	1.8
6	yi ~ 1 + NutritionMode + log(L.span)	4072.450	4.999690e-02	4072.5	1.38	0.051	1.7
7	yi ~ 1 + Treatment + Calcifier + NutritionMode	4072.480	4.925511e-02	4072.5	1.41	0.051	2.2
8	yi ~ 1 + Treatment + Calcifier + log(L.span)	4072.637	4.552823e-02	4072.6	1.56	0.047	1.7

AICc: corrected Akaike Information Criteria; R^2: proportiono f variance explain by the model; Calcifier: calcification mode (calcifier vs non-calcifier); Nutrition mode: autotroph vs heterotroph; L.span: life span; Treatment: ocean acidification, temperature, combination of ocean acidificaiton and temperature.

Table 2. Most parsimonious meta-regression models for the effects of ocean warming and acidification on survival in marine species.

	Model	AICc	Delta	Weights	R^2
1	yi ~ 1 + Treatment + L.stage	1192.8	0.00	0.102	4.7
2	yi ~ 1 + Treatment + log(exposure)	1192.8	0.08	0.098	1.4
3	yi ~ 1 + Treatment + L.stage + log(exposure)	1194.0	1.20	0.056	4.4
4	yi ~ 1 + Treatment + Calcifier + log(exposure)	1194.1	1.33	0.053	1.6
5	yi ~ 1 + Treatment + L.stage + log(L.span)	1194.2	1.41	0.051	5.8

AICc: corrected Akaike Information Criteria; R^2: proportiono f variance explain by the model; Treatment: ocean acidification, temperature, combination of ocean acidificaiton and temperature; L.stage: life stage; exposure: time exposed to treatment; Calcifier: calcification mode (calcifier vs non-calcifier); L.span: life span.



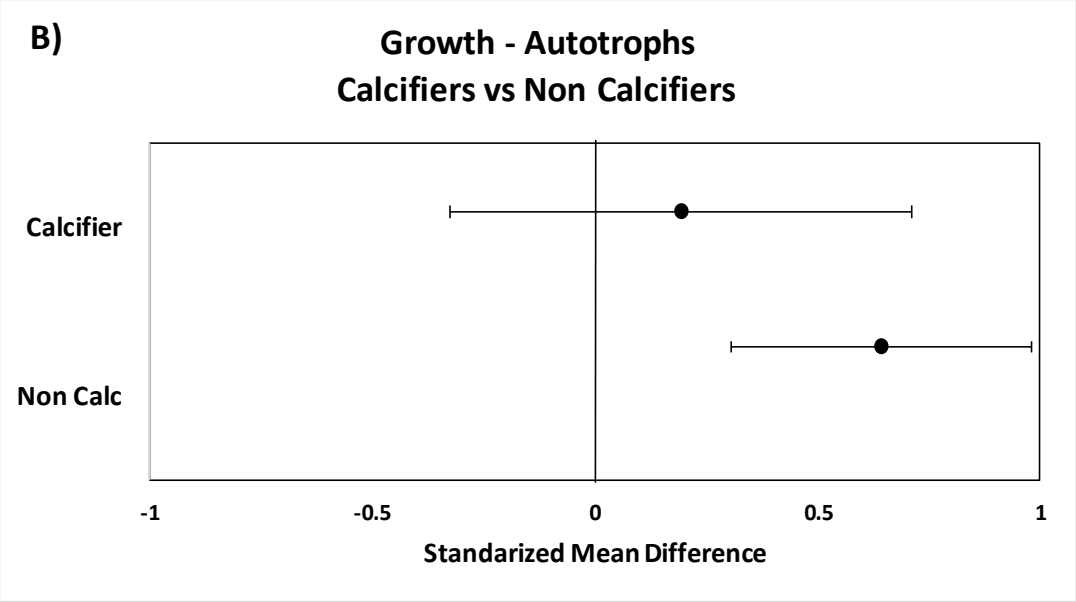
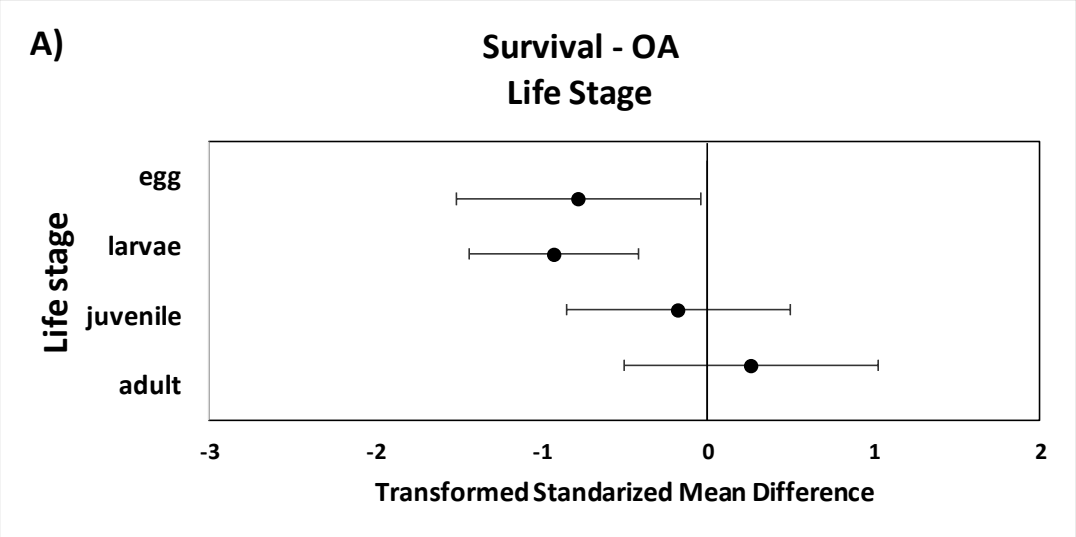
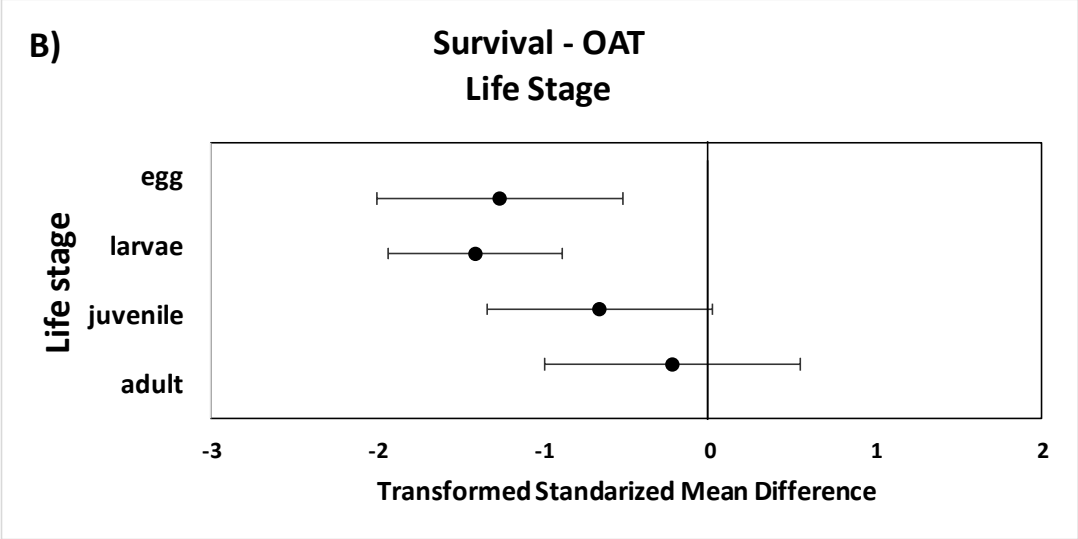


Figure 1. Estimates effects of growth meta-regression with nutrition mode and calcifying mode as moderators. A) Heterotrophs; B) Autotrophs. Error bars represent 95% confidence intervals.





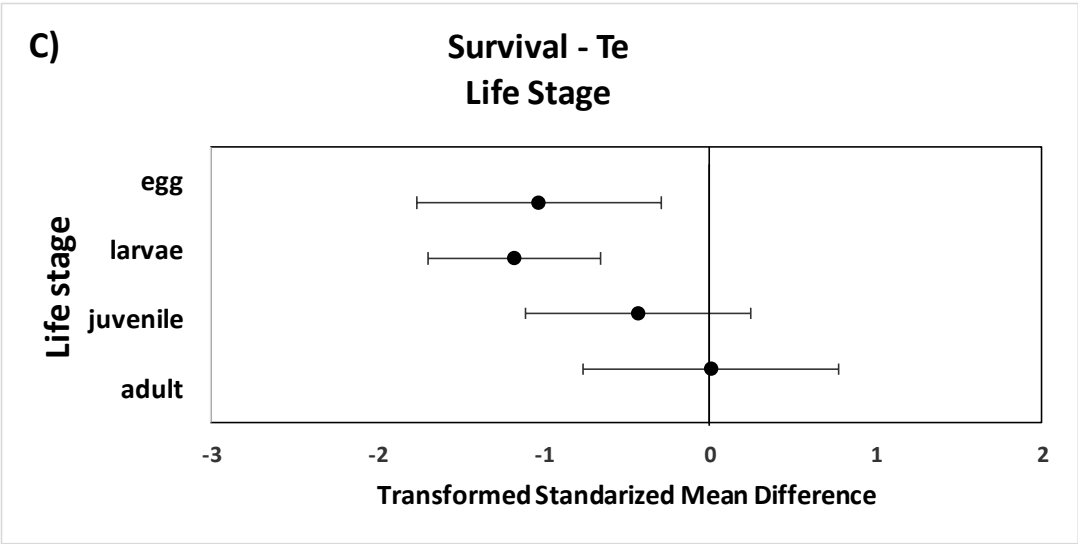


Figure 2. Estimates effects of survival meta-regression with treatment and life stage as moderators. A) Ocean acidification; B) Ocean acidification + Temperature; C) Temperature. Error bars represent 95% confidence intervals.

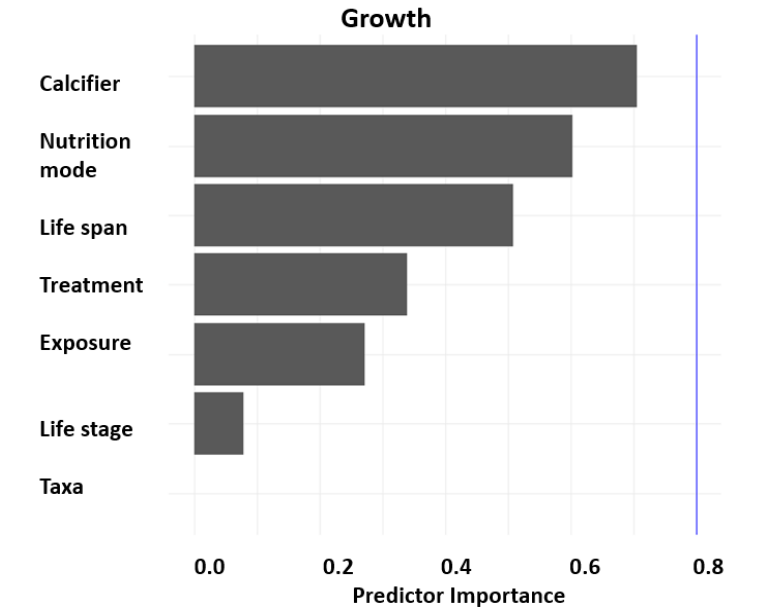


Figure 3. Explanatory variables importance score for growth meta-analysis

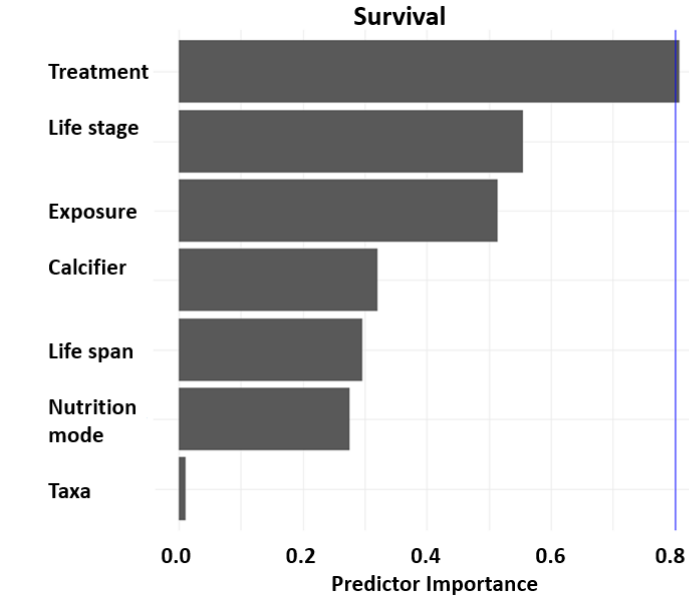


Figure 4. Explanatory variables importance score for survival meta-analysis

Discussion

Our meta-analysis sought to understand key drivers of heterogeneity of growth and survival of marine animals experiencing climatic change. Yet, the variables included in our models only explained a small percentage of the data variability. For growth, calcification mode was selected as the most important predictor variable. Calcifying organisms have been

predicted to be some of the most vulnerable groups to climatic changes, in particular to ocean acidification (Doney et al., 2009; Fitzer et al., 2015; Spalding et al., 2017). We found an overall negative on calcifying organism regardless of the treatment, and a positive effect for non-calcifying species, but neither of these responses was significant. Calcifying species can present different responses (positive or negative) to temperature and ocean acidification (Leung et al., 2017). Previous meta-analyses (Harvey et al., 2013; Kroeker et al., 2013) have found negative effects on calcifying organisms, especially for sessile and low-mobility species. Similarly, experiments and meta-analyses have found positive effects of climatic stressors on the growth of non-calcifying species, in particular on primary producers (Feng et al., 2009; Hancock et al., 2018). Coccolithophores for instance, can present negative responses in their calcifiying rates (Meyer and Riebesell, 2015), but also increases in calcification have been reported (Iglesias-Rodriguez et al., 2008; Shi et al., 2009). On the other hand, non-calcifying primary producers can benefit from elevated levels of CO_2 as a resource for photosynthesis (Gao et al., 2019). In our analysis the large number of categories (n = 18 taxa) included in the variable "taxa" may be responsible for the low predictive score. The requirements of each species to maintain their optimal fitness can influence the inter- and intra specific responses to stressors. Uniform responses across species are unlikely to occur (Harley et al., 2017). Understanding which functional-groups would be most affected and the direction of change may help identify differences in species sensitivities to environmental change. Such functional-group responses could influence community dynamics and ecosystem function.

Analysis of survival identified 'treatment' as the most important predictive variable. When we averaged the models we found that the early life stages (eggs and larvae) showed the strongest effect to the environmental stressors. Previous meta-analyses have also found early life stages to be more sensitive to the effects of climate change (Koeker et al., 2013; Harvey et al., 2013; Pandori et al., 2019). During these vulnerable life stages, physiological functions are not fully developed and energy reserves are not sufficient to support repair of cellular processes in response to environmental change (Pandori et al., 2019; Bulnheim 1974). Similar to the analysis of growth, we included a large number of categorical taxa (12) for the survival meta-analysis, which can also be responsible for the low importance

score for taxa and for the large amount of unexplained variability found in the moderator meta-regressions.

The differences in species-specific responses to global stressors can be more pronounced in certain taxonomic groups than others, and this variation pose challenges to detecting the effects of environmental change (Kroeker et al., 2010). We included a variety of species in our analysis, for which distinct functional groups were incorporated as predictive variables of heterogeneity. A greater variety of species tend to present a greater variety of responses to simulated climate changes due to inter-specific differences in physiological requirements and functions. In addition, other predictive variables not included in this study could have acted as sources of heterogeneity (i.e. behavioural responses or food ratios). In a time of climate change and ocean acidification, it is essential to identify the different drivers that dictate responses of species fitness traits. Understanding which variables will play an essential role in shaping populations in the future will aid in making more accurate predictions for community-level responses and aid in guiding species management approaches.

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Supplementary Information

Table S1. Taxanomic groups included in the meta-analyses of growth and survival

Taxa	Growth	N	Survival	N
Bacteria	✓	12		
Bryozoa	✓	2		
Cephalopod	✓	1	✓	2
Coral	✓	7	✓	3
Crustacean	✓	8	✓	7
Echinoids	✓	15	✓	6
Fish	✓	16	✓	11
Foraminifer	✓	1	✓	1
Jellyfish	✓	2	✓	2
Macroalgae	✓	29	✓	3
Macroalgae (Cca)	✓	8		
Mollusc	✓	33	✓	15
Phytoplankton	✓	27		
Phytoplankton (Coccolithophore)	✓	8		
Polychaete	✓	3	✓	1
Seagrass	✓	1		
Sponges	✓	3	✓	1
Zooplankton	✓	2	✓	1

N = number of studies used for the analyses

Table S2. Rosenthal and Rosenberg fail-safe numbers for growth and survival meta-analyses

	Fail-safe numbers		
	Rosenthal	Rosenberg	5N + 10 criterion
Growth	10550	3451	870
Survival	13753	2210	275

Table S3. Growth, model-averaged coefficients

	Estimate	Std. Error	z value	Pr(>|z|)	
CalcifierN	0.280378	0.265071	1.058	0.2902	
CalcifierY	-0.207589	0.228973	0.907	0.3646	
NutritionM.A	0.437701	0.256650	1.705	0.0881	.
log(L.span)	-0.062383	0.044004	1.418	0.1563	
NutritionM.H	-0.131775	0.217805	0.605	0.5452	
TreatmentOAT	0.242558	0.151408	1.602	0.1092	
TreatmentTemp	0.174271	0.150816	1.156	0.2479	
log(exposure)	0.003494	0.098557	0.035	0.9717	
TreatmentOA	0.107443	0.152037	0.707	0.4798	
L.stageegg	0.317983	0.960538	0.331	0.7406	
L.stagejuvenile	0.321568	0.352316	0.913	0.3614	
L.stagelarvae	0.093696	0.346511	0.270	0.7869	
L.stageadult	0.187720	0.190060	0.988	0.3233	
taxabacteria	1.210926	0.642625	1.884	0.0595	.
taxabryozoa	-0.222988	1.545672	0.144	0.8853	
taxacephalopod	-1.512617	1.786812	0.847	0.3972	
taxacoral	-1.553662	1.284483	1.210	0.2264	
taxacrustacean	0.113322	1.248158	0.091	0.9277	
taxacrustacean (barnacle)	-0.384440	1.517712	0.253	0.8000	
taxaechinoids	0.350668	1.154339	0.304	0.7613	
taxafish	-0.373527	0.926968	0.403	0.6870	
taxaforaminifer	-2.497007	1.749419	1.427	0.1535	
taxajellyfish	-1.366226	1.395417	0.979	0.3275	
taxamacroalgae	-0.366978	0.801659	0.458	0.6471	
taxamacroalgae (CCA)	-1.067001	1.218286	0.876	0.3811	
taxamollusc	-0.440287	1.098163	0.401	0.6885	
taxaphytoplankton	0.218387	0.703826	0.310	0.7563	
taxaphytoplankton (coccolithophore)	-0.617869	1.138812	0.543	0.5874	
taxapolychaete	-0.079824	1.260449	0.063	0.9495	
taxaseagrass	-2.057713	1.781030	1.155	0.2479	
taxasponges	-0.761519	1.208381	0.630	0.5286	
taxazooplankton	-0.491327	1.135633	0.433	0.6653	

Signif. codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Std.Error: standard error; Pr(>|z|): probabilistic value for the Z-statistic; CalcifierN: non-calcifier; CalcifierY: calcifier; NutritionM.A: autotroph; NutritionM.H: heterotroph; L.span: life span; TreatmentOA: ocean acidification; TreatmentTemp: elevated temperature; TreatmentOAT: combination of ocean acidification and elevated temperature; exposure: treatment exposure time; L.stage: life stage.

Table S4. Survival, model-averaged coefficients

	Estimate	Std. Error	z value	Pr(>|z|)	
L.stageadult	0.08567	0.82379	0.104	0.91717	
L.stageegg	-1.90353	0.90153	2.111	0.03473	*
L.stagejuvenile	-0.78740	0.83397	0.944	0.34508	
L.stagelarvae	-2.08903	0.72951	2.864	0.00419	**
TreatmentOAT	-1.24337	0.62610	1.986	0.04704	*
TreatmentTemp	-0.76397	0.62463	1.223	0.22130	
log(exposure)	0.39287	0.26866	1.462	0.14365	
TreatmentOA	-1.37422	0.50311	2.731	0.00631	**
CalcifierN	-1.02485	1.16801	0.877	0.38025	
CalcifierY	-0.63587	0.95169	0.668	0.50404	
log(L.span)	0.10510	0.23019	0.457	0.64798	
NutritionM.H	-0.66604	1.07733	0.618	0.53643	
NutritionM.A	-0.11338	1.52180	0.075	0.94061	
taxacoral	4.12967	2.49546	1.655	0.09795	.
taxacrustacean	0.10797	2.31370	0.047	0.96278	
taxaechinoids	2.49724	2.32110	1.076	0.28198	
taxafish	1.29695	2.26288	0.573	0.56655	
taxaforaminifer	-0.10961	2.64815	0.041	0.96698	
taxajellyfish	3.32030	2.66505	1.246	0.21281	
taxamollusc	1.37551	2.20374	0.624	0.53252	
taxapolychaete	3.76259	2.95058	1.275	0.20224	
taxasponges	3.56970	3.04514	1.172	0.24109	
taxazooplankton	2.35645	3.05360	0.772	0.44029	
taxacephalopod	-4.35415	1.56175	2.788	0.00530	**
taxamacroalgae	0.78455	2.60901	0.301	0.76364	

Signif. codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Std.Error: standard error; Pr(>|z|): probabilistic value for the Z-statistic; L.stage: life stage; TreatmentOA: ocean acidification; TreatmentTemp: elevated temperature; TreatmentOAT: combination of ocean acidification and elevated temperature; exposure: treatment exposure time; CalcifierN: non-calcifier; CalcifierY: calcifier; NutritionM.A: autotroph; NutritionM.H: heterotroph.

Table S5. Studies and categories used for the growth meta-analysis

obs	study	author	year	journal	m1	sd1	n1	m2	sd2	n2	Treatment	Ecol.Level	L.stage	Calcifier	L.span	L.span1	Nutrition mode	Taxa	Exp
1	1	Achlatis	2017	Scientific Reports	41.0	4.7	7	39.3	3.5	7	OA	species	adult	N	100	>10	H	sponges	4
2	1	Achlatis	2017	Scientific Reports	41.0	4.7	7	38.3	6.1	7	Temp	species	adult	N	100	>10	H	sponges	4
3	1	Achlatis	2017	Scientific Reports	41.0	4.7	7	36.3	4.9	7	OAT	species	adult	N	100	>10	H	sponges	4
4	2	Anlauf	2011	JEMBE	18.0	10.0	27	15.0	7.3	13	OA	species	juvenile	Y	100	>10	H	coral	6
5	2	Anlauf	2011	JEMBE	18.0	10.0	27	14.8	2.5	5	Temp	species	juvenile	Y	100	>10	H	coral	6
6	2	Anlauf	2011	JEMBE	18.0	10.0	27	10.9	3.7	14	OAT	species	juvenile	Y	100	>10	H	coral	6
7	3	Anthony	2008	PNAS	2.4	1.3	15	2.1	3.0	15	OA	species	adult	Y	50	>10	A	macroalgae (CCA)	8
8	3	Anthony	2008	PNAS	12.2	3.5	25	10.1	3.5	25	OA	species	adult	Y	100	>10	H	coral	8
9	3	Anthony	2008	PNAS	12.2	5.4	15	10.8	5.4	15	OA	species	adult	Y	100	>10	H	coral	8
10	3	Anthony	2008	PNAS	2.4	1.3	15	3.3	2.2	15	Temp	species	adult	Y	50	>10	A	macroalgae (CCA)	8
11	3	Anthony	2008	PNAS	12.2	3.5	25	9.7	3.8	25	Temp	species	adult	Y	100	>10	H	coral	8
12	3	Anthony	2008	PNAS	12.2	5.4	15	9.6	4.0	15	Temp	species	adult	Y	100	>10	H	coral	8
13	3	Anthony	2008	PNAS	2.4	1.3	15	1.4	3.0	15	OAT	species	adult	Y	50	>10	A	macroalgae (CCA)	8
14	3	Anthony	2008	PNAS	12.2	3.5	25	9.7	6.3	25	OAT	species	adult	Y	100	>10	H	coral	8
15	3	Anthony	2008	PNAS	12.2	5.4	15	11.5	5.4	15	OAT	species	adult	Y	100	>10	H	coral	8
16	4	Alguero-Muniz	2016	Marine Biology	7.5	1.4	5	7.6	1.3	5	OA	species	larvae	N	25	>10	H	jellyfish	1
17	4	Alguero-Muniz	2016	Marine Biology	7.5	1.4	5	5.4	0.3	5	Temp	species	larvae	N	25	>10	H	jellyfish	1
18	4	Alguero-Muniz	2016	Marine Biology	7.5	1.4	5	4.8	1.8	5	OAT	species	larvae	N	25	>10	H	jellyfish	1
19	5	Armstrong	2017	Marine Biology	1.6	5.0	3	3.6	6.0	3	OA	species	egg	Y	1.6	1 to 10	H	mollusc	0.4
20	5	Armstrong	2017	Marine Biology	1.6	5.0	3	11.7	6.7	3	Temp	species	egg	Y	1.6	1 to 10	H	mollusc	0.4
21	5	Armstrong	2017	Marine Biology	1.6	5.0	3	8.9	3.9	3	OAT	species	egg	Y	1.6	1 to 10	H	mollusc	0.4
22	6	Arnold	2013	Global Change Biology	5.0	0.2	2	4.9	0.1	2	OA	species	adult	Y	0.14	<1	A	phytoplankton (coccolithophore)	0.6
23	6	Arnold	2013	Global Change Biology	5.0	0.2	2	4.3	0.1	2	Temp	species	adult	Y	0.14	<1	A	phytoplankton (coccolithophore)	0.6
24	6	Arnold	2013	Global Change Biology	5.0	0.2	2	4.2	0.0	2	OAT	species	adult	Y	0.14	<1	A	phytoplankton (coccolithophore)	0.6
25	7	Baragi	2015	JEMBE	304.4	12.2	3	304.4	12.2	3	OA	species	larvae	Y	6	1 to 10	H	crustacean	0.6
26	7	Baragi	2015	JEMBE	380.9	7.0	3	337.4	5.2	3	OA	species	larvae	Y	6	1 to 10	H	crustacean	0.6
27	7	Baragi	2015	JEMBE	394.8	7.0	3	375.7	12.2	3	OA	species	larvae	Y	6	1 to 10	H	crustacean	0.6
28	7	Baragi	2015	JEMBE	441.7	47.0	3	457.4	31.3	3	OA	species	larvae	Y	6	1 to 10	H	crustacean	0.6
29	7	Baragi	2015	JEMBE	554.8	15.7	3	514.8	5.2	3	OA	species	larvae	Y	6	1 to 10	H	crustacean	0.6
30	7	Baragi	2015	JEMBE	490.4	7.0	3	471.3	15.7	3	OA	species	larvae	Y	6	1 to 10	H	crustacean	0.6
31	7	Baragi	2015	JEMBE	304.4	12.2	3	304.4	12.2	3	Temp	species	larvae	Y	6	1 to 10	H	crustacean	0.6
32	7	Baragi	2015	JEMBE	380.9	7.0	3	346.1	13.9	3	Temp	species	larvae	Y	6	1 to 10	H	crustacean	0.6
33	7	Baragi	2015	JEMBE	394.8	7.0	3	384.4	12.2	3	Temp	species	larvae	Y	6	1 to 10	H	crustacean	0.6
34	7	Baragi	2015	JEMBE	441.7	47.0	3	408.7	36.5	3	Temp	species	larvae	Y	6	1 to 10	H	crustacean	0.6
35	7	Baragi	2015	JEMBE	554.8	15.7	3	495.7	60.9	3	Temp	species	larvae	Y	6	1 to 10	H	crustacean	0.6

36	7	Baragi	2015	JEMBE	490.4	7.0	3	438.3	13.9	3	Temp	species	larvae	Y	6	1 to 10	H	crustacean	0.6
37	7	Baragi	2015	JEMBE	304.4	12.2	3	304.4	12.2	3	OAT	species	larvae	Y	6	1 to 10	H	crustacean	0.6
38	7	Baragi	2015	JEMBE	380.9	7.0	3	363.5	13.9	3	OAT	species	larvae	Y	6	1 to 10	H	crustacean	0.6
39	7	Baragi	2015	JEMBE	394.8	7.0	3	405.2	24.4	3	OAT	species	larvae	Y	6	1 to 10	H	crustacean	0.6
40	7	Baragi	2015	JEMBE	441.7	47.0	3	445.2	17.4	3	OAT	species	larvae	Y	6	1 to 10	H	crustacean	0.6
41	7	Baragi	2015	JEMBE	554.8	15.7	3	532.2	7.0	3	OAT	species	larvae	Y	6	1 to 10	H	crustacean	0.6
42	7	Baragi	2015	JEMBE	490.4	7.0	3	488.7	7.0	3	OAT	species	larvae	Y	6	1 to 10	H	crustacean	0.6
43	8	Baragi	2015	JEMBE	1.8	0.2	3	2.4	0.3	3	OA	species	adult	N	0.02	<1	A	phytoplankton	0.9
44	8	Baragi	2015	JEMBE	18.1	6.1	3	58.2	6.2	3	OA	species	adult	N	0.02	<1	A	phytoplankton	1.1
45	8	Baragi	2015	JEMBE	1.8	0.2	3	1.5	0.2	3	Temp	species	adult	N	0.02	<1	A	phytoplankton	0.9
46	8	Baragi	2015	JEMBE	18.1	6.1	3	9.2	5.1	3	Temp	species	adult	N	0.02	<1	A	phytoplankton	1.1
47	8	Baragi	2015	JEMBE	1.8	0.2	3	2.6	0.3	3	OAT	species	adult	N	0.02	<1	A	phytoplankton	0.9
48	8	Baragi	2015	JEMBE	18.1	6.1	3	62.1	5.0	3	OAT	species	adult	N	0.02	<1	A	phytoplankton	1.1
49	9	Baragi	2015	Hydrobiologia	1.1	0.0	3	1.2	0.1	3	OA	species	adult	N	0.02	<1	A	phytoplankton	2.6
50	9	Baragi	2015	Hydrobiologia	4.5	0.4	3	4.8	0.8	3	OA	species	adult	N	0.02	<1	A	phytoplankton	2.6
51	9	Baragi	2015	Hydrobiologia	1.1	0.0	3	0.7	0.0	3	Temp	species	adult	N	0.02	<1	A	phytoplankton	2.6
52	9	Baragi	2015	Hydrobiologia	4.5	0.4	3	0.7	0.2	3	Temp	species	adult	N	0.02	<1	A	phytoplankton	2.6
53	9	Baragi	2015	Hydrobiologia	1.1	0.0	3	0.6	0.1	3	OAT	species	adult	N	0.02	<1	A	phytoplankton	2.6
54	9	Baragi	2015	Hydrobiologia	4.5	0.4	3	0.4	0.1	3	OAT	species	adult	N	0.02	<1	A	phytoplankton	2.6
55	10	Basso	2015	Estuaries and Coast	0.0	0.1	91	0.1	0.1	91	OA	species	juvenile	Y	25	>10	H	mollusc	5.1
56	10	Basso	2015	Estuaries and Coasts	0.0	0.1	91	0.0	0.1	91	Temp	species	juvenile	Y	25	>10	H	mollusc	5.1
57	10	Basso	2015	Estuaries and Coasts	0.0	0.1	91	0.1	0.6	91	OAT	species	juvenile	Y	25	>10	H	mollusc	5.1
58	11	Bautista-Chamizo	2018	Science of the Total Environment	62346.4	670.4	3	51620.1	3352.0	3	OA	species	adult	N	0.02	<1	A	phytoplankton	0.3
59	11	Bautista-Chamizo	2018	Science of the Total Environment	119529.4	2823.5	3	88470.6	1411.8	3	OA	species	adult	N	0.02	<1	A	phytoplankton	0.3
60	11	Bautista-Chamizo	2018	Science of the Total Environment	62346.4	670.4	3	45139.7	3128.5	3	Temp	species	adult	N	0.02	<1	A	phytoplankton	0.3
61	11	Bautista-Chamizo	2018	Science of the Total Environment	119529.4	2823.5	3	130352.9	5647.1	3	Temp	species	adult	N	0.02	<1	A	phytoplankton	0.3
62	11	Bautista-Chamizo	2018	Science of the Total Environment	62346.4	670.4	3	29050.3	2011.2	3	OAT	species	adult	N	0.02	<1	A	phytoplankton	0.3
63	11	Bautista-Chamizo	2018	Science of the Total Environment	119529.4	2823.5	3	123294.1	1411.8	3	OAT	species	adult	N	0.02	<1	A	phytoplankton	0.3
64	12	Bennett	2017	Global Change Biology	1.4	0.6	14	1.8	0.8	15	OA	species	larvae	N	100	>10	H	sponges	4
65	12	Bennett	2017	Global Change Biology	1.4	0.6	14	0.7	0.6	14	Temp	species	larvae	N	100	>10	H	sponges	4
66	12	Bennett	2017	Global Change Biology	1.4	0.6	14	1.0	0.7	14	OAT	species	larvae	N	100	>10	H	sponges	4
67	13	Bermudez	2015	PLoS One	0.5	0.3	3	0.6	0.3	3	OA	species	adult	N	0.02	<1	A	phytoplankton	52
68	13	Bermudez	2015	PLoS One	0.5	0.3	3	0.7	0.1	3	Temp	species	adult	N	0.02	<1	A	phytoplankton	52
69	13	Bermudez	2015	PLoS One	0.5	0.3	3	0.7	0.2	3	OAT	species	adult	N	0.02	<1	A	phytoplankton	52

70	14	Bignami	2017	ICES Journal of Marine Science	17.1	1.4	3	12.5	1.5	3	OA	species	larvae	N	15	>10	H	fish	2.9
71	14	Bignami	2017	ICES Journal of Marine Science	17.1	1.4	3	21.1	0.5	3	Temp	species	larvae	N	15	>10	H	fish	2.9
72	14	Bignami	2017	ICES Journal of Marine Science	17.1	1.4	3	20.9	1.0	3	OAT	species	larvae	N	15	>10	H	fish	2.9
73	15	Brown	2014	Algae	6.8	1.5	18	6.5	3.7	18	OA	species	adult	N	5	1 to 10	A	macroalgae	1
74	15	Brown	2014	Algae	9.0	1.4	18	8.8	2.7	18	OA	species	adult	N	5	1 to 10	A	macroalgae	2
75	15	Brown	2014	Algae	10.0	2.3	18	9.6	4.2	18	OA	species	adult	N	5	1 to 10	A	macroalgae	3
76	15	Brown	2014	Algae	11.8	3.7	18	11.5	4.0	18	OA	species	adult	N	5	1 to 10	A	macroalgae	4
77	15	Brown	2014	Algae	6.8	1.5	18	6.6	3.5	18	Temp	species	adult	N	5	1 to 10	A	macroalgae	1
78	15	Brown	2014	Algae	9.0	1.4	18	7.8	4.3	18	Temp	species	adult	N	5	1 to 10	A	macroalgae	2
79	15	Brown	2014	Algae	10.0	2.3	18	7.8	3.0	18	Temp	species	adult	N	5	1 to 10	A	macroalgae	3
80	15	Brown	2014	Algae	11.8	3.7	18	7.0	3.9	18	Temp	species	adult	N	5	1 to 10	A	macroalgae	4
81	15	Brown	2014	Algae	6.8	1.5	18	6.8	1.7	18	OAT	species	adult	N	5	1 to 10	A	macroalgae	1
82	15	Brown	2014	Algae	9.0	1.4	18	9.6	2.1	18	OAT	species	adult	N	5	1 to 10	A	macroalgae	2
83	15	Brown	2014	Algae	10.0	2.3	18	11.7	3.3	18	OAT	species	adult	N	5	1 to 10	A	macroalgae	3
84	15	Brown	2014	Algae	11.8	3.7	18	14.8	4.1	18	OAT	species	adult	N	5	1 to 10	A	macroalgae	4
85	16	Bylenga	2017	PLoS One	9.2	0.1	3	9.5	0.4	3	OA	species	larvae	Y	36	>10	H	mollusc	6.4
86	16	Bylenga	2017	PLoS One	9.2	0.1	3	10.1	0.5	3	Temp	species	larvae	Y	36	>10	H	mollusc	6.4
87	16	Bylenga	2017	PLoS One	9.2	0.1	3	9.3	0.1	3	OAT	species	larvae	Y	36	>10	H	mollusc	6.4
88	17	Byrne	2013	JEMBE	377.3	39.0	8	354.3	21.7	8	OA	species	larvae	Y	10	1 to 10	H	echinoids	0.4
89	17	Byrne	2013	JEMBE	377.3	39.0	8	475.5	17.4	8	Temp	species	larvae	Y	10	1 to 10	H	echinoids	0.4
90	17	Byrne	2013	JEMBE	377.3	39.0	8	458.6	30.4	8	OAT	species	larvae	Y	10	1 to 10	H	echinoids	0.4
91	18	Byrne	2013	MEPS	402.6	16.3	7	399.5	34.4	7	OA	species	larvae	Y	10	1 to 10	H	echinoids	0.4
92	18	Byrne	2013	MEPS	402.6	16.3	7	375.9	36.2	7	Temp	species	larvae	Y	10	1 to 10	H	echinoids	0.4
93	18	Byrne	2013	MEPS	402.6	16.3	7	368.4	22.6	7	OAT	species	larvae	Y	10	1 to 10	H	echinoids	0.4
94	19	Chakravarti	2016	Evolutionary Applications	1.5	0.2	72	1.4	0.2	72	OA	species	juvenile	Y	0.6	<1	H	polychaete	1
95	19	Chakravarti	2016	Evolutionary Applications	1.5	0.2	72	1.6	0.3	72	Temp	species	juvenile	Y	0.6	<1	H	polychaete	1
96	19	Chakravarti	2016	Evolutionary Applications	1.5	0.2	72	1.5	0.3	72	OAT	species	juvenile	Y	0.6	<1	H	polychaete	1
97	20	Chavez-Villegas	2017	Revista de Biologia Tropical	850.8	16.4	3	831.2	13.1	3	OA	species	larvae	Y	30	>10	H	mollusc	4.29
98	20	Chavez-Villegas	2017	Revista de Biologia Tropical	850.8	16.4	3	1054.1	16.4	3	Temp	species	larvae	Y	30	>10	H	mollusc	4.29
99	20	Chavez-Villegas	2017	Revista de Biologia Tropical	850.8	16.4	3	1031.2	16.4	3	OAT	species	larvae	Y	30	>10	H	mollusc	4.29
100	21	Chen	2018	Aquaculture	11.5	0.3	3	13.1	1.5	3	OA	species	adult	N	6	1 to 10	A	macroalgae	2
101	21	Chen	2018	Aquaculture	11.5	0.3	3	13.2	0.2	3	Temp	species	adult	N	6	1 to 10	A	macroalgae	2
102	21	Chen	2018	Aquaculture	11.5	0.3	3	16.0	0.4	3	OAT	species	adult	N	6	1 to 10	A	macroalgae	2
103	22	Clark	2013	Ecology and Evolution	20.8	3.4	6	18.9	2.7	6	OA	species	adult	Y	40	>10	H	mollusc	12
104	22	Clark	2013	Ecology and Evolution	20.8	3.4	6	15.3	2.3	6	Temp	species	adult	Y	40	>10	H	mollusc	12
105	22	Clark	2013	Ecology and Evolution	20.8	3.4	6	17.8	2.9	6	OAT	species	adult	Y	40	>10	H	mollusc	12

106	23	Clemments	2018	Conservation Physiology	1.7	0.4	30	1.7	0.4	30	OA	species	adult	Y	24	>10	H	mollusc	12.9
107	23	Clemments	2018	Conservation Physiology	1.7	0.4	30	1.6	0.5	30	Temp	species	adult	Y	24	>10	H	mollusc	12.9
108	23	Clemments	2018	Conservation Physiology	1.7	0.4	30	1.7	0.4	30	OAT	species	adult	Y	24	>10	H	mollusc	12.9
109	24	Cole	2016	Marine Biology	292.7	12.6	3	274.2	9.0	3	OA	species	larvae	Y	10	1 to 10	H	mollusc	0.6
110	24	Cole	2016	Marine Biology	292.7	12.6	3	292.7	12.6	3	Temp	species	larvae	Y	10	1 to 10	H	mollusc	0.6
111	24	Cole	2016	Marine Biology	292.7	12.6	3	284.6	5.4	3	OAT	species	larvae	Y	10	1 to 10	H	mollusc	0.6
112	25	Dahlke	2017	Global Change Biology	1.2	0.1	4	1.1	0.1	4	OA	species	larvae	N	25	>10	H	fish	1.9
113	25	Dahlke	2017	Global Change Biology	1.2	0.1	4	1.0	0.1	5	Temp	species	larvae	N	25	>10	H	fish	1.3
114	25	Dahlke	2017	Global Change Biology	1.2	0.1	4	0.9	0.1	5	OAT	species	larvae	N	25	>10	H	fish	1.3
115	26	Dionisio	2017	MEPS	257.3	4.8	5	232.1	9.1	5	OA	species	larvae	Y	1.8	1 to 10	H	mollusc	1.1
116	26	Dionisio	2017	MEPS	463.7	21.2	5	364.2	25.1	5	OA	species	juvenile	Y	1.8	1 to 10	H	mollusc	2.1
117	26	Dionisio	2017	MEPS	257.3	4.8	5	229.2	6.2	5	Temp	species	larvae	Y	1.8	1 to 10	H	mollusc	1.1
118	26	Dionisio	2017	MEPS	463.7	21.2	5	423.8	32.9	5	Temp	species	juvenile	Y	1.8	1 to 10	H	mollusc	2.1
119	26	Dionisio	2017	MEPS	257.3	4.8	5	232.8	8.0	5	OAT	species	larvae	Y	1.8	1 to 10	H	mollusc	1.1
120	26	Dionisio	2017	MEPS	463.7	21.2	5	350.9	9.4	5	OAT	species	juvenile	Y	1.8	1 to 10	H	mollusc	2.1
121	27	Dong	2018	Marine Environmental Research	0.0	0.0	4	0.0	0.0	4	OA	species	larvae	N	25	>10	H	jellyfish	1
122	27	Dong	2018	Marine Environmental Research	0.0	0.0	4	0.0	0.0	4	Temp	species	larvae	N	25	>10	H	jellyfish	1
123	27	Dong	2018	Marine Environmental Research	0.0	0.0	4	0.0	0.0	4	OAT	species	larvae	N	25	>10	H	jellyfish	1
124	28	Di Santo	2015	JEMBE	6.4	0.5	37	6.1	0.5	37	OA	species	juvenile	N	8	1 to 10	H	fish	0.1
125	28	Di Santo	2015	JEMBE	4.2	1.0	77	3.9	0.4	77	OA	species	juvenile	N	8	1 to 10	H	fish	0.1
126	28	Di Santo	2015	JEMBE	6.4	0.5	37	6.2	1.2	37	Temp	species	juvenile	N	8	1 to 10	H	fish	0.1
127	28	Di Santo	2015	JEMBE	4.2	1.0	77	3.9	1.0	77	Temp	species	juvenile	N	8	1 to 10	H	fish	0.1
128	28	Di Santo	2015	JEMBE	6.4	0.5	37	6.2	0.5	37	OAT	species	juvenile	N	8	1 to 10	H	fish	0.1
129	28	Di Santo	2015	JEMBE	4.2	1.0	77	3.5	0.9	77	OAT	species	juvenile	N	8	1 to 10	H	fish	0.1
130	29	Duarte	2014	Journal of Sea Research	1.3	0.3	5	0.9	0.1	5	OA	species	juvenile	Y	20	>10	H	mollusc	8.6
131	29	Duarte	2014	Journal of Sea Research	1.3	0.3	5	1.4	0.3	7	Temp	species	juvenile	Y	20	>10	H	mollusc	8.6
132	29	Duarte	2014	Journal of Sea Research	1.3	0.3	5	1.2	0.5	5	OAT	species	juvenile	Y	20	>10	H	mollusc	8.6
133	30	Durrant	2013	Marine Biology	32.5	18.5	7	22.5	13.2	7	OA	species	adult	Y	20	>10	H	bryozoa	1.7
134	30	Durrant	2013	Marine Biology	32.5	18.5	7	30.0	13.0	7	Temp	species	adult	Y	20	>10	H	bryozoa	1.7
135	30	Durrant	2013	Marine Biology	32.5	18.5	7	21.0	7.9	7	OAT	species	adult	Y	20	>10	H	bryozoa	1.7

136	31	Sheppard Brennand	2010	PLoS One	138.4	14.5	3	119.0	10.1	3	OA	species	larvae	Y	5	1 to 10	H	echinoids	0.7
137	31	Sheppard Brennand	2010	PLoS One	138.4	14.5	3	178.4	6.7	3	Temp	species	larvae	Y	5	1 to 10	H	echinoids	0.7
138	31	Sheppard Brennand	2010	PLoS One	138.4	14.5	3	137.1	6.7	3	OAT	species	larvae	Y	5	1 to 10	H	echinoids	0.7
139	32	De bodt	2010	Biogeosciences	5.2	0.2	6	5.0	0.2	6	OA	species	adult	Y	0.14	<1	A	phytoplankton (coccolithophore)	8.6
140	32	De bodt	2010	Biogeosciences	5.2	0.2	6	4.9	0.3	6	Temp	species	adult	Y	0.14	<1	A	phytoplankton (coccolithophore)	8.6
141	32	De bodt	2010	Biogeosciences	5.2	0.2	6	4.7	0.2	6	OAT	species	adult	Y	0.14	<1	A	phytoplankton (coccolithophore)	8.6
142	33	Duckworth	2012	MEPS	3.3	0.3	3	3.3	0.5	3	OA	species	adult	N	20	>10	H	sponges	3.4
143	33	Duckworth	2012	MEPS	1.8	0.2	3	1.6	0.3	3	OA	species	adult	N	100	>10	H	sponges	3.4
144	33	Duckworth	2012	MEPS	3.1	0.5	3	3.1	0.4	3	OA	species	adult	N	100	>10	H	sponges	3.4
145	33	Duckworth	2012	MEPS	3.9	0.4	3	3.6	0.3	3	OA	species	adult	N	20	>10	H	sponges	3.4
146	33	Duckworth	2012	MEPS	2.0	0.2	3	2.0	0.3	3	OA	species	adult	N	20	>10	H	sponges	3.4
147	33	Duckworth	2012	MEPS	3.9	0.6	3	3.5	0.3	3	OA	species	adult	N	20	>10	H	sponges	3.4
148	33	Duckworth	2012	MEPS	3.3	0.3	3	3.5	0.4	3	Temp	species	adult	N	20	>10	H	sponges	3.4
149	33	Duckworth	2012	MEPS	1.8	0.2	3	1.8	0.2	3	Temp	species	adult	N	100	>10	H	sponges	3.4
150	33	Duckworth	2012	MEPS	3.1	0.5	3	2.9	0.3	3	Temp	species	adult	N	100	>10	H	sponges	3.4
151	33	Duckworth	2012	MEPS	3.9	0.4	3	3.6	0.4	3	Temp	species	adult	N	20	>10	H	sponges	3.4
152	33	Duckworth	2012	MEPS	2.0	0.2	3	2.0	0.2	3	Temp	species	adult	N	20	>10	H	sponges	3.4
153	33	Duckworth	2012	MEPS	3.9	0.6	3	4.6	0.4	3	Temp	species	adult	N	20	>10	H	sponges	3.4
154	33	Duckworth	2012	MEPS	3.3	0.3	3	3.5	0.9	3	OAT	species	adult	N	20	>10	H	sponges	3.4
155	33	Duckworth	2012	MEPS	1.8	0.2	3	1.9	0.3	3	OAT	species	adult	N	100	>10	H	sponges	3.4
156	33	Duckworth	2012	MEPS	3.1	0.5	3	2.8	0.3	3	OAT	species	adult	N	100	>10	H	sponges	3.4
157	33	Duckworth	2012	MEPS	3.9	0.4	3	4.2	0.5	3	OAT	species	adult	N	20	>10	H	sponges	3.4
158	33	Duckworth	2012	MEPS	2.0	0.2	3	1.8	0.4	3	OAT	species	adult	N	20	>10	H	sponges	3.4
159	33	Duckworth	2012	MEPS	3.9	0.6	3	4.1	0.9	3	OAT	species	adult	N	20	>10	H	sponges	3.4
160	34	Dworjanyn	2018	Proc Roy Soc B	45.2	7.1	7	41.2	9.9	7	OA	species	juvenile	Y	5	1 to 10	H	echinoids	20.9
161	34	Dworjanyn	2018	Proc Roy Soc B	45.2	7.1	7	94.1	12.7	7	Temp	species	juvenile	Y	5	1 to 10	H	echinoids	20.9
162	34	Dworjanyn	2018	Proc Roy Soc B	45.2	7.1	7	74.3	2.8	7	OAT	species	juvenile	Y	5	1 to 10	H	echinoids	20.9
163	35	Edmunds	2011	Limnology & Oceanography	6.9	1.4	10	7.5	2.9	10	OA	species	juvenile	Y	100	>10	H	coral	4.3
164	35	Edmunds	2011	Limnology & Oceanography	6.9	1.4	10	6.0	2.2	10	Temp	species	juvenile	Y	100	>10	H	coral	4.3
165	35	Edmunds	2011	Limnology & Oceanography	6.9	1.4	10	5.7	4.2	10	OAT	species	juvenile	Y	100	>10	H	coral	4.3
166	36	Errera	2014	Harmful Algae	0.3	0.0	3	0.4	0.0	6	OA	species	adult	N	0.02	<1	A	phytoplankton	1.29
167	36	Errera	2014	Harmful Algae	0.3	0.0	3	0.2	0.0	3	Temp	species	adult	N	0.02	<1	A	phytoplankton	1.29
168	36	Errera	2014	Harmful Algae	0.3	0.0	3	0.3	0.0	6	OAT	species	adult	N	0.02	<1	A	phytoplankton	1.29
169	37	Feng	2009	MEPS	26.8	9.4	6	108.2	32.9	6	OA	communities	adult	N	0.02	<1	A	phytoplankton	2
170	37	Feng	2009	MEPS	16.5	4.1	6	21.4	7.0	6	OA	communities	adult	Y	0.14	<1	A	phytoplankton (coccolithophore)	2

171	37	Feng	2009	MEPS	167.6	14.1	6	83.8	35.3	6	OA	communities	adult	N	0.02	<1	A	phytoplankton	2
172	37	Feng	2009	MEPS	26.8	9.4	6	14.5	4.2	6	Temp	communities	adult	N	0.02	<1	A	phytoplankton	2
173	37	Feng	2009	MEPS	16.5	4.1	6	29.1	4.1	6	Temp	communities	adult	Y	0.14	<1	A	phytoplankton (coccolithophore)	2
174	37	Feng	2009	MEPS	167.6	14.1	6	247.1	34.4	6	Temp	communities	adult	N	0.02	<1	A	phytoplankton	2
175	37	Feng	2009	MEPS	26.8	9.4	6	28.6	4.7	6	OAT	communities	adult	N	0.02	<1	A	phytoplankton	2
176	37	Feng	2009	MEPS	16.5	4.1	6	100.6	19.7	6	OAT	communities	adult	Y	0.14	<1	A	phytoplankton (coccolithophore)	2
177	37	Feng	2009	MEPS	167.6	14.1	6	150.0	35.3	6	OAT	communities	adult	N	0.02	<1	A	phytoplankton	2
178	38	Fiorini	2011	Aquatic Microbial Ecology	11.0	2.5	4	10.4	1.2	4	OA	species	adult	Y	0.14	<1	A	phytoplankton (coccolithophore)	1.3
179	38	Fiorini	2011	Aquatic Microbial Ecology	10.6	1.0	4	9.7	1.0	4	OA	species	adult	Y	0.14	<1	A	phytoplankton (coccolithophore)	1.3
180	38	Fiorini	2011	Aquatic Microbial Ecology	11.0	2.5	4	10.9	0.8	4	Temp	species	adult	Y	0.14	<1	A	phytoplankton (coccolithophore)	1.3
181	38	Fiorini	2011	Aquatic Microbial Ecology	10.6	1.0	4	10.5	0.7	4	Temp	species	adult	Y	0.14	<1	A	phytoplankton (coccolithophore)	1.3
182	38	Fiorini	2011	Aquatic Microbial Ecology	11.0	2.5	4	10.9	1.0	4	OAT	species	adult	Y	0.14	<1	A	phytoplankton (coccolithophore)	1.3
183	38	Fiorini	2011	Aquatic Microbial Ecology	10.6	1.0	4	10.5	0.9	4	OAT	species	adult	Y	0.14	<1	A	phytoplankton (coccolithophore)	1.3
184	39	Findlay	2010	Marine Biology	6.1	1.6	3	4.9	1.1	3	OA	species	juvenile	Y	5	1 to 10	H	crustacean	4.3
185	39	Findlay	2010	Marine Biology	14.4	8.4	2	2.9	2.0	2	OA	species	juvenile	Y	7	1 to 10	H	crustacean	4.3
186	39	Findlay	2010	Marine Biology	6.1	1.6	3	6.7	1.0	3	Temp	species	juvenile	Y	5	1 to 10	H	crustacean	4.3
187	39	Findlay	2010	Marine Biology	14.4	8.4	2	4.4	5.5	2	Temp	species	juvenile	Y	7	1 to 10	H	crustacean	4.3
188	39	Findlay	2010	Marine Biology	6.1	1.6	3	3.6	0.4	3	OAT	species	juvenile	Y	5	1 to 10	H	crustacean	4.3
189	39	Findlay	2010	Marine Biology	14.4	8.4	2	6.2	2.9	2	OAT	species	juvenile	Y	7	1 to 10	H	crustacean	4.3
190	40	Fitzer	2015	Ecology and Evolution	1.7	0.6	4	0.9	0.3	4	OA	species	adult	Y	24	>10	H	mollusc	36
191	40	Fitzer	2015	Ecology and Evolution	1.7	0.6	4	1.0	0.1	4	OAT	species	adult	Y	24	>10	H	mollusc	36
192	41	Gao	2017	Marine Pollution Bulletin	4.1	0.9	3	7.9	0.5	3	OA	species	adult	N	0.25	<1	A	macroalgae	1.7
193	41	Gao	2017	Marine Pollution Bulletin	4.1	0.9	3	5.0	0.8	3	Temp	species	adult	N	0.25	<1	A	macroalgae	1.7
194	41	Gao	2017	Marine Pollution Bulletin	4.1	0.9	3	6.0	0.6	3	OAT	species	adult	N	0.25	<1	A	macroalgae	1.7
195	42	Gao	2018	Global Change Biology Bioenergy	2.7	0.2	3	3.2	0.1	3	OA	species	adult	N	0.25	<1	A	macroalgae	6
196	42	Gao	2018	Global Change Biology Bioenergy	2.7	0.2	3	3.5	0.2	3	Temp	species	adult	N	0.25	<1	A	macroalgae	6
197	42	Gao	2018	Global Change Biology Bioenergy	2.7	0.2	3	3.9	0.1	3	OAT	species	adult	N	0.25	<1	A	macroalgae	6
198	43	Garcia	2015	Marine Environmental Research	0.7	0.1	3	0.8	0.0	3	OA	species	larvae	Y	10	1 to 10	H	echinoids	1.4
199	43	Garcia	2015	Marine Environmental Research	0.7	0.1	3	0.7	0.1	3	Temp	species	larvae	Y	10	1 to 10	H	echinoids	1.4

200	43	Garcia	2015	Marine Environmental Research	0.7	0.1	3	0.7	0.1	3	OAT	species	larvae	Y	10	1 to 10	H	echinoids	1.4
201	44	Gardner	2018	Marine Biology	112.8	4.0	15	105.8	9.0	15	OA	species	larvae	Y	3	1 to 10	H	mollusc	0.7
202	44	Gardner	2018	Marine Biology	112.8	4.0	15	104.4	4.8	15	Temp	species	larvae	Y	3	1 to 10	H	mollusc	0.7
203	44	Gardner	2018	Marine Biology	112.8	4.0	15	104.6	5.2	15	OAT	species	larvae	Y	3	1 to 10	H	mollusc	0.7
204	45	Gibbin	2017	Journal of Experimental Biology	1.6	0.2	12	1.7	0.2	7	OA	species	adult	N	0.6	<1	H	polychaete	4.3
205	45	Gibbin	2017	Journal of Experimental Biology	1.6	0.2	12	1.6	0.2	12	Temp	species	adult	N	0.6	<1	H	polychaete	4.3
206	45	Gibbin	2017	Journal of Experimental Biology	1.6	0.2	12	1.7	0.1	3	OAT	species	adult	N	0.6	<1	H	polychaete	4.3
207	46	Gobler	2018	Frontiers in Marine Science	6.4	0.1	4	6.0	0.2	4	OA	species	larvae	N	2	1 to 10	H	fish	1.4
208	46	Gobler	2018	Frontiers in Marine Science	6.4	0.1	4	7.5	0.6	4	Temp	species	larvae	N	2	1 to 10	H	fish	1.4
209	46	Gobler	2018	Frontiers in Marine Science	6.4	0.1	4	7.4	0.3	4	OAT	species	larvae	N	2	1 to 10	H	fish	1.4
210	47	Gonzalez	2018	Marine Pollution Bulletin	7.8	1.5	3	5.9	1.0	3	OA	species	larvae	N	10	1 to 10	A	macroalgae	2.4
211	47	Gonzalez	2018	Marine Pollution Bulletin	12.5	2.1	3	14.0	1.8	3	OA	species	larvae	N	10	1 to 10	A	macroalgae	2.4
212	47	Gonzalez	2018	Marine Pollution Bulletin	7.8	1.5	3	6.5	1.0	3	Temp	species	larvae	N	10	1 to 10	A	macroalgae	2.4
213	47	Gonzalez	2018	Marine Pollution Bulletin	12.5	2.1	3	6.2	1.4	3	Temp	species	larvae	N	10	1 to 10	A	macroalgae	2.4
214	47	Gonzalez	2018	Marine Pollution Bulletin	7.8	1.5	3	6.9	2.1	3	OAT	species	larvae	N	10	1 to 10	A	macroalgae	2.4
215	47	Gonzalez	2018	Marine Pollution Bulletin	12.5	2.1	3	5.3	1.1	3	OAT	species	larvae	N	10	1 to 10	A	macroalgae	2.4
216	48	Gooding	2009	PNAS	140.0	31.0	5	191.0	36.4	6	OA	species	juvenile	Y	20	>10	H	echinoids	10
217	48	Gooding	2009	PNAS	140.0	31.0	5	234.8	86.1	6	Temp	species	juvenile	Y	20	>10	H	echinoids	10
218	48	Gooding	2009	PNAS	140.0	31.0	5	317.4	111.1	5	OAT	species	juvenile	Y	20	>10	H	echinoids	10
219	49	Gordillo	2016	Polar Biology	2.9	0.1	4	3.2	0.8	4	OA	species	adult	N	2	1 to 10	A	macroalgae	1.3
220	49	Gordillo	2016	Polar Biology	0.9	0.2	4	1.1	0.2	4	OA	species	adult	N	4	1 to 10	A	macroalgae	1.3
221	49	Gordillo	2016	Polar Biology	0.9	0.1	4	0.9	0.3	4	OA	species	adult	N	6	1 to 10	A	macroalgae	1.3
222	49	Gordillo	2016	Polar Biology	2.9	0.5	4	4.0	0.2	4	OA	species	adult	N	10	1 to 10	A	macroalgae	1.3
223	49	Gordillo	2016	Polar Biology	0.9	0.5	4	0.0	0.1	4	OA	species	adult	N	0.7	<1	A	macroalgae	1.3
224	49	Gordillo	2016	Polar Biology	2.9	0.1	4	3.7	0.2	4	OA	species	adult	N	6	1 to 10	A	macroalgae	1.3
225	49	Gordillo	2016	Polar Biology	2.9	0.1	4	2.6	0.1	4	Temp	species	adult	N	2	1 to 10	A	macroalgae	1.3
226	49	Gordillo	2016	Polar Biology	0.9	0.2	4	2.3	0.1	4	Temp	species	adult	N	4	1 to 10	A	macroalgae	1.3
227	49	Gordillo	2016	Polar Biology	0.9	0.1	4	1.3	0.0	4	Temp	species	adult	N	6	1 to 10	A	macroalgae	1.3
228	49	Gordillo	2016	Polar Biology	2.9	0.5	4	3.3	0.7	4	Temp	species	adult	N	10	1 to 10	A	macroalgae	1.3
229	49	Gordillo	2016	Polar Biology	0.9	0.5	4	1.5	0.2	4	Temp	species	adult	N	0.7	<1	A	macroalgae	1.3
230	49	Gordillo	2016	Polar Biology	2.9	0.1	4	3.0	0.2	4	Temp	species	adult	N	1.3	1 to 10	A	macroalgae	1.3

231	49	Gordillo	2016	Polar Biology	2.9	0.1	4	3.2	0.3	4	OAT	species	adult	N	2	1 to 10	A	macroalgae	1.3
232	49	Gordillo	2016	Polar Biology	0.9	0.2	4	2.4	0.1	4	OAT	species	adult	N	4	1 to 10	A	macroalgae	1.3
233	49	Gordillo	2016	Polar Biology	0.9	0.1	4	1.1	0.2	4	OAT	species	adult	N	1.3	1 to 10	A	macroalgae	1.3
234	49	Gordillo	2016	Polar Biology	2.9	0.5	4	3.5	0.3	4	OAT	species	adult	N	10	1 to 10	A	macroalgae	1.3
235	49	Gordillo	2016	Polar Biology	0.9	0.5	4	1.2	0.1	4	OAT	species	adult	N	0.7	<1	A	macroalgae	1.3
236	49	Gordillo	2016	Polar Biology	2.9	0.1	4	4.1	0.1	4	OAT	species	adult	N	1.3	1 to 10	A	macroalgae	1.3
237	50	Graba-Lanc	2018	MEPS	75.3	17.7	15	64.8	26.5	15	OA	species	adult	Y	50	>10	A	macroalgae (CCA)	2
238	50	Graba-Lanc	2018	MEPS	39.9	31.2	15	43.7	14.9	15	OA	species	adult	Y	50	>10	A	macroalgae (CCA)	2
239	50	Graba-Lanc	2018	MEPS	174.8	200.8	15	168.1	93.9	15	OA	species	adult	N	8	1 to 10	A	macroalgae	2
240	50	Graba-Lanc	2018	MEPS	198.6	219.0	15	190.3	208.3	15	OA	species	adult	N	4	1 to 10	A	macroalgae	2
241	50	Graba-Lanc	2018	MEPS	50.4	45.9	15	31.5	30.2	15	OA	species	adult	N	5	1 to 10	A	macroalgae	2
242	50	Graba-Lanc	2018	MEPS	40.3	71.1	15	84.7	128.5	15	OA	species	adult	N	0.25	<1	A	macroalgae	2
243	50	Graba-Lanc	2018	MEPS	75.3	17.7	15	61.1	35.3	15	Temp	species	adult	Y	50	>10	A	macroalgae (CCA)	2
244	50	Graba-Lanc	2018	MEPS	39.9	31.2	15	37.8	14.9	15	Temp	species	adult	Y	50	>10	A	macroalgae (CCA)	2
245	50	Graba-Lanc	2018	MEPS	174.8	200.8	15	107.0	35.6	15	Temp	species	adult	N	8	1 to 10	A	macroalgae	2
246	50	Graba-Lanc	2018	MEPS	198.6	219.0	15	233.1	357.9	15	Temp	species	adult	N	4	1 to 10	A	macroalgae	2
247	50	Graba-Lanc	2018	MEPS	50.4	45.9	15	16.4	27.3	15	Temp	species	adult	N	5	1 to 10	A	macroalgae	2
248	50	Graba-Lanc	2018	MEPS	40.3	71.1	15	40.9	57.4	15	Temp	species	adult	N	0.25	<1	A	macroalgae	2
249	50	Graba-Lanc	2018	MEPS	75.3	17.7	15	83.0	33.6	15	OAT	species	adult	Y	50	>10	A	macroalgae (CCA)	2
250	50	Graba-Lanc	2018	MEPS	39.9	31.2	15	56.6	13.5	15	OAT	species	adult	Y	50	>10	A	macroalgae (CCA)	2
251	50	Graba-Lanc	2018	MEPS	174.8	200.8	15	95.3	103.6	15	OAT	species	adult	N	8	1 to 10	A	macroalgae	2
252	50	Graba-Lanc	2018	MEPS	198.6	219.0	15	191.7	203.0	15	OAT	species	adult	N	4	1 to 10	A	macroalgae	2
253	50	Graba-Lanc	2018	MEPS	50.4	45.9	15	50.9	48.8	15	OAT	species	adult	N	5	1 to 10	A	macroalgae	2
254	50	Graba-Lanc	2018	MEPS	40.3	71.1	15	61.6	71.1	15	OAT	species	adult	N	0.25	<1	A	macroalgae	2
255	51	Graiff	2017	Botanica Marina	41.3	3.5	3	30.0	9.8	3	OA	species	adult	N	5	1 to 10	A	macroalgae	10
256	51	Graiff	2017	Botanica Marina	5.2	3.5	3	7.8	1.8	3	OA	species	adult	N	5	1 to 10	A	macroalgae	10
257	51	Graiff	2017	Botanica Marina	8.6	0.5	3	10.7	1.2	3	OA	species	adult	N	5	1 to 10	A	macroalgae	10
258	51	Graiff	2017	Botanica Marina	27.1	3.3	3	31.8	2.3	3	OA	species	adult	N	5	1 to 10	A	macroalgae	10
259	51	Graiff	2017	Botanica Marina	41.3	3.5	3	16.0	1.5	3	Temp	species	adult	N	5	1 to 10	A	macroalgae	10
260	51	Graiff	2017	Botanica Marina	8.6	0.5	3	4.8	2.4	3	Temp	species	adult	N	5	1 to 10	A	macroalgae	10
261	51	Graiff	2017	Botanica Marina	27.1	3.3	3	24.4	1.8	3	Temp	species	adult	N	5	1 to 10	A	macroalgae	10
262	51	Graiff	2017	Botanica Marina	41.3	3.5	3	24.6	1.7	3	OAT	species	adult	N	5	1 to 10	A	macroalgae	10
263	51	Graiff	2017	Botanica Marina	8.6	0.5	3	2.3	4.4	3	OAT	species	adult	N	5	1 to 10	A	macroalgae	10
264	51	Graiff	2017	Botanica Marina	27.1	3.3	3	25.4	6.3	3	OAT	species	adult	N	5	1 to 10	A	macroalgae	10
265	52	Heldt	2016	Scientific Reports	40.1	92.7	12	943.1	3139.7	12	OA	population	adult	Y	0.23	<1	H	crustacean	13
266	52	Heldt	2016	Scientific Reports	40.1	92.7	12	170.6	370.7	12	Temp	population	adult	Y	0.23	<1	H	crustacean	13
267	52	Heldt	2016	Scientific Reports	40.1	92.7	12	1301.0	1958.0	12	OAT	population	adult	Y	0.23	<1	H	crustacean	13
268	53	Hendrix	2017	Aquatic Botany	1.7	0.7	3	1.0	0.7	3	OA	species	adult	N	35	>10	A	seagrass	2
269	53	Hendrix	2017	Aquatic Botany	1.7	0.7	3	0.5	0.5	3	Temp	species	adult	N	35	>10	A	seagrass	2
270	53	Hendrix	2017	Aquatic Botany	1.7	0.7	3	1.3	0.5	3	OAT	species	adult	N	35	>10	A	seagrass	2
271	54	Hiebenthal	2013	Marine Biology	0.1	0.0	4	0.1	0.0	4	OA	species	adult	Y	24	>10	H	mollusc	13
272	54	Hiebenthal	2013	Marine Biology	0.1	0.0	4	0.1	0.0	4	Temp	species	adult	Y	24	>10	H	mollusc	13
273	54	Hiebenthal	2013	Marine Biology	0.1	0.0	4	0.1	0.0	4	OAT	species	adult	Y	24	>10	H	mollusc	13
274	55	Hildebrand	2014	Marine Pollution Bu	2.4	1.3	4	2.5	2.0	4	OA	species	adult	N	2.21	1 to 10	H	zooplankton	25.8
275	55	Hildebrand	2014	Marine Pollution Bu	2.4	1.3	4	2.5	2.3	4	Temp	species	adult	N	2.21	1 to 10	H	zooplankton	25.8
276	55	Hildebrand	2014	Marine Pollution Bu	2.4	1.3	4	1.6	0.8	4	OAT	species	adult	N	2.21	1 to 10	H	zooplankton	25.8
277	56	Hoppe	2018	Biogeosciences	0.9	0.0	3	0.8	0.1	3	OA	species	adult	N	0.02	<1	A	phytoplankton	0.6
278	56	Hoppe	2018	Biogeosciences	0.9	0.0	3	1.1	0.0	3	Temp	species	adult	N	0.02	<1	A	phytoplankton	0.6
279	56	Hoppe	2018	Biogeosciences	0.9	0.0	3	1.3	0.0	3	OAT	species	adult	N	0.02	<1	A	phytoplankton	0.6

280	57	Horvath	2016	Scientific Reports	1388.4	68.5	3	1199.2	91.3	3	OA	species	adult	Y	100	>10	H	coral	2
281	57	Horvath	2016	Scientific Reports	1388.4	68.5	3	1305.4	98.0	3	Temp	species	adult	Y	100	>10	H	coral	2
282	57	Horvath	2016	Scientific Reports	1388.4	68.5	3	1157.4	57.7	3	OAT	species	adult	Y	100	>10	H	coral	2
283	58	Iniguez	2016	Marine Biology	9.1	1.1	4	9.2	1.2	4	OA	species	adult	N	5	1 to 10	A	macroalgae	1
284	58	Iniguez	2016	Marine Biology	1.5	0.2	4	1.8	0.6	4	OA	species	adult	N	6	1 to 10	A	macroalgae	1
285	58	Iniguez	2016	Marine Biology	9.1	1.1	4	12.2	1.7	4	Temp	species	adult	N	5	1 to 10	A	macroalgae	1
286	58	Iniguez	2016	Marine Biology	1.5	0.2	4	1.6	0.3	4	Temp	species	adult	N	6	1 to 10	A	macroalgae	1
287	58	Iniguez	2016	Marine Biology	9.1	1.1	4	11.6	0.3	4	OAT	species	adult	N	5	1 to 10	A	macroalgae	1
288	58	Iniguez	2016	Marine Biology	1.5	0.2	4	1.2	0.4	4	OAT	species	adult	N	6	1 to 10	A	macroalgae	1
289	59	Iniguez	2017	Journal of Experimental Botany	5.6	0.7	6	7.3	1.0	6	OA	species	juvenile	N	0.67	1 to 10	A	macroalgae	1.86
290	59	Iniguez	2017	Journal of Experimental Botany	5.6	0.7	6	4.4	0.8	6	Temp	species	juvenile	N	0.67	1 to 10	A	macroalgae	1.86
291	59	Iniguez	2017	Journal of Experimental Botany	5.6	0.7	6	5.8	0.5	6	OAT	species	juvenile	N	0.67	1 to 10	A	macroalgae	1.86
292	60	Jarrold	2018	Frontiers in Marine Science	0.4	0.0	6	0.4	0.0	6	OA	species	juvenile	N	10	1 to 10	H	fish	11
293	60	Jarrold	2018	Frontiers in Marine Science	0.4	0.0	6	0.3	0.0	6	Temp	species	juvenile	N	10	1 to 10	H	fish	11
294	60	Jarrold	2018	Frontiers in Marine Science	0.4	0.0	6	0.3	0.0	6	OAT	species	juvenile	N	10	1 to 10	H	fish	11
295	61	Jiang	2018	Coral Reefs	0.4	0.0	2	0.4	0.0	2	OA	species	juvenile	Y	100	>10	H	coral	3
296	61	Jiang	2018	Coral Reefs	0.4	0.0	2	0.5	0.0	2	Temp	species	juvenile	Y	100	>10	H	coral	3
297	61	Jiang	2018	Coral Reefs	0.4	0.0	2	0.5	0.0	2	OAT	species	juvenile	Y	100	>10	H	coral	3
298	62	Kamya	2016	Coral Reefs	4.7	1.0	8	4.0	1.1	8	OA	species	juvenile	Y	8	1 to 10	H	echinoids	8
299	62	Kamya	2016	Coral Reefs	4.7	1.0	8	5.3	1.1	8	Temp	species	juvenile	Y	8	1 to 10	H	echinoids	8
300	62	Kamya	2016	Coral Reefs	4.7	1.0	8	6.1	0.7	8	OAT	species	juvenile	Y	8	1 to 10	H	echinoids	8
301	63	Kang	2016	Algae	0.6	0.2	5	0.5	0.1	5	OA	species	adult	N	0.25	<1	A	macroalgae	1.4
302	63	Kang	2016	Algae	0.6	0.2	5	0.6	0.1	5	Temp	species	adult	N	0.25	<1	A	macroalgae	1.4
303	63	Kang	2016	Algae	0.6	0.2	5	0.6	0.1	5	OAT	species	adult	N	0.25	<1	A	macroalgae	1.4
304	64	Keppel	2015	Marine Biology Reseach	0.1	0.0	4	0.1	0.0	4	OA	species	adult	Y	8	1 to 10	H	echinoids	10
305	64	Keppel	2015	Marine Biology Reseach	0.1	0.0	4	0.1	0.0	4	Temp	species	adult	Y	8	1 to 10	H	echinoids	10
306	64	Keppel	2015	Marine Biology Reseach	0.1	0.0	4	0.0	0.0	4	OAT	species	adult	Y	8	1 to 10	H	echinoids	10
307	65	Ko	2014	Environmental Science & Technology	2.8	0.3	4	2.1	0.2	4	OA	species	larvae	Y	40	>10	H	mollusc	2.1
308	65	Ko	2014	Environmental Science & Technology	0.9	0.9	4	8.5	1.3	4	OA	species	larvae	Y	40	>10	H	mollusc	8.3
309	65	Ko	2014	Environmental Science & Technology	2.8	0.3	4	4.0	0.8	4	Temp	species	larvae	Y	40	>10	H	mollusc	2.1

310	65	Ko	2014	Environmental Science & Technology	0.9	0.9	4	0.2	0.1	4	Temp	species	larvae	Y	40	>10	H	mollusc	8.3
311	65	Ko	2014	Environmental Science & Technology	2.8	0.3	4	3.9	0.4	4	OAT	species	larvae	Y	40	>10	H	mollusc	2.1
312	65	Ko	2014	Environmental Science & Technology	0.9	0.9	4	3.9	3.1	4	OAT	species	larvae	Y	40	>10	H	mollusc	8.3
313	66	Kram	2016	ICES Journal of Marine Science	1.3	0.8	10	0.7	0.8	10	OA	species	adult	N	2.9	1 to 10	A	macroalgae	3
314	66	Kram	2016	ICES Journal of Marine Science	-0.2	0.3	10	-1.1	0.5	10	OA	species	adult	Y	10	1 to 10	A	macroalgae (CCA)	4.4
315	66	Kram	2016	ICES Journal of Marine Science	1.3	0.8	10	-0.4	0.6	10	Temp	species	adult	N	2.9	1 to 10	A	macroalgae	3
316	66	Kram	2016	ICES Journal of Marine Science	-0.2	0.3	10	-0.5	0.4	10	Temp	species	adult	Y	10	1 to 10	A	macroalgae (CCA)	4.4
317	66	Kram	2016	ICES Journal of Marine Science	1.3	0.8	10	0.3	0.8	10	OAT	species	adult	N	2.9	1 to 10	A	macroalgae	3
318	66	Kram	2016	ICES Journal of Marine Science	-0.2	0.3	10	-1.0	0.5	10	OAT	species	adult	Y	10	1 to 10	A	macroalgae (CCA)	4.4
319	67	Kroeker	2014	PLoS One	0.6	0.1	3	0.8	0.2	3	OA	species	adult	Y	15	>10	H	mollusc	5.4
320	67	Kroeker	2014	PLoS One	0.6	0.1	3	1.6	0.2	3	Temp	species	adult	Y	15	>10	H	mollusc	5.4
321	67	Kroeker	2014	PLoS One	0.6	0.1	3	0.9	0.3	3	OAT	species	adult	Y	15	>10	H	mollusc	5.4
322	68	Langdon	2018	Limnology & Oceanography	4.4	2.3	18	2.4	1.5	18	OA	species	adult	Y	100	>10	H	coral	8.9
323	68	Langdon	2018	Limnology & Oceanography	140.8	47.1	16	118.6	50.3	13	OA	species	adult	Y	100	>10	H	coral	8.9
324	68	Langdon	2018	Limnology & Oceanography	4.4	2.3	18	-0.4	1.1	16	Temp	species	adult	Y	100	>10	H	coral	8.9
325	68	Langdon	2018	Limnology & Oceanography	140.8	47.1	16	0.0	0.0	17	Temp	species	adult	Y	100	>10	H	coral	8.9
326	68	Langdon	2018	Limnology & Oceanography	4.4	2.3	18	-0.3	1.2	18	OAT	species	adult	Y	100	>10	H	coral	8.9
327	68	Langdon	2018	Limnology & Oceanography	140.8	47.1	16	0.0	0.0	15	OAT	species	adult	Y	100	>10	H	coral	8.9
328	69	Lagos	2016	Aquaculture Environment Interactions	0.2	0.1	5	0.1	0.0	5	OA	species	juvenile	Y	10	1 to 10	H	mollusc	2.6
329	69	Lagos	2016	Aquaculture Environment Interactions	0.2	0.1	5	0.2	0.0	5	Temp	species	juvenile	Y	10	1 to 10	H	mollusc	2.6
330	69	Lagos	2016	Aquaculture Environment Interactions	0.2	0.1	5	0.2	0.0	5	OAT	species	juvenile	Y	10	1 to 10	H	mollusc	2.6
331	70	Lardies	2017	Aquaculture	0.0	0.0	5	0.0	0.0	5	OA	species	juvenile	Y	10	1 to 10	H	mollusc	2.6
332	70	Lardies	2017	Aquaculture	0.0	0.0	5	0.0	0.0	5	Temp	species	juvenile	Y	10	1 to 10	H	mollusc	2.6
333	70	Lardies	2017	Aquaculture	0.0	0.0	5	0.0	0.0	5	OAT	species	juvenile	Y	10	1 to 10	H	mollusc	2.6
334	71	Leal	2017	Marine Biology	32.1	2.2	6	37.3	2.0	6	OA	species	larvae	N	1	1 to 10	A	macroalgae	2.1

335	71	Leal	2017	Marine Biology	31.0	3.3	6	35.4	2.5	6	OA	species	larvae	N	0.61	<1	A	macroalgae	2.1
336	71	Leal	2017	Marine Biology	484.4	56.0	6	766.7	170.4	6	OA	species	larvae	N	1	1 to 10	A	macroalgae	2.1
337	71	Leal	2017	Marine Biology	715.6	85.2	6	764.3	231.2	6	OA	species	larvae	N	0.61	<1	A	macroalgae	2.1
338	71	Leal	2017	Marine Biology	32.1	2.2	6	36.9	2.1	6	Temp	species	larvae	N	1	1 to 10	A	macroalgae	2.1
339	71	Leal	2017	Marine Biology	31.0	3.3	6	37.7	3.9	6	Temp	species	larvae	N	0.61	<1	A	macroalgae	2.1
340	71	Leal	2017	Marine Biology	484.4	56.0	6	725.4	206.9	6	Temp	species	larvae	N	1	1 to 10	A	macroalgae	2.1
341	71	Leal	2017	Marine Biology	715.6	85.2	6	744.8	119.3	6	Temp	species	larvae	N	0.61	<1	A	macroalgae	2.1
342	71	Leal	2017	Marine Biology	32.1	2.2	6	32.0	1.8	6	OAT	species	larvae	N	1	1 to 10	A	macroalgae	2.1
343	71	Leal	2017	Marine Biology	31.0	3.3	6	33.3	3.4	6	OAT	species	larvae	N	0.61	<1	A	macroalgae	2.1
344	71	Leal	2017	Marine Biology	484.4	56.0	6	506.3	68.2	6	OAT	species	larvae	N	1	1 to 10	A	macroalgae	2.1
345	71	Leal	2017	Marine Biology	715.6	85.2	6	910.3	68.2	6	OAT	species	larvae	N	0.61	<1	A	macroalgae	2.1
346	72	Leal	2018	Scientific Reports	1779.7	134.1	4	1791.2	46.0	4	OA	species	larvae	N	1	1 to 10	A	macroalgae	1.7
347	72	Leal	2018	Scientific Reports	1273.9	249.0	4	1055.6	92.0	4	OA	species	larvae	N	1	1 to 10	A	macroalgae	1.7
348	72	Leal	2018	Scientific Reports	1146.2	211.5	4	1057.7	184.6	4	OA	species	larvae	N	0.61	<1	A	macroalgae	1.7
349	72	Leal	2018	Scientific Reports	1330.8	250.0	4	1019.2	138.5	4	OA	species	larvae	N	0.61	<1	A	macroalgae	1.7
350	72	Leal	2018	Scientific Reports	23.9	0.4	4	30.6	2.1	4	OA	species	larvae	N	0.61	<1	A	macroalgae	1.7
351	72	Leal	2018	Scientific Reports	28.4	3.2	4	31.1	2.2	4	OA	species	larvae	N	0.61	<1	A	macroalgae	1.7
352	72	Leal	2018	Scientific Reports	1779.7	134.1	4	1680.1	463.6	4	Temp	species	larvae	N	1	1 to 10	A	macroalgae	1.7
353	72	Leal	2018	Scientific Reports	1273.9	249.0	4	779.7	153.3	4	Temp	species	larvae	N	1	1 to 10	A	macroalgae	1.7
354	72	Leal	2018	Scientific Reports	1146.2	211.5	4	1150.0	80.8	4	Temp	species	larvae	N	0.61	<1	A	macroalgae	1.7
355	72	Leal	2018	Scientific Reports	1330.8	250.0	4	984.6	200.0	4	Temp	species	larvae	N	0.61	<1	A	macroalgae	1.7
356	72	Leal	2018	Scientific Reports	23.9	0.4	4	28.6	1.2	4	Temp	species	larvae	N	0.61	<1	A	macroalgae	1.7
357	72	Leal	2018	Scientific Reports	28.4	3.2	4	25.5	1.5	4	Temp	species	larvae	N	0.61	<1	A	macroalgae	1.7
358	72	Leal	2018	Scientific Reports	1779.7	134.1	4	2055.6	245.2	4	OAT	species	larvae	N	1	1 to 10	A	macroalgae	1.7
359	72	Leal	2018	Scientific Reports	1273.9	249.0	4	1404.2	256.7	4	OAT	species	larvae	N	1	1 to 10	A	macroalgae	1.7
360	72	Leal	2018	Scientific Reports	1146.2	211.5	4	1080.8	173.1	4	OAT	species	larvae	N	0.61	<1	A	macroalgae	1.7
361	72	Leal	2018	Scientific Reports	1330.8	250.0	4	869.2	226.9	4	OAT	species	larvae	N	0.61	<1	A	macroalgae	1.7
362	72	Leal	2018	Scientific Reports	23.9	0.4	4	31.2	0.9	4	OAT	species	larvae	N	0.61	<1	A	macroalgae	1.7
363	72	Leal	2018	Scientific Reports	28.4	3.2	4	25.9	1.4	4	OAT	species	larvae	N	0.61	<1	A	macroalgae	1.7
364	73	Le Moullac	2016	Estuarine Coastal ar	-6.2	10.5	4	-12.9	12.4	4	OA	species	juvenile	Y	14	>10	H	mollusc	1.3
365	73	Le Moullac	2016	Estuarine Coastal ar	-6.2	10.5	4	6.2	16.2	4	Temp	species	juvenile	Y	14	>10	H	mollusc	1.3
366	73	Le Moullac	2016	Estuarine Coastal ar	-6.2	10.5	4	14.3	11.0	4	OAT	species	juvenile	Y	14	>10	H	mollusc	1.3
367	74	Leo	2018	Conservation Physiology	10.0	0.5	6	9.8	0.8	6	OA	species	larvae	N	20	>10	H	fish	27
368	74	Leo	2018	Conservation Physiology	10.0	0.5	6	9.8	0.7	6	Temp	species	larvae	N	20	>10	H	fish	16
369	74	Leo	2018	Physiology	10.0	0.5	6	9.1	0.9	6	OAT	species	larvae	N	20	>10	H	fish	16
370	75	Leung	2017	Scientific Reports	0.0	0.0	22	0.0	0.0	21	OA	species	adult	Y	1	1 to 10	H	mollusc	8
371	75	Leung	2017	Scientific Reports	0.0	0.0	22	0.0	0.0	8	Temp	species	adult	Y	1	1 to 10	H	mollusc	8
372	75	Leung	2017	Scientific Reports	0.0	0.0	22	0.0	0.0	5	OAT	species	adult	Y	1	1 to 10	H	mollusc	8
373	76	Leung	2018	Science of the Total Environment	1185.6	381.2	3	1080.1	182.8	3	OA	species	juvenile	Y	1	1 to 10	H	mollusc	26
374	76	Leung	2018	Science of the Total Environment	1185.6	381.2	3	431.1	252.8	3	Temp	species	juvenile	Y	1	1 to 10	H	mollusc	26

375	76	Leung	2018	Science of the Total Environment	1185.6	381.2	3	27.0	143.9	3	OAT	species	juvenile	Y	1	1 to 10	H	mollusc	26
376	77	Li	2017	PLoS One	0.4	0.0	3	0.3	0.0	3	OA	species	adult	N	0.02	<1	A	phytoplankton	1.6
377	77	Li	2017	PLoS One	0.4	0.0	3	0.4	0.0	3	Temp	species	adult	N	0.02	<1	A	phytoplankton	1.6
378	77	Li	2017	PLoS One	0.4	0.0	3	0.2	0.0	3	OAT	species	adult	N	0.02	<1	A	phytoplankton	1.6
379	78	Li	2018	ICES Journal of Marine Science	1.3	0.0	3	1.2	0.0	3	OA	species	adult	N	0.02	<1	A	phytoplankton	15.6
380	78	Li	2018	ICES Journal of Marine Science	1.3	0.0	3	1.3	0.1	3	Temp	species	adult	N	0.02	<1	A	phytoplankton	15.6
381	78	Li	2018	ICES Journal of Marine Science	1.3	0.0	3	1.4	0.0	3	OAT	species	adult	N	0.02	<1	A	phytoplankton	15.6
382	79	Li	2018	Progress in Oceanography	0.1	0.0	3	0.2	0.0	3	OA	species	adult	N	0.02	<1	A	bacteria	0.14
383	79	Li	2018	Progress in Oceanography	0.1	0.0	3	0.1	0.0	3	Temp	species	adult	N	0.02	<1	A	bacteria	0.14
384	79	Li	2018	Progress in Oceanography	0.1	0.0	3	0.2	0.0	3	OAT	species	adult	N	0.02	<1	A	bacteria	0.14
385	80	Liu	2015	Marine Biology Reseach	7.4	0.2	3	8.4	0.8	3	OA	species	adult	N	0.25	<1	A	macroalgae	3
386	80	Liu	2015	Marine Biology Reseach	7.4	0.2	3	9.7	0.6	3	Temp	species	adult	N	0.25	<1	A	macroalgae	3
387	80	Liu	2015	Marine Biology Reseach	7.4	0.2	3	11.2	2.3	3	OAT	species	adult	N	0.25	<1	A	macroalgae	3
388	81	Liu	2015	Hydrobiologia	5.1	0.1	3	6.5	0.1	3	OA	species	adult	N	6	1 to 10	A	macroalgae	3
389	81	Liu	2015	Hydrobiologia	5.1	0.1	3	3.5	1.1	3	Temp	species	adult	N	6	1 to 10	A	macroalgae	3
390	81	Liu	2015	Hydrobiologia	5.1	0.1	3	4.8	1.0	3	OAT	species	adult	N	6	1 to 10	A	macroalgae	3
391	82	Liu	2018	Journal of Applied Phycology	7.5	0.6	3	7.6	0.7	3	OA	species	adult	N	6	1 to 10	A	macroalgae	1.4
392	82	Liu	2018	Journal of Applied Phycology	7.5	0.6	3	9.5	0.8	3	Temp	species	adult	N	6	1 to 10	A	macroalgae	1.4
393	82	Liu	2018	Journal of Applied Phycology	7.5	0.6	3	10.0	0.3	3	OAT	species	adult	N	6	1 to 10	A	macroalgae	1.4
394	83	Lord	2017	MEPS	0.3	0.1	8	0.3	0.2	8	OA	species	juvenile	Y	2	1 to 10	H	mollusc	10
395	83	Lord	2017	MEPS	0.1	0.0	8	0.0	0.0	8	OA	species	juvenile	Y	35	>10	H	mollusc	10
396	83	Lord	2017	MEPS	0.3	0.1	8	0.4	0.2	8	Temp	species	juvenile	Y	2	1 to 10	H	mollusc	10
397	83	Lord	2017	MEPS	0.1	0.0	8	0.0	0.0	8	Temp	species	juvenile	Y	35	>10	H	mollusc	10
398	83	Lord	2017	MEPS	0.3	0.1	8	0.3	0.2	8	OAT	species	juvenile	Y	2	1 to 10	H	mollusc	10
399	83	Lord	2017	MEPS	0.1	0.0	8	0.0	0.0	8	OAT	species	juvenile	Y	35	>10	H	mollusc	10
400	84	Manno	2012	Polar Biology	170.2	7.4	3	140.8	6.3	3	OA	species	juvenile	Y	0.55	<1	A	foraminifer	0.9
401	84	Manno	2012	Polar Biology	310.4	13.4	3	249.8	10.6	3	OA	species	adult	Y	0.55	<1	A	foraminifer	0.9
402	84	Manno	2012	Polar Biology	170.2	7.4	3	170.2	7.4	3	Temp	species	juvenile	Y	0.55	<1	A	foraminifer	0.9
403	84	Manno	2012	Polar Biology	310.4	13.4	3	310.4	13.4	3	Temp	species	adult	Y	0.55	<1	A	foraminifer	0.9
404	84	Manno	2012	Polar Biology	170.2	7.4	3	150.8	6.7	3	OAT	species	juvenile	Y	0.55	<1	A	foraminifer	0.9
405	84	Manno	2012	Polar Biology	310.4	13.4	3	270.8	12.0	3	OAT	species	adult	Y	0.55	<1	A	foraminifer	0.9
406	85	Manriquez	2016	PLoS One	0.6	0.1	3	0.4	0.1	3	OA	species	juvenile	Y	10	1 to 10	H	mollusc	1.5
407	85	Manriquez	2016	PLoS One	0.6	0.1	3	0.7	0.1	3	Temp	species	juvenile	Y	10	1 to 10	H	mollusc	1.5
408	85	Manriquez	2016	PLoS One	0.6	0.1	3	0.5	0.1	3	OAT	species	juvenile	Y	10	1 to 10	H	mollusc	1.5

409	86	Melatunan	2013	MEPS	6.4	1.9	16	1.6	2.3	16	OA	species	adult	Y	10	1 to 10	H	mollusc	4.3
410	86	Melatunan	2013	MEPS	6.4	1.9	16	1.4	1.7	16	Temp	species	adult	Y	10	1 to 10	H	mollusc	4.3
411	86	Melatunan	2013	MEPS	6.4	1.9	16	-1.8	1.4	16	OAT	species	adult	Y	10	1 to 10	H	mollusc	4.3
412	87	Mensch	2016	Frontiers in Microbiology	1.4	0.1	11	1.5	0.2	11	OA	species	adult	N	5	1 to 10	A	macroalgae	11
413	87	Mensch	2016	Frontiers in Microbiology	1.4	0.1	11	1.3	0.2	11	Temp	species	adult	N	5	1 to 10	A	macroalgae	11
414	87	Mensch	2016	Frontiers in Microbiology	1.4	0.1	11	1.4	0.2	11	OAT	species	adult	N	5	1 to 10	A	macroalgae	11
415	88	Miller	2012	Nature Climate Change	29.8	5.3	35	33.3	6.8	37	OA	species	juvenile	N	10	1 to 10	H	fish	4.6
416	88	Miller	2012	Nature Climate Change	29.8	5.3	35	30.0	6.9	39	Temp	species	juvenile	N	10	1 to 10	H	fish	4.6
417	88	Miller	2012	Nature Climate Change	29.8	5.3	35	31.2	7.2	35	OAT	species	juvenile	N	10	1 to 10	H	fish	4.6
418	89	Miller	2015	Ecological Applications	3.2	0.0	4	3.3	0.0	5	OA	species	larvae	N	10	1 to 10	H	fish	1.2
419	89	Miller	2015	Ecological Applications	3.2	0.0	4	3.1	0.0	4	Temp	species	larvae	N	10	1 to 10	H	fish	1.2
420	89	Miller	2015	Ecological Applications	3.2	0.0	4	3.0	0.0	4	OAT	species	larvae	N	10	1 to 10	H	fish	1.2
421	90	Milner	2016	Limnology & Oceanography	0.8	0.0	4	0.8	0.0	4	OA	species	adult	Y	0.14	<1	A	phytoplankton (coccolithophore)	1
422	90	Milner	2016	Limnology & Oceanography	0.8	0.0	4	1.0	0.0	4	Temp	species	adult	Y	0.14	<1	A	phytoplankton (coccolithophore)	1
423	90	Milner	2016	Limnology & Oceanography	0.8	0.0	4	1.0	0.1	4	OAT	species	adult	Y	0.14	<1	A	phytoplankton (coccolithophore)	1
424	91	Minich	2018	PLoS One	11.8	2.6	18	11.5	4.2	18	OA	species	adult	N	5	1 to 10	A	macroalgae	4
425	91	Minich	2018	PLoS One	11.8	2.6	18	7.0	3.6	18	Temp	species	adult	N	5	1 to 10	A	macroalgae	4
426	91	Minich	2018	PLoS One	11.8	2.6	18	14.8	3.7	18	OAT	species	adult	N	5	1 to 10	A	macroalgae	4
427	92	Mos	2019	Science of the Total Environment	716.5	93.4	5	767.0	73.7	5	OA	species	larvae	Y	5	1 to 10	H	echinoids	2
428	92	Mos	2019	Science of the Total Environment	716.5	93.4	5	760.4	44.2	5	Temp	species	larvae	Y	5	1 to 10	H	echinoids	2
429	92	Mos	2019	Science of the Total Environment	716.5	93.4	5	782.4	49.1	5	OAT	species	larvae	Y	5	1 to 10	H	echinoids	2
430	93	Munoz	2018	Aquatic Botany	0.0	0.0	3	0.1	0.1	3	OA	species	adult	Y	6	1 to 10	A	macroalgae (CCA)	0.3
431	93	Munoz	2018	Aquatic Botany	0.0	0.0	3	-0.4	0.1	3	Temp	species	adult	Y	6	1 to 10	A	macroalgae (CCA)	0.3
432	93	Munoz	2018	Aquatic Botany	0.0	0.0	3	0.1	0.0	3	OAT	species	adult	Y	6	1 to 10	A	macroalgae (CCA)	0.3
433	94	Murray	2018	Diversity-Basel	0.3	0.1	10	0.3	0.0	10	OA	species	larvae	N	2	1 to 10	H	fish	2.3
434	94	Murray	2018	Diversity-Basel	0.3	0.1	10	0.5	0.1	10	Temp	species	larvae	N	2	1 to 10	H	fish	2
435	94	Murray	2018	Diversity-Basel	0.3	0.1	10	0.4	0.1	10	OAT	species	larvae	N	2	1 to 10	H	fish	2

436	95	Nguyen	2012	Global Change Biology	579.5	39.4	12	556.8	118.1	12	OA	species	larvae	Y	10	1 to 10	H	echinoids	0.7
437	95	Nguyen	2012	Global Change Biology	579.5	39.4	12	550.0	39.4	12	Temp	species	larvae	Y	10	1 to 10	H	echinoids	0.7
438	95	Nguyen	2012	Global Change Biology	579.5	39.4	12	547.7	70.9	12	OAT	species	larvae	Y	10	1 to 10	H	echinoids	0.7
439	96	Nguyen	2014	JEMBE	463.4	25.7	6	462.0	19.7	6	OA	species	juvenile	Y	10	1 to 10	H	echinoids	4
440	96	Nguyen	2014	JEMBE	463.4	25.7	6	454.1	30.9	6	Temp	species	juvenile	Y	10	1 to 10	H	echinoids	4
441	96	Nguyen	2014	JEMBE	463.4	25.7	6	448.4	20.1	6	OAT	species	juvenile	Y	10	1 to 10	H	echinoids	4
442	97	Ni	2018	Biogeosciences	6.2	1.1	3	7.2	1.2	3	OA	species	juvenile	Y	1.3	1 to 10	H	polychaete	2.4
443	97	Ni	2018	Biogeosciences	1.9	0.5	3	1.6	0.2	3	OA	species	juvenile	Y	1.3	1 to 10	H	polychaete	2.6
444	97	Ni	2018	Biogeosciences	0.7	0.1	3	0.7	0.1	3	OA	species	juvenile	Y	1.3	1 to 10	H	polychaete	2.7
445	97	Ni	2018	Biogeosciences	6.2	1.1	3	8.1	1.5	3	Temp	species	juvenile	Y	1.3	1 to 10	H	polychaete	2.4
446	97	Ni	2018	Biogeosciences	1.9	0.5	3	1.6	0.5	3	Temp	species	juvenile	Y	1.3	1 to 10	H	polychaete	2.6
447	97	Ni	2018	Biogeosciences	0.7	0.1	3	0.8	0.3	3	Temp	species	juvenile	Y	1.3	1 to 10	H	polychaete	2.7
448	97	Ni	2018	Biogeosciences	6.2	1.1	3	7.0	0.2	3	OAT	species	juvenile	Y	1.3	1 to 10	H	polychaete	2.4
449	97	Ni	2018	Biogeosciences	1.9	0.5	3	1.7	0.6	3	OAT	species	juvenile	Y	1.3	1 to 10	H	polychaete	2.6
450	97	Ni	2018	Biogeosciences	0.7	0.1	3	0.4	0.1	3	OAT	species	juvenile	Y	1.3	1 to 10	H	polychaete	2.7
451	98	Nishida	2018	Geochimica Et Cosmochimica Acta	27.2	1.2	11	26.7	1.2	11	OA	species	juvenile	Y	20	>10	H	mollusc	6.3
452	98	Nishida	2018	Geochimica Et Cosmochimica Acta	27.2	1.2	11	37.9	1.2	11	Temp	species	juvenile	Y	20	>10	H	mollusc	7.9
453	98	Nishida	2018	Geochimica Et Cosmochimica Acta	27.2	1.2	11	37.4	1.2	11	OAT	species	juvenile	Y	20	>10	H	mollusc	7.9
454	99	Olischlager	2013	Journal of Experimental Botany	8.1	2.8	6	8.9	1.2	6	OA	species	adult	N	6	1 to 10	A	macroalgae	2
455	99	Olischlager	2013	Journal of Experimental Botany	2.9	0.3	3	5.9	0.3	3	OA	species	adult	N	6	1 to 10	A	macroalgae	2.9
456	99	Olischlager	2013	Journal of Experimental Botany	8.1	2.8	6	12.8	1.1	6	Temp	species	adult	N	6	1 to 10	A	macroalgae	2
457	99	Olischlager	2013	Journal of Experimental Botany	2.9	0.3	3	11.3	0.3	6	Temp	species	adult	N	6	1 to 10	A	macroalgae	2.9
458	99	Olischlager	2013	Journal of Experimental Botany	8.1	2.8	6	14.0	1.0	6	OAT	species	adult	N	6	1 to 10	A	macroalgae	2
459	99	Olischlager	2013	Journal of Experimental Botany	2.9	0.3	3	11.6	1.4	6	OAT	species	adult	N	6	1 to 10	A	macroalgae	2.9
460	100	Olischlager	2017	Planta	6.7	0.4	3	7.6	1.0	3	OA	species	adult	N	4	1 to 10	A	macroalgae	2.6
461	100	Olischlager	2017	Planta	12.5	1.4	3	12.7	0.8	3	OA	species	adult	N	4	1 to 10	A	macroalgae	2.6
462	100	Olischlager	2017	Planta	6.7	0.4	3	10.5	0.7	3	Temp	species	adult	N	4	1 to 10	A	macroalgae	2.6
463	100	Olischlager	2017	Planta	12.5	1.4	3	12.6	0.8	3	Temp	species	adult	N	4	1 to 10	A	macroalgae	2.6

464	100	Olischlager	2017	Planta	6.7	0.4	3	12.1	1.4	3	OAT	species	adult	N	4	1 to 10	A	macroalgae	2.6
465	100	Olischlager	2017	Planta	12.5	1.4	3	13.3	0.6	3	OAT	species	adult	N	4	1 to 10	A	macroalgae	2.6
466	101	Ordoꝺez	2017	PLoS One	8.8	2.4	3	7.9	2.4	3	OA	species	larvae	Y	50	>10	A	macroalgae (CCA)	0.3
467	101	Ordoꝺez	2017	PLoS One	8.8	2.4	3	8.7	1.3	3	Temp	species	larvae	Y	50	>10	A	macroalgae (CCA)	0.3
468	101	Ordoꝺez	2017	PLoS One	8.8	2.4	3	8.9	1.2	3	OAT	species	larvae	Y	50	>10	A	macroalgae (CCA)	0.3
469	102	Ou	2017	Harmful Algae	0.2	0.1	3	0.4	0.1	3	OA	species	adult	N	0.02	<1	A	phytoplankton	13
470	102	Ou	2017	Harmful Algae	0.2	0.1	3	0.3	0.1	3	Temp	species	adult	N	0.02	<1	A	phytoplankton	13
471	102	Ou	2017	Harmful Algae	0.2	0.1	3	0.4	0.0	3	OAT	species	adult	N	0.02	<1	A	phytoplankton	13
472	103	Padilla-Gar	2013	Proc Roy Soc B	0.3	0.1	3	0.3	0.0	3	OA	species	larvae	Y	20	>10	H	echinoids	0.4
473	103	Padilla-Gar	2013	Proc Roy Soc B	0.3	0.1	3	0.3	0.1	3	Temp	species	larvae	Y	20	>10	H	echinoids	0.4
474	103	Padilla-Gar	2013	Proc Roy Soc B	0.3	0.1	3	0.3	0.1	3	OAT	species	larvae	Y	20	>10	H	echinoids	0.4
475	104	Pansch	2013	Marine Biology	0.0	0.0	8	0.0	0.0	8	OA	species	juvenile	Y	2	1 to 10	H	crustacean	8
476	104	Pansch	2013	Marine Biology	0.0	0.0	8	0.0	0.0	8	Temp	species	juvenile	Y	2	1 to 10	H	crustacean	8
477	104	Pansch	2013	Marine Biology	0.0	0.0	8	0.0	0.0	8	OAT	species	juvenile	Y	2	1 to 10	H	crustacean	8
478	105	Pimentel	2014	Journal of Experimental Biology	13.3	1.4	60	10.3	1.0	60	OA	species	larvae	N	40	>10	H	fish	4.3
479	105	Pimentel	2014	Journal of Experimental Biology	13.3	1.4	60	19.4	1.1	60	Temp	species	larvae	N	40	>10	H	fish	4.3
480	105	Pimentel	2014	Journal of Experimental Biology	13.3	1.4	60	15.4	1.9	60	OAT	species	larvae	N	40	>10	H	fish	4.3
481	106	Pimentel	2016	Climatic Change	0.1	0.0	12	0.1	0.0	12	OA	species	larvae	N	11	>10	H	fish	2.1
482	106	Pimentel	2016	Climatic Change	0.1	0.0	12	0.1	0.0	12	OA	species	larvae	N	30	>10	H	fish	2.1
483	106	Pimentel	2016	Climatic Change	0.1	0.0	12	0.1	0.0	12	Temp	species	larvae	N	11	>10	H	fish	2.1
484	106	Pimentel	2016	Climatic Change	0.1	0.0	12	0.1	0.0	12	Temp	species	larvae	N	30	>10	H	fish	2.1
485	106	Pimentel	2016	Climatic Change	0.1	0.0	12	0.1	0.0	12	OAT	species	larvae	N	11	>10	H	fish	2.1
486	106	Pimentel	2016	Climatic Change	0.1	0.0	12	0.1	0.0	12	OAT	species	larvae	N	30	>10	H	fish	2.1
487	107	Pistevos	2015	Scientific Reports	0.7	0.2	3	0.2	0.1	3	OA	species	juvenile	N	35	>10	H	fish	9.7
488	107	Pistevos	2015	Scientific Reports	0.7	0.2	3	0.5	0.2	3	Temp	species	juvenile	N	35	>10	H	fish	9.7
489	107	Pistevos	2015	Scientific Reports	0.7	0.2	3	0.2	0.1	3	OAT	species	juvenile	N	35	>10	H	fish	9.7
490	108	Poore	2016	Marine Biology	39.6	6.7	3	53.1	8.6	3	OA	species	adult	N	3	1 to 10	A	macroalgae	2
491	108	Poore	2016	Marine Biology	22.7	10.4	3	47.8	20.2	3	OA	species	adult	N	3	1 to 10	A	macroalgae	2
492	108	Poore	2016	Marine Biology	38.6	4.9	3	41.4	19.8	3	OA	species	adult	N	6	1 to 10	A	macroalgae	2
493	108	Poore	2016	Marine Biology	10.5	2.7	3	16.3	2.8	3	OA	species	adult	N	6	1 to 10	A	macroalgae	2
494	108	Poore	2016	Marine Biology	32.8	6.9	3	33.0	6.6	3	OA	species	adult	N	6	1 to 10	A	macroalgae	2
495	108	Poore	2016	Marine Biology	71.2	8.4	3	62.8	8.4	3	OA	species	adult	N	4	1 to 10	A	macroalgae	2
496	108	Poore	2016	Marine Biology	39.6	6.7	3	37.9	8.6	3	Temp	species	adult	N	3	1 to 10	A	macroalgae	2
497	108	Poore	2016	Marine Biology	22.7	10.4	3	54.5	15.9	3	Temp	species	adult	N	3	1 to 10	A	macroalgae	2
498	108	Poore	2016	Marine Biology	38.6	4.9	3	55.7	13.0	3	Temp	species	adult	N	6	1 to 10	A	macroalgae	2
499	108	Poore	2016	Marine Biology	10.5	2.7	3	11.5	2.7	3	Temp	species	adult	N	6	1 to 10	A	macroalgae	2
500	108	Poore	2016	Marine Biology	32.8	6.9	3	35.5	6.6	3	Temp	species	adult	N	6	1 to 10	A	macroalgae	2
501	108	Poore	2016	Marine Biology	71.2	8.4	3	56.2	7.7	3	Temp	species	adult	N	4	1 to 10	A	macroalgae	2
502	108	Poore	2016	Marine Biology	39.6	6.7	3	48.1	9.2	3	OAT	species	adult	N	3	1 to 10	A	macroalgae	2

503	108	Poore	2016	Marine Biology	22.7	10.4	3	37.9	10.4	3	OAT	species	adult	N	3	1 to 10	A	macroalgae	2
504	108	Poore	2016	Marine Biology	38.6	4.9	3	58.9	13.0	3	OAT	species	adult	N	6	1 to 10	A	macroalgae	2
505	108	Poore	2016	Marine Biology	10.5	2.7	3	11.1	2.5	3	OAT	species	adult	N	6	1 to 10	A	macroalgae	2
506	108	Poore	2016	Marine Biology	32.8	6.9	3	25.4	7.2	3	OAT	species	adult	N	6	1 to 10	A	macroalgae	2
507	108	Poore	2016	Marine Biology	71.2	8.4	3	76.1	11.5	3	OAT	species	adult	N	4	1 to 10	A	macroalgae	2
508	109	Pope	2014	Biogeosciences	11.1	0.4	3	10.5	0.5	3	OA	species	larvae	N	15	>10	H	fish	6
509	109	Pope	2014	Biogeosciences	11.1	0.4	3	11.1	0.8	3	Temp	species	larvae	N	15	>10	H	fish	6
510	109	Pope	2014	Biogeosciences	11.1	0.4	3	11.2	0.5	3	OAT	species	larvae	N	15	>10	H	fish	6
511	110	Qu	2018	Limnology & Oceanography	0.6	0.0	3	0.6	0.0	3	OA	species	adult	N	0.02	<1	A	phytoplankton	0.3
512	110	Qu	2018	Limnology & Oceanography	0.6	0.0	3	0.9	0.0	3	Temp	species	adult	N	0.02	<1	A	phytoplankton	0.3
513	110	Qu	2018	Limnology & Oceanography	0.6	0.0	3	0.9	0.1	3	OAT	species	adult	N	0.02	<1	A	phytoplankton	0.3
514	111	Rosa	2014	Proc Roy Soc B	1.3	0.2	3	1.3	0.3	3	OA	species	egg	N	20	>10	H	fish	13.1
515	111	Rosa	2014	Proc Roy Soc B	1.3	0.2	3	1.8	0.3	3	Temp	species	egg	N	20	>10	H	fish	13.1
516	111	Rosa	2014	Proc Roy Soc B	1.3	0.2	3	1.6	0.2	3	OAT	species	egg	N	20	>10	H	fish	13.1
517	112	Rosa	2014	Journal of Experimental Biology	8.3	3.5	10	3.4	0.5	10	OA	species	egg	N	3.5	1 to 10	H	cephalopod	3.9
518	112	Rosa	2014	Journal of Experimental Biology	8.3	3.5	10	7.5	2.0	10	Temp	species	egg	N	3.5	1 to 10	H	cephalopod	2
519	112	Rosa	2014	Journal of Experimental Biology	8.3	3.5	10	4.2	3.4	10	OAT	species	egg	N	3.5	1 to 10	H	cephalopod	2
520	113	Roth-Schul	2018	Limnology and Oceanography	0.8	0.1	3	0.8	0.1	3	OA	communities	adult	N	0.001	<1	A	bacteria	3
521	113	Roth-Schul	2018	Limnology and Oceanography	0.8	0.1	3	1.1	0.0	3	Temp	communities	adult	N	0.001	<1	A	bacteria	3
522	113	Roth-Schul	2018	Limnology and Oceanography	0.8	0.1	3	1.3	0.1	3	OAT	communities	adult	N	0.001	<1	A	bacteria	3
523	114	Sampaio	2017	Marine Environmental Research	0.1	0.0	3	0.2	0.1	3	OA	species	adult	N	0.25	<1	A	macroalgae	1
524	114	Sampaio	2017	Marine Environmental Research	0.1	0.0	3	0.1	0.1	3	Temp	species	adult	N	0.25	<1	A	macroalgae	1
525	114	Sampaio	2017	Marine Environmental Research	0.1	0.0	3	0.1	0.1	3	OAT	species	adult	N	0.25	<1	A	macroalgae	1
526	115	Sarker	2013	Botanica Marina	7.2	0.7	5	6.7	0.5	5	OA	species	adult	N	10	1 to 10	A	macroalgae	0.6
527	115	Sarker	2013	Botanica Marina	8.4	0.8	5	9.3	0.3	5	OA	species	adult	N	10	1 to 10	A	macroalgae	1.1
528	115	Sarker	2013	Botanica Marina	7.2	0.7	5	5.3	0.4	5	Temp	species	adult	N	10	1 to 10	A	macroalgae	0.6
529	115	Sarker	2013	Botanica Marina	8.4	0.8	5	7.3	0.6	5	Temp	species	adult	N	10	1 to 10	A	macroalgae	1.1
530	115	Sarker	2013	Botanica Marina	7.2	0.7	5	7.1	0.4	5	OAT	species	adult	N	10	1 to 10	A	macroalgae	0.6
531	115	Sarker	2013	Botanica Marina	8.4	0.8	5	9.3	0.5	5	OAT	species	adult	N	10	1 to 10	A	macroalgae	1.1
532	116	Schluter	2014	Nature Climate Change	1.1	0.0	5	1.1	0.0	5	OA	species	adult	Y	0.14	<1	A	phytoplankton (coccolithophore)	52

533	116	Schluter	2014	Nature Climate Change	1.1	0.0	5	1.3	0.0	5	Temp	species	adult	Y	0.14	<1	A	phytoplankton (coccolithophore)	52
534	116	Schluter	2014	Nature Climate Change	1.1	0.0	5	1.2	0.0	5	OAT	species	adult	Y	0.14	<1	A	phytoplankton (coccolithophore)	52
535	117	Schoenrock	2015	Marine Biology	-6.1	10.0	12	1.7	8.2	12	OA	species	adult	N	0.7	<1	A	macroalgae	11.3
536	117	Schoenrock	2015	Marine Biology	3.3	20.9	12	-2.2	12.2	12	OA	species	adult	N	0.7	<1	A	macroalgae	11.3
537	117	Schoenrock	2015	Marine Biology	-6.1	10.0	12	-10.3	10.9	12	Temp	species	adult	N	0.7	<1	A	macroalgae	11.3
538	117	Schoenrock	2015	Marine Biology	3.3	20.9	12	3.6	7.8	12	Temp	species	adult	N	0.7	<1	A	macroalgae	11.3
539	117	Schoenrock	2015	Marine Biology	-6.1	10.0	12	0.1	10.9	12	OAT	species	adult	N	0.7	<1	A	macroalgae	11.3
540	117	Schoenrock	2015	Marine Biology	3.3	20.9	12	2.5	8.7	12	OAT	species	adult	N	0.7	<1	A	macroalgae	11.3
541	118	Schoenrock	2016	JEMBE	0.1	0.7	18	0.2	0.9	18	OA	species	adult	Y	50	>10	A	macroalgae (CCA)	6.7
542	118	Schoenrock	2016	JEMBE	0.1	0.3	18	0.0	0.3	18	OA	species	adult	Y	50	>10	A	macroalgae (CCA)	6.7
543	118	Schoenrock	2016	JEMBE	0.1	0.7	18	0.0	0.8	18	Temp	species	adult	Y	50	>10	A	macroalgae (CCA)	6.7
544	118	Schoenrock	2016	JEMBE	0.1	0.3	18	0.2	0.3	18	Temp	species	adult	Y	50	>10	A	macroalgae (CCA)	6.7
545	118	Schoenrock	2016	JEMBE	0.1	0.7	18	0.1	0.6	18	OAT	species	adult	Y	50	>10	A	macroalgae (CCA)	6.7
546	118	Schoenrock	2016	JEMBE	0.1	0.3	18	0.0	0.3	18	OAT	species	adult	Y	50	>10	A	macroalgae (CCA)	6.7
547	119	Schram	2016	Ices Journal of Marine Science	-0.1	0.1	18	0.0	0.1	18	OA	species	adult	Y	60	>10	H	mollusc	6
548	119	Schram	2016	Ices Journal of Marine Science	4.5	6.5	18	7.4	6.0	18	OA	species	adult	Y	60	>10	H	mollusc	6
549	119	Schram	2016	Ices Journal of Marine Science	-0.1	0.1	18	-0.1	0.1	18	Temp	species	adult	Y	60	>10	H	mollusc	6
550	119	Schram	2016	Ices Journal of Marine Science	4.5	6.5	18	4.5	3.7	18	Temp	species	adult	Y	60	>10	H	mollusc	6
551	119	Schram	2016	Ices Journal of Marine Science	-0.1	0.1	18	-0.1	0.1	18	OAT	species	adult	Y	60	>10	H	mollusc	6
552	119	Schram	2016	Ices Journal of Marine Science	4.5	6.5	18	3.7	7.1	18	OAT	species	adult	Y	60	>10	H	mollusc	6
553	120	Schram	2016	MEPS	-3.0	12.1	12	-7.9	12.1	12	OA	species	adult	Y	3	1 to 10	H	mollusc	12.9
554	120	Schram	2016	MEPS	-5.9	13.9	12	-2.4	8.8	11	OA	species	adult	Y	1	1 to 10	H	mollusc	12.9
555	120	Schram	2016	MEPS	-3.0	12.1	12	-0.3	10.9	7	Temp	species	adult	Y	3	1 to 10	H	mollusc	12.9
556	120	Schram	2016	MEPS	-5.9	13.9	12	-8.0	26.1	6	Temp	species	adult	Y	1	1 to 10	H	mollusc	12.9
557	120	Schram	2016	MEPS	-3.0	12.1	12	-9.5	12.4	7	OAT	species	adult	Y	3	1 to 10	H	mollusc	12.9
558	120	Schram	2016	MEPS	-5.9	13.9	12	5.7	10.7	5	OAT	species	adult	Y	1	1 to 10	H	mollusc	12.9
559	121	Shuka	2017	Phycologia	19.1	11.4	15	25.8	13.5	15	OA	species	larvae	N	5	1 to 10	A	macroalgae	15
560	121	Shuka	2017	Phycologia	19.1	11.4	15	18.4	19.7	15	Temp	species	larvae	N	5	1 to 10	A	macroalgae	15
561	121	Shuka	2017	Phycologia	19.1	11.4	15	33.4	10.7	15	OAT	species	larvae	N	5	1 to 10	A	macroalgae	15
562	122	Sinutok	2011	Limnology & Oceanography	0.0	0.0	4	0.0	0.0	4	OA	species	adult	Y	2	1 to 10	A	macroalgae (CCA)	4
563	122	Sinutok	2011	Limnology & Oceanography	0.0	0.0	4	0.0	0.0	4	OA	species	adult	Y	2	1 to 10	A	macroalgae (CCA)	4
564	122	Sinutok	2011	Limnology & Oceanography	0.0	0.0	4	0.0	0.0	4	Temp	species	adult	Y	2	1 to 10	A	macroalgae (CCA)	4
565	122	Sinutok	2011	Limnology & Oceanography	0.0	0.0	4	-0.2	0.4	4	Temp	species	adult	Y	2	1 to 10	A	macroalgae (CCA)	4
566	122	Sinutok	2011	Limnology & Oceanography	0.0	0.0	4	0.0	0.0	4	OAT	species	adult	Y	2	1 to 10	A	macroalgae (CCA)	4
567	122	Sinutok	2011	Limnology & Oceanography	0.0	0.0	4	0.0	0.0	4	OAT	species	adult	Y	2	1 to 10	A	macroalgae (CCA)	4

568	123	Small	2016	Marine Biology	5.7	9.4	18	7.0	23.5	18	OA	species	juvenile	Y	50	>10	H	crustacean	5
569	123	Small	2016	Marine Biology	5.7	9.4	18	17.1	18.1	18	Temp	species	juvenile	Y	50	>10	H	crustacean	5
570	123	Small	2016	Marine Biology	5.7	9.4	18	14.3	23.5	18	OAT	species	juvenile	Y	50	>10	H	crustacean	5
571	124	Speights	2017	Ecology and Evolution	0.9	1.7	92	1.0	3.1	92	OA	species	juvenile	Y	20	>10	H	mollusc	21.7
572	124	Speights	2017	Ecology and Evolution	0.9	1.7	92	1.2	4.7	92	Temp	species	juvenile	Y	20	>10	H	mollusc	21.7
573	124	Speights	2017	Ecology and Evolution	0.9	1.7	92	1.1	2.5	92	OAT	species	juvenile	Y	20	>10	H	mollusc	21.7
574	125	Sswat	2018	PLoS One	0.0	0.0	3	0.0	0.0	3	OA	species	larvae	N	20	>10	H	fish	4.6
575	125	Sswat	2018	PLoS One	0.0	0.0	3	0.0	0.0	3	Temp	species	larvae	N	20	>10	H	fish	4.6
576	125	Sswat	2018	PLoS One	0.0	0.0	3	0.0	0.0	3	OAT	species	larvae	N	20	>10	H	fish	4.6
577	126	Stevens	2018	MEPS	0.1	0.0	4	0.1	0.0	4	OA	species	juvenile	Y	24	>10	H	mollusc	4
578	126	Stevens	2018	MEPS	0.0	0.0	4	0.0	0.0	4	OA	species	juvenile	Y	20	>10	H	mollusc	4
579	126	Stevens	2018	MEPS	0.1	0.0	4	0.1	0.1	4	OA	species	juvenile	Y	2	1 to 10	H	mollusc	4
580	126	Stevens	2018	MEPS	0.0	0.0	4	0.0	0.0	4	OA	species	juvenile	Y	40	>10	H	mollusc	4
581	126	Stevens	2018	MEPS	0.1	0.0	4	0.0	0.0	4	Temp	species	juvenile	Y	24	>10	H	mollusc	4
582	126	Stevens	2018	MEPS	0.0	0.0	4	0.0	0.0	4	Temp	species	juvenile	Y	20	>10	H	mollusc	4
583	126	Stevens	2018	MEPS	0.1	0.0	4	0.1	0.0	4	Temp	species	juvenile	Y	2	1 to 10	H	mollusc	4
584	126	Stevens	2018	MEPS	0.0	0.0	4	0.0	0.0	4	Temp	species	juvenile	Y	40	>10	H	mollusc	4
585	126	Stevens	2018	MEPS	0.1	0.0	4	0.0	0.0	4	OAT	species	juvenile	Y	24	>10	H	mollusc	4
586	126	Stevens	2018	MEPS	0.0	0.0	4	0.0	0.0	4	OAT	species	juvenile	Y	20	>10	H	mollusc	4
587	126	Stevens	2018	MEPS	0.1	0.0	4	0.1	0.0	4	OAT	species	juvenile	Y	2	1 to 10	H	mollusc	4
588	126	Stevens	2018	MEPS	0.0	0.0	4	0.0	0.0	4	OAT	species	juvenile	Y	40	>10	H	mollusc	4
589	127	Swezey	2017	Proc Roy Soc B	1.4	0.5	8	1.6	0.6	8	OA	species	adult	Y	1	1 to 10	H	bryozoa	8
590	127	Swezey	2017	Proc Roy Soc B	1.4	0.5	8	1.5	0.5	8	Temp	species	adult	Y	1	1 to 10	H	bryozoa	8
591	127	Swezey	2017	Proc Roy Soc B	1.4	0.5	8	1.6	0.6	8	OAT	species	adult	Y	1	1 to 10	H	bryozoa	8
592	128	Swiney	2017	Ices Journal of Marine Science	4.9	5.3	10	3.7	6.3	6	OA	species	juvenile	Y	20	>10	H	crustacean	26.3
593	128	Swiney	2017	Ices Journal of Marine Science	4.9	5.3	10	2.6	3.3	7	Temp	species	juvenile	Y	20	>10	H	crustacean	26.3
594	128	Swiney	2017	Ices Journal of Marine Science	4.9	5.3	10	2.1	3.2	11	OAT	species	juvenile	Y	20	>10	H	crustacean	26.3
595	129	Talmage	2011	PLoS One	460.6	30.3	4	352.7	36.4	4	OA	species	larvae	Y	40	>10	H	mollusc	2.9
596	129	Talmage	2011	PLoS One	480.7	30.7	4	333.2	34.4	4	OA	species	larvae	Y	2	1 to 10	H	mollusc	2.9
597	129	Talmage	2011	PLoS One	0.1	0.0	3	0.1	0.0	3	OA	species	juvenile	Y	40	>10	H	mollusc	6.4
598	129	Talmage	2011	PLoS One	0.4	0.1	3	0.2	0.1	3	OA	species	juvenile	Y	20	>10	H	mollusc	6.4
599	129	Talmage	2011	PLoS One	0.2	0.1	3	0.1	0.0	3	OA	species	juvenile	Y	2	1 to 10	H	mollusc	6.4
600	129	Talmage	2011	PLoS One	460.6	30.3	4	450.9	24.2	4	Temp	species	larvae	Y	40	>10	H	mollusc	2.9
601	129	Talmage	2011	PLoS One	480.7	30.7	4	461.1	22.1	4	Temp	species	larvae	Y	2	1 to 10	H	mollusc	2.9
602	129	Talmage	2011	PLoS One	0.1	0.0	3	0.0	0.0	3	Temp	species	juvenile	Y	40	>10	H	mollusc	6.4
603	129	Talmage	2011	PLoS One	0.4	0.1	3	0.2	0.2	3	Temp	species	juvenile	Y	20	>10	H	mollusc	6.4
604	129	Talmage	2011	PLoS One	0.2	0.1	3	0.0	0.0	3	Temp	species	juvenile	Y	2	1 to 10	H	mollusc	6.4
605	129	Talmage	2011	PLoS One	460.6	30.3	4	327.3	18.2	4	OAT	species	larvae	Y	40	>10	H	mollusc	2.9
606	129	Talmage	2011	PLoS One	480.7	30.7	4	313.5	34.4	4	OAT	species	larvae	Y	2	1 to 10	H	mollusc	2.9
607	129	Talmage	2011	PLoS One	0.1	0.0	3	0.1	0.0	3	OAT	species	juvenile	Y	40	>10	H	mollusc	6.4
608	129	Talmage	2011	PLoS One	0.4	0.1	3	0.3	0.2	3	OAT	species	juvenile	Y	20	>10	H	mollusc	6.4
609	129	Talmage	2011	PLoS One	0.2	0.1	3	0.0	0.0	3	OAT	species	juvenile	Y	2	1 to 10	H	mollusc	6.4

610	130	Tatters	2013	Harmful Algae	0.1	0.0	3	0.1	0.0	3	OA	species	adult	N	0.02	<1	A	phytoplankton	34.7
611	130	Tatters	2013	Harmful Algae	0.1	0.0	3	0.1	0.0	3	Temp	species	adult	N	0.02	<1	A	phytoplankton	34.7
612	130	Tatters	2013	Harmful Algae	0.1	0.0	3	0.1	0.0	3	OAT	species	adult	N	0.02	<1	A	phytoplankton	34.7
613	131	Thiyagaraja	2012	Aquaculture	7.3	0.5	4	7.5	0.8	4	OA	species	larvae	Y	20	>10	H	mollusc	0.7
614	131	Thiyagaraja	2012	Aquaculture	7.3	0.5	4	6.5	1.0	4	Temp	species	larvae	Y	20	>10	H	mollusc	0.7
615	131	Thiyagaraja	2012	Aquaculture	7.3	0.5	4	6.1	0.5	4	OAT	species	larvae	Y	20	>10	H	mollusc	0.7
616	132	Tong	2019	Biogeosciences	0.7	0.0	3	0.6	0.1	3	OA	species	adult	Y	0.14	<1	A	phytoplankton (coccolithophore)	1.4
617	132	Tong	2019	Biogeosciences	0.7	0.0	3	1.2	0.0	3	Temp	species	adult	Y	0.14	<1	A	phytoplankton (coccolithophore)	1.4
618	132	Tong	2019	Biogeosciences	0.7	0.0	3	1.2	0.1	3	OAT	species	adult	Y	0.14	<1	A	phytoplankton (coccolithophore)	1.4
619	133	Torstensso	2012	Polar Biology	0.2	0.0	4	0.2	0.0	4	OA	species	adult	N	1	1 to 10	A	phytoplankton	1
620	133	Torstensso	2012	Polar Biology	0.2	0.0	4	0.3	0.0	4	Temp	species	adult	N	1	1 to 10	A	phytoplankton	1
621	133	Torstensso	2012	Polar Biology	0.2	0.0	4	0.3	0.0	4	OAT	species	adult	N	1	1 to 10	A	phytoplankton	1
622	134	Torstensso	2013	Biogeosciences	0.2	0.0	4	0.2	0.0	4	OA	species	adult	N	0.02	<1	A	phytoplankton	2
623	134	Torstensso	2013	Biogeosciences	0.2	0.0	4	0.3	0.0	4	Temp	species	adult	N	0.02	<1	A	phytoplankton	2
624	134	Torstensso	2013	Biogeosciences	0.2	0.0	4	0.3	0.0	4	OAT	species	adult	N	0.02	<1	A	phytoplankton	2
625	135	Towle	2015	PLoS One	1.4	0.1	10	1.0	0.1	10	OA	species	adult	Y	100	>10	H	coral	8
626	135	Towle	2015	PLoS One	1.4	0.1	10	1.0	0.1	10	Temp	species	adult	Y	100	>10	H	coral	8
627	135	Towle	2015	PLoS One	1.4	0.1	10	0.7	0.1	10	OAT	species	adult	Y	100	>10	H	coral	8
628	136	Vaz-Pinto	2013	Biological Invasions	0.2	0.0	16	0.2	0.0	16	OA	species	larvae	N	4	1 to 10	A	macroalgae	1.4
629	136	Vaz-Pinto	2013	Biological Invasions	0.2	0.0	16	0.5	0.2	16	Temp	species	larvae	N	4	1 to 10	A	macroalgae	1.4
630	136	Vaz-Pinto	2013	Biological Invasions	0.2	0.0	16	0.2	0.0	16	OAT	species	larvae	N	4	1 to 10	A	macroalgae	1.4
631	137	Visconti	2017	Ices Journal of Marine Science	161.6	11.0	25	235.0	8.8	25	OA	species	larvae	Y	10	1 to 10	H	echinoids	0.3
632	137	Visconti	2017	Ices Journal of Marine Science	161.6	11.0	25	173.9	13.2	25	Temp	species	larvae	Y	10	1 to 10	H	echinoids	0.3
633	137	Visconti	2017	Ices Journal of Marine Science	161.6	11.0	25	225.7	13.2	25	OAT	species	larvae	Y	10	1 to 10	H	echinoids	0.3
634	138	Waller	2017	Ices Journal of Marine Science	3.5	0.1	3	3.8	0.1	3	OA	species	larvae	Y	50	>10	H	crustacean	2.1
635	138	Waller	2017	Ices Journal of Marine Science	4.5	0.0	3	4.8	0.0	3	OA	species	larvae	Y	50	>10	H	crustacean	3.6
636	138	Waller	2017	Ices Journal of Marine Science	3.5	0.1	3	3.6	0.1	3	Temp	species	larvae	Y	50	>10	H	crustacean	1.1
637	138	Waller	2017	Ices Journal of Marine Science	4.5	0.0	3	4.5	0.2	3	Temp	species	larvae	Y	50	>10	H	crustacean	1.9
638	138	Waller	2017	Ices Journal of Marine Science	3.5	0.1	3	3.6	0.1	3	OAT	species	larvae	Y	50	>10	H	crustacean	1.2
639	138	Waller	2017	Ices Journal of Marine Science	4.5	0.0	3	4.4	0.1	3	OAT	species	larvae	Y	50	>10	H	crustacean	1.6
640	139	Walther	2010	MEPS	357.7	43.4	7	399.0	50.0	7	OA	species	larvae	Y	6	1 to 10	H	crustacean	10.7
641	139	Walther	2010	MEPS	357.7	43.4	7	590.0	70.0	7	Temp	species	larvae	Y	6	1 to 10	H	crustacean	10.7
642	139	Walther	2010	MEPS	357.7	43.4	7	505.0	90.0	7	OAT	species	larvae	Y	6	1 to 10	H	crustacean	10.7

643	140	Wang	2015	Science of the Total Environment	8.1	0.1	3	6.5	1.2	3	OA	species	juvenile	Y	20	>10	H	mollusc	2
644	140	Wang	2015	Science of the Total Environment	8.1	0.1	3	1.9	1.5	3	Temp	species	juvenile	Y	20	>10	H	mollusc	2
645	140	Wang	2015	Science of the Total Environment	8.1	0.1	3	2.0	0.4	3	OAT	species	juvenile	Y	20	>10	H	mollusc	2
646	141	Watson	2018	Global Change Biology	5.9	0.1	6	6.0	0.1	6	OA	species	larvae	N	12	>10	H	fish	1.6
647	141	Watson	2018	Global Change Biology	8.7	0.4	6	9.0	0.3	6	OA	species	juvenile	N	12	>10	H	fish	3
648	141	Watson	2018	Global Change Biology	5.9	0.1	6	6.0	0.1	6	Temp	species	larvae	N	12	>10	H	fish	1.6
649	141	Watson	2018	Global Change Biology	8.7	0.4	6	12.5	0.5	6	Temp	species	juvenile	N	12	>10	H	fish	3
650	141	Watson	2018	Global Change Biology	5.9	0.1	6	6.0	0.1	6	OAT	species	larvae	N	12	>10	H	fish	1.6
651	141	Watson	2018	Global Change Biology	8.7	0.4	6	13.5	0.7	6	OAT	species	juvenile	N	12	>10	H	fish	3
652	142	Werner	2016	Oecologia	51.5	14.2	3	32.9	25.5	3	OA	species	adult	N	5	1 to 10	A	macroalgae	6
653	142	Werner	2016	Oecologia	49.4	5.2	3	74.5	19.5	3	OA	species	adult	N	5	1 to 10	A	macroalgae	10.7
654	142	Werner	2016	Oecologia	37.7	25.5	3	39.8	12.8	3	OA	species	adult	N	5	1 to 10	A	macroalgae	9.6
655	142	Werner	2016	Oecologia	30.3	15.0	3	48.5	8.3	3	OA	species	adult	N	5	1 to 10	A	macroalgae	8.9
656	142	Werner	2016	Oecologia	51.5	14.2	3	29.0	11.2	3	Temp	species	adult	N	5	1 to 10	A	macroalgae	6
657	142	Werner	2016	Oecologia	49.4	5.2	3	13.9	3.0	3	Temp	species	adult	N	5	1 to 10	A	macroalgae	10.7
658	142	Werner	2016	Oecologia	37.7	25.5	3	17.3	13.5	3	Temp	species	adult	N	5	1 to 10	A	macroalgae	9.6
659	142	Werner	2016	Oecologia	30.3	15.0	3	39.4	9.8	3	Temp	species	adult	N	5	1 to 10	A	macroalgae	8.9
660	142	Werner	2016	Oecologia	51.5	14.2	3	22.1	8.3	3	OAT	species	adult	N	5	1 to 10	A	macroalgae	6
661	142	Werner	2016	Oecologia	49.4	5.2	3	21.2	3.8	3	OAT	species	adult	N	5	1 to 10	A	macroalgae	10.7
662	142	Werner	2016	Oecologia	37.7	25.5	3	19.5	9.8	3	OAT	species	adult	N	5	1 to 10	A	macroalgae	9.6
663	142	Werner	2016	Oecologia	30.3	15.0	3	40.7	17.3	3	OAT	species	adult	N	5	1 to 10	A	macroalgae	8.9
664	143	Wolfe	2013	Cahiers De Biologie Marine	454.7	9.2	4	465.8	12.9	4	OA	species	juvenile	Y	10	1 to 10	H	echinoids	2
665	143	Wolfe	2013	Cahiers De Biologie Marine	454.7	9.2	4	460.3	7.4	4	Temp	species	juvenile	Y	10	1 to 10	H	echinoids	2
666	143	Wolfe	2013	Cahiers De Biologie Marine	454.7	9.2	4	464.0	7.4	4	OAT	species	juvenile	Y	10	1 to 10	H	echinoids	2
667	144	Wolfe	2013	Global Change Biology	256.7	7.6	4	262.6	13.0	4	OA	species	juvenile	Y	10	1 to 10	H	echinoids	2
668	144	Wolfe	2013	Global Change Biology	256.7	7.6	4	204.7	19.5	4	Temp	species	juvenile	Y	10	1 to 10	H	echinoids	2
669	144	Wolfe	2013	Global Change Biology	256.7	7.6	4	185.7	6.5	4	OAT	species	juvenile	Y	10	1 to 10	H	echinoids	2
670	145	Zhang	2015	Marine Envrionmental Research	0.5	0.2	5	0.5	0.2	5	OA	species	adult	Y	1.21	1 to 10	H	mollusc	4.4

671	145	Zhang	2015	Marine Envrionmental Research	0.5	0.2	5	2.3	0.8	5	Temp	species	adult	Y	1.21	1 to 10	H	mollusc	4.4
672	145	Zhang	2015	Marine Envrionmental Research	0.5	0.2	5	1.7	0.4	5	OAT	species	adult	Y	1.21	1 to 10	H	mollusc	4.4
673	146	Zhang	2016	Ices Journal of Marine Science	0.1	0.2	3	0.5	0.3	3	OA	species	adult	Y	1.21	1 to 10	H	mollusc	0.4
674	146	Zhang	2016	Ices Journal of Marine Science	0.7	0.4	3	0.6	0.1	3	OA	species	adult	Y	1.21	1 to 10	H	mollusc	4.4
675	146	Zhang	2016	Ices Journal of Marine Science	0.1	0.2	3	0.5	0.5	3	Temp	species	adult	Y	1.21	1 to 10	H	mollusc	0.4
676	146	Zhang	2016	Ices Journal of Marine Science	0.7	0.4	3	0.6	0.4	3	Temp	species	adult	Y	1.21	1 to 10	H	mollusc	4.4
677	146	Zhang	2016	Ices Journal of Marine Science	0.1	0.2	3	-0.1	0.2	3	OAT	species	adult	Y	1.21	1 to 10	H	mollusc	0.4
678	146	Zhang	2016	Ices Journal of Marine Science	0.7	0.4	3	0.6	0.1	3	OAT	species	adult	Y	1.21	1 to 10	H	mollusc	4.4
679	147	Zhao	2017	JEMBE	36.0	6.1	5	21.8	10.3	5	OA	species	adult	Y	24	>10	H	mollusc	5
680	147	Zhao	2017	JEMBE	33.7	8.4	5	26.5	9.6	5	OA	species	adult	Y	12	>10	H	mollusc	5
681	147	Zhao	2017	JEMBE	36.0	6.1	5	38.2	5.4	5	Temp	species	adult	Y	24	>10	H	mollusc	5
682	147	Zhao	2017	JEMBE	33.7	8.4	5	23.0	8.8	5	Temp	species	adult	Y	12	>10	H	mollusc	5
683	147	Zhao	2017	JEMBE	36.0	6.1	5	24.5	17.6	3	OAT	species	adult	Y	24	>10	H	mollusc	5
684	147	Zhao	2017	JEMBE	33.7	8.4	5	17.3	9.2	3	OAT	species	adult	Y	12	>10	H	mollusc	5
685	148	Baragi	2016	Marine Pollution Bulletin	4697500.0	174937.1	3	5657000.0	349874.3	3	OA	communities	adult	N	0.02	<1	A	phytoplankton	1.4
686	148	Baragi	2016	Marine Pollution Bulletin	51795353.8	2664666.9	3	55897876.9	3552889.2	3	OA	communities	adult	N	0.02	<1	A	phytoplankton	1.4
687	148	Baragi	2016	Marine Pollution Bulletin	72539134.7	7179413.4	3	62176544.0	5384560.1	3	OA	communities	adult	N	0.02	<1	A	bacteria	1.4
688	148	Baragi	2016	Marine Pollution Bulletin	4697500.0	174937.1	3	2829000.0	349874.3	3	Temp	communities	adult	N	0.02	<1	A	phytoplankton	1.4
689	148	Baragi	2016	Marine Pollution Bulletin	51795353.8	2664666.9	3	54872246.2	2664666.9	3	Temp	communities	adult	N	0.02	<1	A	phytoplankton	1.4
690	148	Baragi	2016	Marine Pollution Bulletin	72539134.7	7179413.4	3	81347336.8	1794853.4	3	Temp	communities	adult	N	0.02	<1	A	bacteria	1.4
691	148	Baragi	2016	Marine Pollution Bulletin	4697500.0	174937.1	3	2374500.0	787217.1	3	OAT	communities	adult	N	0.02	<1	A	phytoplankton	1.4
692	148	Baragi	2016	Marine Pollution Bulletin	51795353.8	2664666.9	3	53333800.0	2664666.9	3	OAT	communities	adult	N	0.02	<1	A	phytoplankton	1.4
693	148	Baragi	2016	Marine Pollution Bulletin	72539134.7	7179413.4	3	68394098.4	5384560.1	3	OAT	communities	adult	N	0.02	<1	A	bacteria	1.4
694	149	Baragi	2017	Estuarine Coastal and Shelf Science	574820.1	82961.9	9	637041.5	72591.7	9	OA	communities	adult	N	0.02	<1	A	phytoplankton	1.4
695	149	Baragi	2017	Estuarine Coastal and Shelf Science	789138.4	31110.7	9	840989.6	41481.0	9	OA	communities	adult	N	0.02	<1	A	phytoplankton	1.4
696	149	Baragi	2017	Estuarine Coastal and Shelf Science	72785862.1	5167241.4	9	71407931.0	4133793.1	9	OA	communities	adult	N	0.001	<1	A	bacteria	1.4

697	149	Baragi	2017	Estuarine Coastal and Shelf Science	42815862.1	6200689.7	9	53839310.3	2066896.6	9	OA	communities	adult	N	0.001	<1	A	bacteria	1.4
698	149	Baragi	2017	Estuarine Coastal and Shelf Science	574820.1	82961.9	9	474574.4	114072.7	9	Temp	communities	adult	N	0.02	<1	A	phytoplankton	1.4
699	149	Baragi	2017	Estuarine Coastal and Shelf Science	789138.4	31110.7	9	630128.0	31110.7	9	Temp	communities	adult	N	0.02	<1	A	phytoplankton	1.4
700	149	Baragi	2017	Estuarine Coastal and Shelf Science	72785862.1	5167241.4	9	74852758.6	3100344.8	9	Temp	communities	adult	N	0.001	<1	A	bacteria	1.4
701	149	Baragi	2017	Estuarine Coastal and Shelf Science	42815862.1	6200689.7	9	55561724.1	13434827.6	9	Temp	communities	adult	N	0.001	<1	A	bacteria	1.4
702	149	Baragi	2017	Estuarine Coastal and Shelf Science	574820.1	82961.9	9	453833.9	62221.5	9	OAT	communities	adult	N	0.02	<1	A	phytoplankton	1.4
703	149	Baragi	2017	Estuarine Coastal and Shelf Science	789138.4	31110.7	9	685436.0	82961.9	9	OAT	communities	adult	N	0.02	<1	A	phytoplankton	1.4
704	149	Baragi	2017	Estuarine Coastal and Shelf Science	72785862.1	5167241.4	9	76230689.7	4133793.1	9	OAT	communities	adult	N	0.001	<1	A	bacteria	1.4
705	149	Baragi	2017	Estuarine Coastal and Shelf Science	42815862.1	6200689.7	9	63140344.8	3100344.8	9	OAT	communities	adult	N	0.001	<1	A	bacteria	1.4
706	150	Benard	2018	Biogeosciences	19.6	14.5	5	14.9	9.2	5	OA	communities	adult	N	0.001	<1	A	phytoplankton	1.9
707	150	Benard	2018	Biogeosciences	6.2	4.5	9	4.3	5.1	9	OA	communities	adult	N	0.001	<1	A	phytoplankton	1.9
708	150	Benard	2018	Biogeosciences	1.0	1.2	9	0.8	1.3	9	OA	communities	adult	N	0.001	<1	A	phytoplankton	1.9
709	150	Benard	2018	Biogeosciences	19.6	14.5	5	26.8	20.0	5	Temp	communities	adult	N	0.001	<1	A	phytoplankton	1.9
710	150	Benard	2018	Biogeosciences	6.2	4.5	9	13.3	1.5	9	Temp	communities	adult	N	0.001	<1	A	phytoplankton	1.9
711	150	Benard	2018	Biogeosciences	1.0	1.2	9	1.1	1.3	9	Temp	communities	adult	N	0.001	<1	A	phytoplankton	1.9
712	150	Benard	2018	Biogeosciences	19.6	14.5	5	28.6	25.6	5	OAT	communities	adult	N	0.001	<1	A	phytoplankton	1.9
713	150	Benard	2018	Biogeosciences	6.2	4.5	9	8.2	2.5	9	OAT	communities	adult	N	0.001	<1	A	phytoplankton	1.9
714	150	Benard	2018	Biogeosciences	1.0	1.2	9	1.0	1.4	9	OAT	communities	adult	N	0.001	<1	A	phytoplankton	1.9
715	151	Burrel	2017	Aquatic Microbial Ecology	624203.8	66193.0	3	662420.4	71709.1	3	OA	communities	adult	N	0.001	<1	A	bacteria	0.9
716	151	Burrel	2017	Aquatic Microbial Ecology	936305.7	55160.9	3	926751.6	55160.9	3	OA	communities	adult	N	0.001	<1	A	bacteria	0.9
717	151	Burrel	2017	Aquatic Microbial Ecology	901273.9	38612.6	3	917197.5	22064.3	3	OA	communities	adult	N	0.001	<1	A	bacteria	0.9
718	151	Burrel	2017	Aquatic Microbial Ecology	894904.5	44128.7	3	907643.3	55160.9	3	OA	communities	adult	N	0.001	<1	A	bacteria	0.9
719	151	Burrel	2017	Aquatic Microbial Ecology	624203.8	66193.0	3	726114.7	27580.4	3	Temp	communities	adult	N	0.001	<1	A	bacteria	0.9
720	151	Burrel	2017	Aquatic Microbial Ecology	936305.7	55160.9	3	684713.4	93773.5	3	Temp	communities	adult	N	0.001	<1	A	bacteria	0.9
721	151	Burrel	2017	Aquatic Microbial Ecology	901273.9	38612.6	3	850318.5	66193.0	3	Temp	communities	adult	N	0.001	<1	A	bacteria	0.9
722	151	Burrel	2017	Aquatic Microbial Ecology	894904.5	44128.7	3	433121.0	27580.4	3	Temp	communities	adult	N	0.001	<1	A	bacteria	0.9
723	151	Burrel	2017	Aquatic Microbial Ecology	624203.8	66193.0	3	729299.4	66193.0	3	OAT	communities	adult	N	0.001	<1	A	bacteria	0.9
724	151	Burrel	2017	Aquatic Microbial Ecology	936305.7	55160.9	3	754777.1	88257.4	3	OAT	communities	adult	N	0.001	<1	A	bacteria	0.9
725	151	Burrel	2017	Aquatic Microbial Ecology	901273.9	38612.6	3	837579.6	126870.0	3	OAT	communities	adult	N	0.001	<1	A	bacteria	0.9

726	151	Burrel	2017	Aquatic Microbial Ecology	894904.5	44128.7	3	496815.3	27580.4	3	OAT	communities	adult	N	0.001	<1	A	bacteria	0.9
727	152	Currie	2017	Frontiers in Microbiology	21.6	1.6	3	29.1	4.1	3	OA	communities	adult	N	0.001	<1	A	bacteria	4
728	152	Currie	2017	Frontiers in Microbiology	12.6	2.4	3	16.5	1.1	3	OA	communities	adult	N	0.001	<1	A	bacteria	4
729	152	Currie	2017	Frontiers in Microbiology	19.8	2.3	3	9.7	3.8	3	OA	communities	adult	N	0.001	<1	A	bacteria	4
730	152	Currie	2017	Frontiers in Microbiology	10.5	2.2	3	7.6	1.1	3	OA	communities	adult	N	0.001	<1	A	bacteria	4
731	152	Currie	2017	Frontiers in Microbiology	2.4	0.5	3	4.3	0.6	3	OA	communities	adult	N	0.001	<1	A	bacteria	4
732	152	Currie	2017	Frontiers in Microbiology	1.2	0.3	3	3.6	1.2	3	OA	communities	adult	N	0.001	<1	A	bacteria	4
733	152	Currie	2017	Frontiers in Microbiology	1.0	0.3	3	1.9	0.2	3	OA	communities	adult	N	0.001	<1	A	bacteria	4
734	152	Currie	2017	Frontiers in Microbiology	1.0	0.3	3	1.2	0.2	3	OA	communities	adult	N	0.001	<1	A	bacteria	4
735	152	Currie	2017	Frontiers in Microbiology	21.6	1.6	3	22.5	3.4	3	Temp	communities	adult	N	0.001	<1	A	bacteria	4
736	152	Currie	2017	Frontiers in Microbiology	12.6	2.4	3	14.6	2.0	3	Temp	communities	adult	N	0.001	<1	A	bacteria	4
737	152	Currie	2017	Frontiers in Microbiology	19.8	2.3	3	18.4	3.7	3	Temp	communities	adult	N	0.001	<1	A	bacteria	4
738	152	Currie	2017	Frontiers in Microbiology	10.5	2.2	3	10.5	1.3	3	Temp	communities	adult	N	0.001	<1	A	bacteria	4
739	152	Currie	2017	Frontiers in Microbiology	2.4	0.5	3	2.7	0.5	3	Temp	communities	adult	N	0.001	<1	A	bacteria	4
740	152	Currie	2017	Frontiers in Microbiology	1.2	0.3	3	1.2	0.3	3	Temp	communities	adult	N	0.001	<1	A	bacteria	4
741	152	Currie	2017	Frontiers in Microbiology	1.0	0.3	3	1.4	0.2	3	Temp	communities	adult	N	0.001	<1	A	bacteria	4
742	152	Currie	2017	Frontiers in Microbiology	1.0	0.3	3	1.3	0.2	3	Temp	communities	adult	N	0.001	<1	A	bacteria	4
743	152	Currie	2017	Frontiers in Microbiology	21.6	1.6	3	26.2	5.0	3	OAT	communities	adult	N	0.001	<1	A	bacteria	4
744	152	Currie	2017	Frontiers in Microbiology	12.6	2.4	3	15.1	1.9	3	OAT	communities	adult	N	0.001	<1	A	bacteria	4
745	152	Currie	2017	Frontiers in Microbiology	19.8	2.3	3	15.6	6.2	3	OAT	communities	adult	N	0.001	<1	A	bacteria	4
746	152	Currie	2017	Frontiers in Microbiology	10.5	2.2	3	9.5	3.4	3	OAT	communities	adult	N	0.001	<1	A	bacteria	4
747	152	Currie	2017	Frontiers in Microbiology	2.4	0.5	3	2.8	1.3	3	OAT	communities	adult	N	0.001	<1	A	bacteria	4
748	152	Currie	2017	Frontiers in Microbiology	1.2	0.3	3	2.6	1.9	3	OAT	communities	adult	N	0.001	<1	A	bacteria	4
749	152	Currie	2017	Frontiers in Microbiology	1.0	0.3	3	1.4	0.5	3	OAT	communities	adult	N	0.001	<1	A	bacteria	4
750	152	Currie	2017	Frontiers in Microbiology	1.0	0.3	3	1.0	0.1	3	OAT	communities	adult	N	0.001	<1	A	bacteria	4

751	154	Garzke	2016	PLoS One	121.1	75.9	3	171.8	151.8	3	OA	communities	adult	N	0.02	<1	A	phytoplankton	3.4
752	154	Garzke	2016	PLoS One	121.1	75.9	3	20.8	105.9	3	Temp	communities	adult	N	0.02	<1	A	phytoplankton	3.4
753	154	Garzke	2016	PLoS One	121.1	75.9	3	6.9	40.0	3	OAT	communities	adult	N	0.02	<1	A	phytoplankton	3.4
754	155	Hare	2007	MEPS	16505.0	6553.0	3	1544.0	1247.0	3	OA	communities	adult	N	0.02	<1	A	phytoplankton	1.4
755	155	Hare	2007	MEPS	7550.0	262.0	3	1987.0	616.0	3	OA	communities	adult	N	0.02	<1	A	phytoplankton	1.4
756	155	Hare	2007	MEPS	8542.0	1380.0	3	5754.0	1109.0	3	OA	communities	adult	N	0.02	<1	A	phytoplankton	1.4
757	155	Hare	2007	MEPS	6600.0	990.0	3	7300.0	2500.0	3	OA	communities	adult	N	0.02	<1	A	phytoplankton	1.4
758	155	Hare	2007	MEPS	16505.0	6553.0	3	4807.0	2865.0	3	Temp	communities	adult	N	0.02	<1	A	phytoplankton	1.4
759	155	Hare	2007	MEPS	7550.0	262.0	3	11412.0	6431.0	3	Temp	communities	adult	N	0.02	<1	A	phytoplankton	1.4
760	155	Hare	2007	MEPS	8542.0	1380.0	3	7778.0	1049.0	3	Temp	communities	adult	N	0.02	<1	A	phytoplankton	1.4
761	155	Hare	2007	MEPS	6600.0	990.0	3	19600.0	8773.0	3	Temp	communities	adult	N	0.02	<1	A	phytoplankton	1.4
762	155	Hare	2007	MEPS	16505.0	6553.0	3	1242.0	421.0	3	OAT	communities	adult	N	0.02	<1	A	phytoplankton	1.4
763	155	Hare	2007	MEPS	7550.0	262.0	3	1080.0	555.0	3	OAT	communities	adult	N	0.02	<1	A	phytoplankton	1.4
764	155	Hare	2007	MEPS	8542.0	1380.0	3	6475.0	1561.0	3	OAT	communities	adult	N	0.02	<1	A	phytoplankton	1.4
765	155	Hare	2007	MEPS	6600.0	990.0	3	27200.0	37206.0	3	OAT	communities	adult	N	0.02	<1	A	phytoplankton	1.4
766	156	Horn	2016	ICES Journal of Marine Science	0.3	0.0	3	0.3	0.0	3	OA	communities	adult	N	0.04	<1	H	zooplankton	0.6
767	156	Horn	2016	ICES Journal of Marine Science	0.1	0.0	3	0.1	0.0	3	OA	communities	adult	N	0.04	<1	H	zooplankton	1
768	156	Horn	2016	ICES Journal of Marine Science	1.5	0.3	3	1.0	0.3	3	OA	communities	adult	N	0.04	<1	H	zooplankton	1.6
769	156	Horn	2016	ICES Journal of Marine Science	5.1	2.1	3	4.4	0.0	3	OA	communities	adult	N	0.04	<1	H	zooplankton	2
770	156	Horn	2016	ICES Journal of Marine Science	26.0	12.2	3	24.8	8.3	3	OA	communities	adult	N	0.04	<1	H	zooplankton	2.6
771	156	Horn	2016	ICES Journal of Marine Science	19.2	2.2	3	17.0	5.6	3	OA	communities	adult	N	0.04	<1	H	zooplankton	3
772	156	Horn	2016	ICES Journal of Marine Science	0.3	0.0	3	0.5	0.2	3	Temp	communities	adult	N	0.04	<1	H	zooplankton	0.6
773	156	Horn	2016	ICES Journal of Marine Science	0.1	0.0	3	1.5	0.4	3	Temp	communities	adult	N	0.04	<1	H	zooplankton	1
774	156	Horn	2016	ICES Journal of Marine Science	1.5	0.3	3	22.6	8.7	3	Temp	communities	adult	N	0.04	<1	H	zooplankton	1.6
775	156	Horn	2016	ICES Journal of Marine Science	5.1	2.1	3	4.5	0.4	3	Temp	communities	adult	N	0.04	<1	H	zooplankton	2
776	156	Horn	2016	ICES Journal of Marine Science	26.0	12.2	3	2.8	2.0	3	Temp	communities	adult	N	0.04	<1	H	zooplankton	2.6
777	156	Horn	2016	ICES Journal of Marine Science	19.2	2.2	3	2.0	0.5	3	Temp	communities	adult	N	0.04	<1	H	zooplankton	3
778	156	Horn	2016	ICES Journal of Marine Science	0.3	0.0	3	0.2	0.1	3	OAT	communities	adult	N	0.04	<1	H	zooplankton	0.6
779	156	Horn	2016	ICES Journal of Marine Science	0.1	0.0	3	2.0	0.9	3	OAT	communities	adult	N	0.04	<1	H	zooplankton	1
780	156	Horn	2016	ICES Journal of Marine Science	1.5	0.3	3	16.3	4.9	3	OAT	communities	adult	N	0.04	<1	H	zooplankton	1.6
781	156	Horn	2016	ICES Journal of Marine Science	5.1	2.1	3	5.6	2.9	3	OAT	communities	adult	N	0.04	<1	H	zooplankton	2
782	156	Horn	2016	ICES Journal of Marine Science	26.0	12.2	3	7.4	5.8	3	OAT	communities	adult	N	0.04	<1	H	zooplankton	2.6

783	156	Horn	2016	ICES Journal of Marine Science	19.2	2.2	3	1.6	0.4	3	OAT	communities	adult	N	0.04	<1	H	zooplankton	3
784	157	Johnson	2017	Coral Reefs	0.0	0.0	6	0.0	0.0	6	OA	communities	adult	N	0.4	<1	A	macroalgae	3
785	157	Johnson	2017	Coral Reefs	0.0	0.0	6	0.0	0.0	6	OA	communities	adult	N	0.4	<1	A	macroalgae	3
786	157	Johnson	2017	Coral Reefs	0.0	0.0	6	0.0	0.0	6	Temp	communities	adult	N	0.4	<1	A	macroalgae	3
787	157	Johnson	2017	Coral Reefs	0.0	0.0	6	0.0	0.0	6	Temp	communities	adult	N	0.4	<1	A	macroalgae	3
788	157	Johnson	2017	Coral Reefs	0.0	0.0	6	0.0	0.0	6	OAT	communities	adult	N	0.4	<1	A	macroalgae	3
789	157	Johnson	2017	Coral Reefs	0.0	0.0	6	0.0	0.0	6	OAT	communities	adult	N	0.4	<1	A	macroalgae	3
790	158	Keys	2018	Biogeosciences	166.2	41.6	80	2216.1	187.0	80	OA	communities	adult	N	0.02	<1	A	phytoplankton	5.1
791	158	Keys	2018	Biogeosciences	200.1	16.6	80	237.6	20.8	80	OA	communities	adult	N	0.02	<1	A	phytoplankton	5.1
792	158	Keys	2018	Biogeosciences	5.6	1.3	80	14.8	8.2	80	OA	communities	adult	N	0.02	<1	A	phytoplankton	5.1
793	158	Keys	2018	Biogeosciences	6.9	1.6	80	6.6	0.8	80	OA	communities	adult	N	0.02	<1	A	phytoplankton	5.1
794	158	Keys	2018	Biogeosciences	3.5	0.5	80	6.9	0.6	80	OA	communities	adult	N	0.02	<1	A	phytoplankton	5.1
795	158	Keys	2018	Biogeosciences	0.2	0.2	80	0.4	0.1	80	OA	communities	adult	N	0.02	<1	A	phytoplankton	5.1
796	158	Keys	2018	Biogeosciences	1.5	0.5	80	1.2	0.2	80	OA	communities	adult	Y	0.02	<1	A	phytoplankton (coccolithophore)	5.1
797	158	Keys	2018	Biogeosciences	166.2	41.6	80	1488.9	166.2	80	Temp	communities	adult	N	0.02	<1	A	phytoplankton	5.1
798	158	Keys	2018	Biogeosciences	200.1	16.6	80	152.8	10.8	80	Temp	communities	adult	N	0.02	<1	A	phytoplankton	5.1
799	158	Keys	2018	Biogeosciences	5.6	1.3	80	57.7	6.9	80	Temp	communities	adult	N	0.02	<1	A	phytoplankton	5.1
800	158	Keys	2018	Biogeosciences	6.9	1.6	80	30.3	6.0	80	Temp	communities	adult	N	0.02	<1	A	phytoplankton	5.1
801	158	Keys	2018	Biogeosciences	3.5	0.5	80	4.2	0.5	80	Temp	communities	adult	N	0.02	<1	A	phytoplankton	5.1
802	158	Keys	2018	Biogeosciences	0.2	0.2	80	0.4	0.2	80	Temp	communities	adult	N	0.02	<1	A	phytoplankton	5.1
803	158	Keys	2018	Biogeosciences	1.5	0.5	80	1.7	0.4	80	Temp	communities	adult	Y	0.02	<1	A	phytoplankton (coccolithophore)	5.1
804	158	Keys	2018	Biogeosciences	166.2	41.6	80	235.5	20.8	80	OAT	communities	adult	N	0.02	<1	A	phytoplankton	5.1
805	158	Keys	2018	Biogeosciences	200.1	16.6	80	126.2	19.1	80	OAT	communities	adult	N	0.02	<1	A	phytoplankton	5.1
806	158	Keys	2018	Biogeosciences	5.6	1.3	80	90.5	16.7	80	OAT	communities	adult	N	0.02	<1	A	phytoplankton	5.1
807	158	Keys	2018	Biogeosciences	6.9	1.6	80	59.3	4.6	80	OAT	communities	adult	N	0.02	<1	A	phytoplankton	5.1
808	158	Keys	2018	Biogeosciences	3.5	0.5	80	11.3	0.7	80	OAT	communities	adult	N	0.02	<1	A	phytoplankton	5.1
809	158	Keys	2018	Biogeosciences	0.2	0.2	80	1.0	0.1	80	OAT	communities	adult	N	0.02	<1	A	phytoplankton	5.1
810	158	Keys	2018	Biogeosciences	1.5	0.5	80	0.6	0.1	80	OAT	communities	adult	Y	0.02	<1	A	phytoplankton (coccolithophore)	5.1
811	159	Legrand	2017	Biogeosciences	0.6	0.5	5	1.8	1.9	5	OA	communities	adult	Y	50	>10	A	macroalgae (CCA)	13
812	159	Legrand	2017	Biogeosciences	2.5	0.2	5	2.3	0.8	5	OA	communities	adult	Y	50	>10	A	macroalgae (CCA)	13
813	159	Legrand	2017	Biogeosciences	0.6	0.5	5	0.9	1.0	5	Temp	communities	adult	Y	50	>10	A	macroalgae (CCA)	13
814	159	Legrand	2017	Biogeosciences	2.5	0.2	5	0.4	0.2	5	Temp	communities	adult	Y	50	>10	A	macroalgae (CCA)	13
815	159	Legrand	2017	Biogeosciences	0.6	0.5	5	1.7	1.8	5	OAT	communities	adult	Y	50	>10	A	macroalgae (CCA)	13
816	159	Legrand	2017	Biogeosciences	2.5	0.2	5	3.8	2.8	5	OAT	communities	adult	Y	50	>10	A	macroalgae (CCA)	13
817	160	Lindh	2013	Environmental Microbiology Reports	2.1	0.6	3	1.5	0.1	3	OA	communities	adult	N	0.001	<1	A	bacteria	3
818	160	Lindh	2013	Environmental Microbiology Reports	2.1	0.6	3	5.2	1.5	3	Temp	communities	adult	N	0.001	<1	A	bacteria	3

819	160	Lindh	2013	Environmental Microbiology Reports	2.1	0.6	3	3.0	0.6	3	OAT	communities	adult	N	0.001	<1	A	bacteria	3
820	161	Maugendre	2015	ICES Journal of Marine Science	541261.3	92304.8	3	402702.7	48924.1	2	OA	communities	adult	N	0.001	<1	A	bacteria	1.7
821	161	Maugendre	2015	ICES Journal of Marine Science	94871.8	25459.9	3	81562.9	19153.3	3	OA	communities	adult	N	0.001	<1	A	bacteria	1.7
822	161	Maugendre	2015	ICES Journal of Marine Science	541261.3	92304.8	3	482342.3	56819.4	3	Temp	communities	adult	N	0.001	<1	A	bacteria	1.7
823	161	Maugendre	2015	ICES Journal of Marine Science	94871.8	25459.9	3	75335.8	24719.4	3	Temp	communities	adult	N	0.001	<1	A	bacteria	1.7
824	161	Maugendre	2015	ICES Journal of Marine Science	541261.3	92304.8	3	465946.0	48386.7	3	OAT	communities	adult	N	0.001	<1	A	bacteria	1.7
825	161	Maugendre	2015	ICES Journal of Marine Science	94871.8	25459.9	3	90415.1	39707.0	3	OAT	communities	adult	N	0.001	<1	A	bacteria	1.7
826	162	Muller	2017	PlosOne	54.9	13.8	8	45.5	14.7	8	OA	communities	adult	N	0.001	<1	A	bacteria	2.3
827	162	Muller	2017	PlosOne	28.7	18.6	8	79.0	30.9	8	OA	communities	adult	N	0.001	<1	A	bacteria	2.3
828	162	Muller	2017	PlosOne	54.9	13.8	8	30.2	9.4	8	Temp	communities	adult	N	0.001	<1	A	bacteria	2.3
829	162	Muller	2017	PlosOne	28.7	18.6	8	35.1	35.5	8	Temp	communities	adult	N	0.001	<1	A	bacteria	2.3
830	162	Muller	2017	PlosOne	54.9	13.8	8	56.2	15.8	8	OAT	communities	adult	N	0.001	<1	A	bacteria	2.3
831	162	Muller	2017	PlosOne	28.7	18.6	8	31.8	21.0	8	OAT	communities	adult	N	0.001	<1	A	bacteria	2.3
832	163	Pancic	2015	Biogeosciences	0.3	0.0	5	0.4	0.0	5	OA	communities	adult	N	0.02	<1	A	phytoplankton	0.7
833	163	Pancic	2015	Biogeosciences	0.3	0.0	5	0.3	0.0	5	Temp	communities	adult	N	0.02	<1	A	phytoplankton	0.7
834	163	Pancic	2015	Biogeosciences	0.3	0.0	5	0.4	0.0	5	OAT	communities	adult	N	0.02	<1	A	phytoplankton	0.7
835	164	Paul	2015	MEPS	1.8	1.1	3	2.3	0.6	3	OA	communities	adult	N	0.02	<1	A	phytoplankton	3
836	164	Paul	2015	MEPS	1.8	1.1	3	2.2	1.0	3	Temp	communities	adult	N	0.02	<1	A	phytoplankton	3
837	164	Paul	2015	MEPS	1.8	1.1	3	3.7	2.8	3	OAT	communities	adult	N	0.02	<1	A	phytoplankton	3
838	165	Piontek	2015	Limnology and Oceanography	0.4	0.2	3	0.6	0.2	3	OA	communities	adult	N	0.001	<1	A	bacteria	0.6
839	165	Piontek	2015	Limnology and Oceanography	0.4	0.2	3	0.3	0.1	3	Temp	communities	adult	N	0.001	<1	A	bacteria	0.6
840	165	Piontek	2015	Limnology and Oceanography	0.4	0.2	3	0.3	0.1	3	OAT	communities	adult	N	0.001	<1	A	bacteria	0.6
841	166	Roth-Schul	2018	Limnology and Oceanography	0.8	0.1	3	0.8	0.1	3	OA	communities	adult	N	0.001	<1	A	bacteria	3
842	166	Roth-Schul	2018	Limnology and Oceanography	0.8	0.1	3	1.1	0.0	3	Temp	communities	adult	N	0.001	<1	A	bacteria	3
843	166	Roth-Schul	2018	Limnology and Oceanography	0.8	0.1	3	1.3	0.1	3	OAT	communities	adult	N	0.001	<1	A	bacteria	3
844	167	Russell	2013	Philos Trans R Soc B	46.8	8.2	4	31.5	12.8	4	OA	communities	adult	N	0.02	<1	A	phytoplankton	5
845	167	Russell	2013	Philos Trans R Soc B	46.8	8.2	4	76.3	16.3	4	Temp	communities	adult	N	0.02	<1	A	phytoplankton	5
846	167	Russell	2013	Philos Trans R Soc B	46.8	8.2	4	72.6	29.7	4	OAT	communities	adult	N	0.02	<1	A	phytoplankton	5
847	168	Tatters	2013	Philos Trans R Soc B	0.4	0.0	3	0.4	0.0	3	OA	communities	adult	N	0.02	<1	A	phytoplankton	52

848	168	Tatters	2013	Philos Trans R Soc B	0.4	0.0	3	0.4	0.0	3	OA	communities	adult	N	0.02	<1	A	phytoplankton	52
849	168	Tatters	2013	Philos Trans R Soc B	0.4	0.0	3	0.3	0.0	3	OA	communities	adult	N	0.02	<1	A	phytoplankton	52
850	168	Tatters	2013	Philos Trans R Soc B	0.3	0.0	3	0.3	0.0	3	OA	communities	adult	N	0.02	<1	A	phytoplankton	52
851	168	Tatters	2013	Philos Trans R Soc B	0.4	0.0	3	0.4	0.0	3	OA	communities	adult	N	0.02	<1	A	phytoplankton	52
852	168	Tatters	2013	Philos Trans R Soc B	0.4	0.0	3	0.4	0.0	3	OA	communities	adult	N	0.02	<1	A	phytoplankton	52
853	168	Tatters	2013	Philos Trans R Soc B	0.4	0.0	3	0.3	0.0	3	Temp	communities	adult	N	0.02	<1	A	phytoplankton	52
854	168	Tatters	2013	Philos Trans R Soc B	0.4	0.0	3	0.4	0.0	3	Temp	communities	adult	N	0.02	<1	A	phytoplankton	52
855	168	Tatters	2013	Philos Trans R Soc B	0.4	0.0	3	0.4	0.0	3	Temp	communities	adult	N	0.02	<1	A	phytoplankton	52
856	168	Tatters	2013	Philos Trans R Soc B	0.3	0.0	3	0.4	0.0	3	Temp	communities	adult	N	0.02	<1	A	phytoplankton	52
857	168	Tatters	2013	Philos Trans R Soc B	0.4	0.0	3	0.4	0.0	3	Temp	communities	adult	N	0.02	<1	A	phytoplankton	52
858	168	Tatters	2013	Philos Trans R Soc B	0.4	0.0	3	0.5	0.0	3	Temp	communities	adult	N	0.02	<1	A	phytoplankton	52
859	168	Tatters	2013	Philos Trans R Soc B	0.4	0.0	3	0.3	0.0	3	OAT	communities	adult	N	0.02	<1	A	phytoplankton	52
860	168	Tatters	2013	Philos Trans R Soc B	0.4	0.0	3	0.4	0.0	3	OAT	communities	adult	N	0.02	<1	A	phytoplankton	52
861	168	Tatters	2013	Philos Trans R Soc B	0.4	0.0	3	0.4	0.0	3	OAT	communities	adult	N	0.02	<1	A	phytoplankton	52
862	168	Tatters	2013	Philos Trans R Soc B	0.3	0.0	3	0.4	0.0	3	OAT	communities	adult	N	0.02	<1	A	phytoplankton	52
863	168	Tatters	2013	Philos Trans R Soc B	0.4	0.0	3	0.4	0.0	3	OAT	communities	adult	N	0.02	<1	A	phytoplankton	52
864	168	Tatters	2013	Philos Trans R Soc B	0.4	0.0	3	0.4	0.0	3	OAT	communities	adult	N	0.02	<1	A	phytoplankton	52
865	169	Taucher	2015	Limnology and Oceanography	35017.8	2717.7	2	46334.5	1811.8	2	OA	communities	adult	N	0.02	<1	A	phytoplankton	1.6
866	169	Taucher	2015	Limnology and Oceanography	13918.0	1893.6	2	15739.5	1128.5	2	OA	communities	adult	N	0.02	<1	A	phytoplankton	1.3
867	169	Taucher	2015	Limnology and Oceanography	35017.8	2717.7	2	43345.2	2415.7	2	Temp	communities	adult	N	0.02	<1	A	phytoplankton	1.6
868	169	Taucher	2015	Limnology and Oceanography	13918.0	1893.6	2	9846.3	1763.2	2	Temp	communities	adult	N	0.02	<1	A	phytoplankton	1.3
869	169	Taucher	2015	Limnology and Oceanography	35017.8	2717.7	2	55089.0	2717.7	2	OAT	communities	adult	N	0.02	<1	A	phytoplankton	1.6
870	169	Taucher	2015	Limnology and Oceanography	13918.0	1893.6	2	13275.2	2634.3	2	OAT	communities	adult	N	0.02	<1	A	phytoplankton	1.3
871	170	Troedsson	2013	Marine Biology	0.5	0.5	9	0.4	0.3	9	OA	communities	adult	N	0.02	<1	A	phytoplankton	2.3

872	170	Troedsson	2013	Marine Biology	0.5	0.4	9	0.4	0.4	9	OA	communities	adult	N	0.02	<1	A	phytoplankton	2.3
873	170	Troedsson	2013	Marine Biology	0.6	0.5	9	0.5	0.6	9	OA	communities	adult	N	0.02	<1	A	phytoplankton	2.3
874	170	Troedsson	2013	Marine Biology	3.0	3.6	9	2.6	2.8	9	OA	communities	adult	N	0.02	<1	A	phytoplankton	2.3
875	170	Troedsson	2013	Marine Biology	0.5	0.5	9	0.2	0.2	9	Temp	communities	adult	N	0.02	<1	A	phytoplankton	2.3
876	170	Troedsson	2013	Marine Biology	0.5	0.4	9	0.5	0.4	9	Temp	communities	adult	N	0.02	<1	A	phytoplankton	2.3
877	170	Troedsson	2013	Marine Biology	0.6	0.5	9	0.9	0.8	9	Temp	communities	adult	N	0.02	<1	A	phytoplankton	2.3
878	170	Troedsson	2013	Marine Biology	3.0	3.6	9	2.2	3.9	9	Temp	communities	adult	N	0.02	<1	A	phytoplankton	2.3
879	170	Troedsson	2013	Marine Biology	0.5	0.5	9	0.2	0.3	9	OAT	communities	adult	N	0.02	<1	A	phytoplankton	2.3
880	170	Troedsson	2013	Marine Biology	0.5	0.4	9	0.4	0.4	9	OAT	communities	adult	N	0.02	<1	A	phytoplankton	2.3
881	170	Troedsson	2013	Marine Biology	0.6	0.5	9	1.0	1.1	9	OAT	communities	adult	N	0.02	<1	A	phytoplankton	2.3
882	170	Troedsson	2013	Marine Biology	3.0	3.6	9	1.9	2.8	9	OAT	communities	adult	N	0.02	<1	A	phytoplankton	2.3
883	171	Wessel	2017	Fems Microbiology Ecology	27.6	7.4	12	22.5	6.9	12	OA	communities	adult	N	0.001	<1	A	bacteria	1.7
884	171	Wessel	2017	Fems Microbiology Ecology	27.6	7.4	12	23.0	9.2	12	Temp	communities	adult	N	0.001	<1	A	bacteria	1.7
885	171	Wessel	2017	Fems Microbiology Ecology	27.6	7.4	12	23.0	8.0	11	OAT	communities	adult	N	0.001	<1	A	bacteria	1.7
886	172	Wolf	2018	Limnology and Oceanography	1.1	0.0	3	1.0	0.1	3	OA	communities	adult	N	0.02	<1	A	phytoplankton	1.6
887	172	Wolf	2018	Limnology and Oceanography	1.1	0.0	3	1.2	0.1	3	Temp	communities	adult	N	0.02	<1	A	phytoplankton	1.6
888	172	Wolf	2018	Limnology and Oceanography	1.1	0.0	3	1.2	0.0	3	OAT	communities	adult	N	0.02	<1	A	phytoplankton	1.6

obs: observations; m1: mean of the control; sd1: standard deviation of the control; n1: control sample size; m2: mean of the treatment; sd2: standard deviation of the treatment; n2: treatment sample size; Ecol.Level: ecological level; L.stage: life stage; L.span: life span; L.span1: life span by categories; Exp: exposure time to treatments; OA: ocean acidification; Temp: elevated temperature; OAT: combination of ocean acidification and elevated temperature; N: non-califier; Y: calcifier; H: heterotroph; A: autotroph; CCA: crustose coralline algae.

Table S6. Studies and categories used for the survival meta-analysis

obs	study	author	year	journal	m1	sd1	n1	m2	sd2	n2	Treatment	Ecol.Level	L.stage	Calcifier	L.span	L.span1	Nutrition mode	Taxa	Exp
1	1	Alguero-Muniz	2016	Marine Biology	92.4	11.22	5	100	0.001	5	OA	species	juvenile	N	25	>10-50	H	jellyfish	1
2	1	Alguero-Muniz	2016	Marine Biology	92.4	11.22	5	95.7	8	5	Temp	species	juvenile	N	25	>10-50	H	jellyfish	1
3	1	Alguero-Muniz	2016	Marine Biology	92.4	11.22	5	68.5	31.5	5	OAT	species	juvenile	N	25	>10-50	H	jellyfish	1
4	2	Bahr	2016	Coral Reefs	7.7	13	20	12.4	18.9	20	OA	species	adult	Y	100	>50	H	coral	8
5	2	Bahr	2016	Coral Reefs	10.1	11.8	20	22.2	17.7	20	OA	species	adult	Y	100	>50	H	coral	8
6	2	Bahr	2016	Coral Reefs	15.1	14.2	20	67.2	17.7	20	OA	species	adult	Y	100	>50	H	coral	8
7	2	Bahr	2016	Coral Reefs	7.7	13	20	58.2	30.8	20	Temp	species	adult	Y	100	>50	H	coral	8
8	2	Bahr	2016	Coral Reefs	10.1	11.8	20	40.7	33.1	20	Temp	species	adult	Y	100	>50	H	coral	8
9	2	Bahr	2016	Coral Reefs	15.1	14.2	20	61.1	30.8	20	Temp	species	adult	Y	100	>50	H	coral	8
10	2	Bahr	2016	Coral Reefs	7.7	13	20	40.7	27.21	20	OAT	species	adult	Y	100	>50	H	coral	8
11	2	Bahr	2016	Coral Reefs	10.1	11.8	20	44.2	27.21	20	OAT	species	adult	Y	100	>50	H	coral	8
12	2	Bahr	2016	Coral Reefs	15.1	14.2	20	91.3	26.03	20	OAT	species	adult	Y	100	>50	H	coral	8
13	3	Baragi	2015	JEMBE	79.86	7.55	3	66.19	6.47	3	OA	species	larvae	Y	6	>5-10	H	crustacean	0.6
14	3	Baragi	2015	JEMBE	79.86	7.55	3	41.01	9.71	3	Temp	species	larvae	Y	6	>5-10	H	crustacean	0.6
15	3	Baragi	2015	JEMBE	79.86	7.55	3	20.14	5.4	3	OAT	species	larvae	Y	6	>5-10	H	crustacean	0.6
16	4	Baria	2015	Zoological Science	69.06	19.61	3	61.88	5.25	3	OA	species	larvae	Y	31	>10-50	H	coral	1.1
17	4	Baria	2015	Zoological Science	60.14	6.83	3	56.34	13.94	3	OA	species	larvae	Y	31	>10-50	H	coral	1.1
18	4	Baria	2015	Zoological Science	69.06	19.61	3	67.13	8.84	3	Temp	species	larvae	Y	31	>10-50	H	coral	1.1
19	4	Baria	2015	Zoological Science	60.14	6.83	3	64.09	4.1	3	Temp	species	larvae	Y	31	>10-50	H	coral	1.1
20	4	Baria	2015	Zoological Science	69.06	19.61	3	56.08	17.4	3	OAT	species	larvae	Y	31	>10-50	H	coral	1.1
21	4	Baria	2015	Zoological Science	60.14	6.83	3	61.66	8.2	3	OAT	species	larvae	Y	31	>10-50	H	coral	1.1
22	5	Baumann	2018	Marine Biology	46.7	24.8	5	41.8	23.2	5	OA	species	larvae	N	2	1 to 5	H	fish	0.6
23	5	Baumann	2018	Marine Biology	46.7	24.8	5	39.4	16.6	4	Temp	species	larvae	N	2	1 to 5	H	fish	0.6
24	5	Baumann	2018	Marine Biology	46.7	24.8	5	30.8	21.4	6	OAT	species	larvae	N	2	1 to 5	H	fish	0.6
25	6	Bennett	2017	Global Change Biology	82.14	17.17	18	85	15.66	18	OA	species	larvae	N	100	>50	H	sponges	4
26	6	Bennett	2017	Global Change Biology	82.14	17.17	18	74.76	17.17	18	Temp	species	larvae	N	100	>50	H	sponges	4

27	6	Bennett	2017	Global Change Biology	82.14	17.17	18	83.81	15.66	18	OAT	species	larvae	N	100	>50	H	sponges	4
28	7	Byrne	2013	MEPS	64.8	3.6	9	59.4	4.8	9	OA	species	larvae	N	10	>5-10	H	echinoids	0.14
29	7	Byrne	2013	MEPS	89.3	5.6	9	93.7	4.4	9	OA	species	larvae	N	10	>5-10	H	echinoids	0.09
30	7	Byrne	2013	MEPS	64.8	3.6	9	58.8	9.6	9	Temp	species	larvae	N	10	>5-10	H	echinoids	0.14
31	7	Byrne	2013	MEPS	89.3	5.6	9	81	6.4	9	Temp	species	larvae	N	10	>5-10	H	echinoids	0.09
32	7	Byrne	2013	MEPS	64.8	3.6	9	56.1	3.2	9	OAT	species	larvae	N	10	>5-10	H	echinoids	0.14
33	7	Byrne	2013	MEPS	89.3	5.6	9	83.1	6	9	OAT	species	larvae	N	10	>5-10	H	echinoids	0.09
34	8	Cardoso	2017	Estuarine Coastal and Shelf Science	45.96	13.09	3	81.34	2.51	3	OA	species	adult	Y	3	1 to 5	H	mollusc	2.1
35	8	Cardoso	2017	Estuarine Coastal and Shelf Science	45.96	13.09	3	7.8	5.85	3	Temp	species	adult	Y	3	1 to 5	H	mollusc	2.1
36	8	Cardoso	2017	Estuarine Coastal and Shelf Science	45.96	13.09	3	48.47	10.58	3	OAT	species	adult	Y	3	1 to 5	H	mollusc	2.1
37	9	Chavez-Ville	2017	Revista de Biologia Tropical	52.46	7.1	3	66.67	7.65	3	OA	species	larvae	Y	30	>10-50	H	mollusc	4.29
38	9	Chavez-Ville	2017	Revista de Biologia Tropical	52.46	7.1	3	44.81	7.65	3	Temp	species	larvae	Y	30	>10-50	H	mollusc	4.29
39	9	Chavez-Ville	2017	Revista de Biologia Tropical	52.46	7.1	3	42.62	10.93	3	OAT	species	larvae	Y	30	>10-50	H	mollusc	4.29
40	10	Clemments	2018	Conservation Physiology	95.26	3.41	30	96.1	7.35	30	OA	species	adult	Y	24	>10-50	H	mollusc	12.9
41	10	Clemments	2018	Conservation Physiology	95.26	3.41	30	81.89	7.35	30	Temp	species	adult	Y	24	>10-50	H	mollusc	12.9
42	10	Clemments	2018	Conservation Physiology	95.26	3.41	30	84.24	5.25	30	OAT	species	adult	Y	24	>10-50	H	mollusc	12.9
43	11	Cole	2016	Marine Biology	96.13	6.7	3	93.2	11.27	3	OA	species	larvae	Y	10	>5-10	H	mollusc	0.6
44	11	Cole	2016	Marine Biology	96.13	6.7	3	82.74	23.2	3	Temp	species	larvae	Y	10	>5-10	H	mollusc	0.6
45	11	Cole	2016	Marine Biology	96.13	6.7	3	89.05	1.54	3	OAT	species	larvae	Y	10	>5-10	H	mollusc	0.6
46	12	Davis	2013	PLoS One	53.9	47.1	8	37.1	38.8	8	OA	species	egg	Y	8	>5-10	H	mollusc	0.4
47	12	Davis	2013	PLoS One	50.8	54.4	6	15.1	28.4	6	OA	species	egg	N	1	1 to 5	H	mollusc	0.4
48	12	Davis	2013	PLoS One	53.9	47.1	8	96.1	2.2	8	Temp	species	egg	Y	8	>5-10	H	mollusc	0.4
49	12	Davis	2013	PLoS One	50.8	54.4	6	72	38.3	6	Temp	species	egg	N	1	1 to 5	H	mollusc	0.4
50	12	Davis	2013	PLoS One	53.9	47.1	8	81.4	33.3	8	OAT	species	egg	Y	8	>5-10	H	mollusc	0.4
51	12	Davis	2013	PLoS One	50.8	54.4	6	60.4	30.7	6	OAT	species	egg	N	1	1 to 5	H	mollusc	0.4

52	13	Dionisio	2017	MEPS	95.6	4.21	5	85.2	10.94	5 OA	species	larvae	N	1.8	1 to 5	H	mollusc	1.1
53	13	Dionisio	2017	MEPS	95.6	4.21	5	19.2	2.86	5 Temp	species	larvae	N	1.8	1 to 5	H	mollusc	1.1
54	13	Dionisio	2017	MEPS	95.6	4.21	5	14.3	8.92	5 OAT	species	larvae	N	1.8	1 to 5	H	mollusc	1.1
55	14	Dong	2018	Marine Environment al Research	86.5	23.5	4	76.2	15.3	4 OA	species	larvae	N	25	>10-50	H	jellyfish	1
56	14	Dong	2018	Marine Environment al Research	86.5	23.5	4	68.1	12.8	4 Temp	species	larvae	N	25	>10-50	H	jellyfish	1
57	14	Dong	2018	Marine Environment al Research	86.5	23.5	4	67.01	22.6	4 OAT	species	larvae	N	25	>10-50	H	jellyfish	1
58	15	Di Santo	2015	JEMBE	75.13	152.83	37	70.32	120.43	37 OA	species	juvenile	N	8	>5-10	H	fish	24
59	15	Di Santo	2015	JEMBE	93.36	58.4	77	93.37	59.86	77 OA	species	juvenile	N	8	>5-10	H	fish	25.6
60	15	Di Santo	2015	JEMBE	75.13	152.83	37	87.73	76.92	37 Temp	species	juvenile	N	8	>5-10	H	fish	24
61	15	Di Santo	2015	JEMBE	93.36	58.4	77	90.15	87.6	77 Temp	species	juvenile	N	8	>5-10	H	fish	25.6
62	15	Di Santo	2015	JEMBE	75.13	152.83	37	100	1.98	37 OAT	species	juvenile	N	8	>5-10	H	fish	24
63	15	Di Santo	2015	JEMBE	93.36	58.4	77	99.98256	4.34	77 OAT	species	juvenile	N	8	>5-10	H	fish	25.6
64	16	Findlay	2010	Marine Biology	89	19.91	3	78.5	5.93	3 OA	species	juvenile	Y	5	1 to 5	H	crustacean	4.3
65	16	Findlay	2010	Marine Biology	76.4	4.33	2	79.8	2.92	2 OA	species	juvenile	Y	7	>5-10	H	crustacean	4.3
66	16	Findlay	2010	Marine Biology	89	19.91	3	54.2	7.03	3 Temp	species	juvenile	Y	5	1 to 5	H	crustacean	4.3
67	16	Findlay	2010	Marine Biology	76.4	4.33	2	71	8.23	2 Temp	species	juvenile	Y	7	>5-10	H	crustacean	4.3
68	16	Findlay	2010	Marine Biology	89	19.91	3	26.4	4.62	3 OAT	species	juvenile	Y	5	1 to 5	H	crustacean	4.3
69	16	Findlay	2010	Conservation Biology	76.4	4.33	2	69.4	5.47	2 OAT	species	juvenile	Y	7	>5-10	H	crustacean	4.3
70	17	Flynn	2015	Conservation Physiology	88.76	8.81	3	89.79	9.45	3 OA	species	egg	N	11	>10-50	H	fish	3
71	17	Flynn	2015	Conservation Physiology	88.76	8.81	3	84.21	10.92	3 Temp	species	egg	N	11	>10-50	H	fish	3
72	17	Flynn	2015	Physiology	88.76	8.81	3	80.86	12.51	3 OAT	species	egg	N	11	>10-50	H	fish	3
73	18	Foster	2015	Coral Reefs	63.49	13.76	4	59.44	25.4	4 OA	species	larvae	Y	100	>50	H	coral	4.4
74	18	Foster	2015	Coral Reefs	63.49	13.76	4	62.61	15.52	4 Temp	species	larvae	Y	100	>50	H	coral	4.4
75	18	Foster	2015	Coral Reefs	63.49	13.76	4	69.66	15.17	4 OAT	species	larvae	Y	100	>50	H	coral	4.4
76	19	Gardner	2018	Marine Biology	100	34.09	15	67	42.98	15 OA	species	larvae	Y	3	1 to 5	H	mollusc	0.7
77	19	Gardner	2018	Marine Biology	100	34.09	15	87.4	36.16	15 Temp	species	larvae	Y	3	1 to 5	H	mollusc	0.7
78	19	Gardner	2018	Biology	100	34.09	15	80.8	39.13	15 OAT	species	larvae	Y	3	1 to 5	H	mollusc	0.7

79	20	Gibbin	2017	Journal of Experimental Biology	69.82	15	12	75.33	4.3	7 OA	species	adult	N	0.6 <1	H	polychaete	4.3
80	20	Gibbin	2017	Journal of Experimental Biology	69.82	15	12	81.67	10.85	12 Temp	species	adult	N	0.6 <1	H	polychaete	4.3
81	20	Gibbin	2017	Journal of Experimental Biology	69.82	15	12	80.3	8.45	3 OAT	species	adult	N	0.6 <1	H	polychaete	4.3
82	21	Gobler	2018	Frontiers in Marine Science	66.8	4.25	4	54.05	5.4	4 OA	species	larvae	N	2 1 to 5	H	fish	1.4
83	21	Gobler	2018	Frontiers in Marine Science	66.8	4.25	4	70.27	4.63	4 Temp	species	larvae	N	2 1 to 5	H	fish	1.4
84	21	Gobler	2018	Frontiers in Marine Science	66.8	4.25	4	72.2	7.34	4 OAT	species	larvae	N	2 1 to 5	H	fish	1.4
85	22	Gaitan - Esp	2014	JEMBE	94.66	1.29	7	93.68	1.93	7 OA	species	egg	N	5 1 to 5	A	macroalgae	1
86	22	Gaitan - Esp	2014	JEMBE	94.66	1.29	7	76.19	10.93	7 Temp	species	egg	N	5 1 to 5	A	macroalgae	1
87	22	Gaitan - Esp	2014	JEMBE	94.66	1.29	7	58.7	21.85	7 OAT	species	egg	N	5 1 to 5	A	macroalgae	1
88	23	Gianguzza	2014	Marine Environmental Research	88.87	15.09	3	41.29	31.3	3 OA	species	larvae	Y	10 >5-10	H	echinoids	0.3
89	23	Gianguzza	2014	Marine Environmental Research	88.87	15.09	3	62.42	27.1	3 Temp	species	larvae	Y	10 >5-10	H	echinoids	0.3
90	23	Gianguzza	2014	Marine Environmental Research	88.87	15.09	3	49.52	27.38	3 OAT	species	larvae	Y	10 >5-10	H	echinoids	0.3
91	24	Gravinese	2018	Estuarine Coastal and Shelf Science	0.5	0.1	8	0.34	0.1	8 OA	species	larvae	Y	7 >5-10	H	crustacean	4
92	24	Gravinese	2018	Estuarine Coastal and Shelf Science	0.5	0.1	8	0.09	0.04	8 Temp	species	larvae	Y	7 >5-10	H	crustacean	4
93	24	Gravinese	2018	Estuarine Coastal and Shelf Science	0.5	0.1	8	0.07	0.03	8 OAT	species	larvae	Y	7 >5-10	H	crustacean	4
94	25	Haynert	2014	Journal of Foraminiferal Research	75	16.74	40	69.34	16.74	40 OA	species	adult	Y	0.5 <1	A	foraminifer	6
95	25	Haynert	2014	Journal of Foraminiferal Research	75	16.74	40	69.83	34.12	40 Temp	species	adult	Y	0.5 <1	A	foraminifer	6

96	25 Haynert	2014	Journal of Foraminiferal Research	75	16.74	40	61.77	20.17	40 OAT	species	adult	Y	0.5 <1	A	foraminifer	6
97	26 Hildebrandt	2014	Marine Pollution Bulletin	81.86	14.3	4	88.11	12.1	4 OA	species	adult	N	2.21 1 to 5	H	zooplankton	29.8
98	26 Hildebrandt	2014	Marine Pollution Bulletin	81.86	14.3	4	82.56	10.2	4 Temp	species	adult	N	2.21 1 to 5	H	zooplankton	29.8
99	26 Hildebrandt	2014	Marine Pollution Bulletin	81.86	14.3	4	82.07	18.3	4 OAT	species	adult	N	2.21 1 to 5	H	zooplankton	29.8
100	27 Jarrold	2018	Frontiers in Marine Science	63.65	10.1	6	75.64	16.8	6 OA	species	juvenile	N	10 >5-10	H	fish	11
101	27 Jarrold	2018	Frontiers in Marine Science	63.65	10.1	6	52.65	13.96	6 Temp	species	juvenile	N	10 >5-10	H	fish	11
102	27 Jarrold	2018	Frontiers in Marine Science	63.65	10.1	6	50.29	36.6	6 OAT	species	juvenile	N	10 >5-10	H	fish	11
103	28 Leung	2017	Scientific Reports	82.19	7.12	3	78.31	22.54	3 OA	species	adult	Y	1 1 to 5	H	mollusc	8
104	28 Leung	2017	Scientific Reports	82.19	7.12	3	29.91	13.45	3 Temp	species	adult	Y	1 1 to 5	H	mollusc	8
105	28 Leung	2017	Scientific Reports	82.19	7.12	3	18.04	22.14	3 OAT	species	adult	Y	1 1 to 5	H	mollusc	8
106	29 Leung	2018	Science of the Total Environment	31.67	14.2	3	33.28	10.02	3 OA	species	juvenile	Y	1 1 to 5	H	mollusc	26
107	29 Leung	2018	Science of the Total Environment	31.67	14.2	3	45.18	30.07	3 Temp	species	juvenile	Y	1 1 to 5	H	mollusc	26
108	29 Leung	2018	Science of the Total Environment	31.67	14.2	3	94.86	5.57	3 OAT	species	juvenile	Y	1 1 to 5	H	mollusc	26
109	30 Lischka	2012	Global Change Biology	100	0.001	3	100	0.001	3 OA	species	juvenile	Y	1 1 to 5	H	mollusc	1
110	30 Lischka	2012	Global Change Biology	89	15.7	3	100	0.001	3 OA	species	juvenile	Y	1 1 to 5	H	mollusc	1

111	30	Lischka	2012	Global Change Biology	100	0.001	3	100	0.001	3 Temp	species	juvenile	Y	1	1 to 5	H	mollusc	1
112	30	Lischka	2012	Global Change Biology	89	15.7	3	67	23.6	6 Temp	species	juvenile	Y	1	1 to 5	H	mollusc	1
113	30	Lischka	2012	Global Change Biology	100	0.001	3	100	0.001	3 OAT	species	juvenile	Y	1	1 to 5	H	mollusc	1
114	30	Lischka	2012	Global Change Biology	89	15.7	3	39	28.3	3 OAT	species	juvenile	Y	1	1 to 5	H	mollusc	1
115	31	Mos	2019	Science of the Total Environment	14.46	12.08	7	21.74	16.39	6 OA	species	larvae	Y	5	1 to 5	H	echinoids	4
116	31	Mos	2019	Science of the Total Environment	14.46	12.08	7	19.24	19.27	7 Temp	species	larvae	Y	5	1 to 5	H	echinoids	4
117	31	Mos	2019	Science of the Total Environment	14.46	12.08	7	27.17	21.57	7 OAT	species	larvae	Y	5	1 to 5	H	echinoids	4
118	32	Murray	2018	Diversity-Basel	62	9	10	51	7	10 OA	species	egg	N	2	1 to 5	H	fish	0.9
119	32	Murray	2018	Diversity-Basel	33	10	10	36	32	10 OA	species	larvae	N	2	1 to 5	H	fish	2.3
120	32	Murray	2018	Diversity-Basel	62	9	10	46	5	10 Temp	species	egg	N	2	1 to 5	H	fish	0.9
121	32	Murray	2018	Diversity-Basel	33	10	10	31	35	10 Temp	species	larvae	N	2	>5-10	H	fish	2.3
122	32	Murray	2018	Diversity-Basel	62	9	10	49	3	10 OAT	species	egg	N	2	>5-10	H	fish	0.9
123	32	Murray	2018	Diversity-Basel	33	10	10	40	27	10 OAT	species	larvae	N	2	>5-10	H	fish	2.3
124	33	Nguyen	2012	Global Change Biology	82.1	11	12	74.9	22	12 OA	species	larvae	N	10	>5-10	H	echinoids	0.4
125	33	Nguyen	2012	Global Change Biology	75.8	3.1	12	61	26.2	12 OA	species	larvae	N	10	>5-10	H	echinoids	0.7
126	33	Nguyen	2012	Global Change Biology	82.1	11	12	65.1	11	12 Temp	species	larvae	N	10	>5-10	H	echinoids	0.4
127	33	Nguyen	2012	Global Change Biology	75.8	3.1	12	56.2	10.5	12 Temp	species	larvae	N	10	>5-10	H	echinoids	0.7
128	33	Nguyen	2012	Global Change Biology	82.1	11	12	64.6	9	12 OAT	species	larvae	N	10	>5-10	H	echinoids	0.4

129	33	Nguyen	2012	Global Change Biology	75.8	3.1	12	54.7	15.7	12	OAT	species	larvae	N	10	>5-10	H	echinoids	0.7
130	34	Nguyen	2014	JEMBE	91.7	9.8	6	88.4	14.5	6	OA	species	juvenile	Y	10	1 to 5	H	echinoids	4
131	34	Nguyen	2014	JEMBE	91.7	9.8	6	86.6	10.3	6	Temp	species	juvenile	Y	10	1 to 5	H	echinoids	4
132	34	Nguyen	2014	JEMBE	91.7	9.8	6	78.2	14.3	6	OAT	species	juvenile	Y	10	1 to 5	H	echinoids	4
133	35	Pansch	2012	JEMBE	8	3.8	6	8.9	4.4	6	OA	species	larvae	Y	2	1 to 5	H	crustacean	8.1
134	35	Pansch	2012	JEMBE	76	19.5	6	77.3	17.2	6	OA	species	larvae	Y	2	1 to 5	H	crustacean	4.1
135	35	Pansch	2012	JEMBE	8	3.8	6	22.2	6.1	6	Temp	species	larvae	Y	2	1 to 5	H	crustacean	8.1
136	35	Pansch	2012	JEMBE	76	19.5	6	54.1	18.1	6	Temp	species	larvae	Y	2	>10-50	H	crustacean	4.1
137	35	Pansch	2012	JEMBE	8	3.8	6	20.1	8.2	6	OAT	species	larvae	Y	2	>10-50	H	crustacean	8.1
138	35	Pansch	2012	JEMBE	76	19.5	6	50.8	27.9	6	OAT	species	larvae	Y	2	>10-50	H	crustacean	4.1
139	36	Pimentel	2014	Journal of Experimental Biology	45.7	1.9	3	39.36	1.18	3	OA	species	larvae	N	40	>10-50	H	fish	4.3
140	36	Pimentel	2014	Journal of Experimental Biology	45.7	1.9	3	38.91	1.55	3	Temp	species	larvae	N	40	>10-50	H	fish	4.3
141	36	Pimentel	2014	Journal of Experimental Biology	45.7	1.9	3	32.8	2.45	3	OAT	species	larvae	N	40	>10-50	H	fish	4.3
142	37	Pimentel	2016	Climatic Change	42.5	2.52	3	38.36	6.31	3	OA	species	larvae	N	11	>10-50	H	fish	2.1
143	37	Pimentel	2016	Climatic Change	39.84	10.22	3	28.42	7.55	3	OA	species	larvae	N	30	>10-50	H	fish	2.1
144	37	Pimentel	2016	Climatic Change	42.5	2.52	3	19.75	4.97	3	Temp	species	larvae	N	11	>10-50	H	fish	2.1
145	37	Pimentel	2016	Climatic Change	39.84	10.22	3	21.54	7.78	3	Temp	species	larvae	N	30	1 to 5	H	fish	2.1
146	37	Pimentel	2016	Climatic Change	42.5	2.52	3	14.23	3.8	3	OAT	species	larvae	N	11	1 to 5	H	fish	2.1
147	37	Pimentel	2016	Climatic Change	39.84	10.22	3	20.02	5.02	3	OAT	species	larvae	N	30	1 to 5	H	fish	2.1
148	38	Poore	2013	Oecologia	14.2	4.4	5	9.2	2.2	6	OA	species	juvenile	Y	1	1 to 5	H	crustacean	2
149	38	Poore	2013	Oecologia	14.2	4.4	5	4.4	5.2	7	Temp	species	juvenile	Y	1	1 to 5	H	crustacean	2
150	38	Poore	2013	Oecologia	14.2	4.4	5	0.8	1.9	7	OAT	species	juvenile	Y	1	1 to 5	H	crustacean	2
151	39	Rosa	2013	Proc Roy Soc B	93.7	7.6	3	90.3	2.6	3	OA	species	larvae	N	2	>10-50	H	cephalopod	7.1
152	39	Rosa	2013	Proc Roy Soc B	93.7	7.6	3	63.2	18.4	3	Temp	species	larvae	N	2	>10-50	H	cephalopod	7.1
153	39	Rosa	2013	Proc Roy Soc B	93.7	7.6	3	31.8	11.8	3	OAT	species	larvae	N	2	>10-50	H	cephalopod	7.1
154	40	Rosa	2014	Proc Roy Soc B	100	0.001	3	100	0.001	3	OA	species	egg	N	20	>10-50	H	fish	13.1
155	40	Rosa	2014	Proc Roy Soc B	100	0.001	3	59.7	10.3	3	OA	species	juvenile	N	20	>10-50	H	fish	4.3
156	40	Rosa	2014	Proc Roy Soc B	100	0.001	3	79.9	10	3	Temp	species	egg	N	20	>10-50	H	fish	13.1
157	40	Rosa	2014	Proc Roy Soc B	100	0.001	3	71.3	6.1	3	Temp	species	juvenile	N	20	>10-50	H	fish	4.3
158	40	Rosa	2014	Proc Roy Soc B	100	0.001	3	88.8	5	3	OAT	species	egg	N	20	>10-50	H	fish	13.1
159	40	Rosa	2014	Proc Roy Soc B	100	0.001	3	44.3	8.9	3	OAT	species	juvenile	N	20	>10-50	H	fish	4.3

160	41	Rosa	2014	Journal of Experimental Biology	91.34	6.6	10	91	3.3	10	OA	species	egg	N	3.5	1 to 5	H	cephalopod	3.9
161	41	Rosa	2014	Journal of Experimental Biology	91.34	6.6	10	70.56	6.6	10	Temp	species	egg	N	3.5	1 to 5	H	cephalopod	3.9
162	41	Rosa	2014	Journal of Experimental Biology	91.34	6.6	10	46.67	3.3	10	OAT	species	egg	N	3.5	1 to 5	H	cephalopod	3.9
163	42	Schalkhauss	2013	Marine Biology	68.2	18	15	55.4	32.2	18	OA	species	adult	Y	20	>10-50	H	mollusc	8.6
164	42	Schalkhauss	2013	Marine Biology	68.2	18	15	100	0.001	18	Temp	species	adult	Y	20	>10-50	H	mollusc	8.6
165	42	Schalkhauss	2013	Biology	68.2	18	15	97.1	2.4	18	OAT	species	adult	Y	20	>10-50	H	mollusc	8.6
166	43	Shuka	2017	Phycologia	57.32	12.78	5	27.68	21.16	5	OA	species	egg	N	5	1 to 5	A	macroalgae	11
167	43	Shuka	2017	Phycologia	57.32	12.78	5	54.82	16.37	5	Temp	species	egg	N	5	1 to 5	A	macroalgae	11
168	43	Shuka	2017	Phycologia	57.32	12.78	5	59.29	27.55	5	OAT	species	egg	N	5	1 to 5	A	macroalgae	11
169	44	Small	2016	Marine Biology	99.84	1.32	18	83.41	40.78	18	OA	species	juvenile	Y	50	>10-50	H	crustacean	5
170	44	Small	2016	Marine Biology	99.84	1.32	18	100	0.001	18	Temp	species	juvenile	Y	50	>10-50	H	crustacean	5
171	44	Small	2016	Biology	99.84	1.32	18	94.26	22.36	18	OAT	species	juvenile	Y	50	>10-50	H	crustacean	5
172	45	Sswat	2018	PLoS One	0.2	0.02	3	0.1	0.01	3	OA	species	larvae	N	20	>10-50	H	fish	4.6
173	45	Sswat	2018	PLoS One	0.2	0.02	3	0.22	0.02	3	Temp	species	larvae	N	20	>10-50	H	fish	4.6
174	45	Sswat	2018	PLoS One	0.2	0.02	3	0.11	0.01	3	OAT	species	larvae	N	20	>10-50	H	fish	4.6
175	46	Stevens	2018	MEPS	100	0.001	4	93.66	1.15	4	OA	species	juvenile	Y	24	>10-50	H	mollusc	4
176	46	Stevens	2018	MEPS	100	0.001	4	97.51	1.42	4	OA	species	juvenile	Y	20	>10-50	H	mollusc	4
177	46	Stevens	2018	MEPS	73.63	3.66	4	51.65	2.2	4	OA	species	juvenile	Y	2	1 to 5	H	mollusc	4
178	46	Stevens	2018	MEPS	73.28	1.53	4	56.49	5.34	4	OA	species	juvenile	Y	40	>10-50	H	mollusc	4
179	46	Stevens	2018	MEPS	100	0.001	4	100	0.001	4	Temp	species	juvenile	Y	24	>10-50	H	mollusc	4
180	46	Stevens	2018	MEPS	100	0.001	4	100	0.001	4	Temp	species	juvenile	Y	20	>10-50	H	mollusc	4
181	46	Stevens	2018	MEPS	73.63	3.66	4	78.75	2.2	4	Temp	species	juvenile	Y	2	1 to 5	H	mollusc	4
182	46	Stevens	2018	MEPS	73.28	1.53	4	87.02	0.76	4	Temp	species	juvenile	Y	40	>10-50	H	mollusc	4
183	46	Stevens	2018	MEPS	100	0.001	4	100	0.001	4	OAT	species	juvenile	Y	24	>10-50	H	mollusc	4
184	46	Stevens	2018	MEPS	100	0.001	4	100	0.001	4	OAT	species	juvenile	Y	20	>10-50	H	mollusc	4
185	46	Stevens	2018	MEPS	73.63	3.66	4	64.1	2.93	4	OAT	species	juvenile	Y	2	1 to 5	H	mollusc	4
186	46	Stevens	2018	MEPS	73.28	1.53	4	82.06	1.53	4	OAT	species	juvenile	Y	40	>10-50	H	mollusc	4
187	47	Talmage	2011	PLoS One	29.8	2.2	4	19.7	0.3	4	OA	species	larvae	Y	40	>10-50	H	mollusc	2.9
188	47	Talmage	2011	PLoS One	74.2	1	4	54.1	2.1	4	OA	species	larvae	Y	2	1 to 5	H	mollusc	2.9
189	47	Talmage	2011	PLoS One	72.8	16	3	43.2	6.1	3	OA	species	juvenile	Y	2	1 to 5	H	mollusc	6.4
190	47	Talmage	2011	PLoS One	29.8	2.2	4	14	1.1	4	Temp	species	larvae	Y	40	>10-50	H	mollusc	2.9
191	47	Talmage	2011	PLoS One	74.2	1	4	33.3	2.1	4	Temp	species	larvae	Y	2	1 to 5	H	mollusc	2.9
192	47	Talmage	2011	PLoS One	72.8	16	3	51.7	15.5	3	Temp	species	juvenile	Y	2	1 to 5	H	mollusc	6.4

193	47	Talmage	2011	PLoS One	29.8	2.2	4	7.9	0.6	4	OAT	species	larvae	Y	40	>10-50	H	mollusc	2.9
194	47	Talmage	2011	PLoS One	74.2	1	4	27	1.7	4	OAT	species	larvae	Y	2	1 to 5	H	mollusc	2.9
195	47	Talmage	2011	PLoS One	72.8	16	3	33.6	13.6	3	OAT	species	juvenile	Y	2	1 to 5	H	mollusc	6.4
196	48	Vaz-Pinto	2013	Biological Invasions	63	10	16	63.5	12	16	OA	species	egg	N	4	1 to 5	A	macroalgae	1.4
197	48	Vaz-Pinto	2013	Biological Invasions	63	10	16	50	12	16	Temp	species	egg	N	4	1 to 5	A	macroalgae	1.4
198	48	Vaz-Pinto	2013	Biological Invasions	63	10	16	60	10	16	OAT	species	egg	N	4	1 to 5	A	macroalgae	1.4
199	49	Waller	2017	Ices Journal of Marine Science	21.86	0.33	3	30.18	0.49	3	OA	species	larvae	Y	51	>50	H	crustacean	1.4
200	49	Waller	2017	Ices Journal of Marine Science	3.75	0.65	3	6.85	0.82	3	OA	species	larvae	Y	51	>50	H	crustacean	2.6
201	49	Waller	2017	Ices Journal of Marine Science	21.86	0.33	3	4.24	3.43	3	Temp	species	larvae	Y	51	>50	H	crustacean	1.4
202	49	Waller	2017	Ices Journal of Marine Science	3.75	0.65	3	0.98	0.65	3	Temp	species	larvae	Y	51	>50	H	crustacean	2.6
203	49	Waller	2017	Ices Journal of Marine Science	21.86	0.33	3	6.852	5.22	3	OAT	species	larvae	Y	51	>50	H	crustacean	1.4
204	49	Waller	2017	Ices Journal of Marine Science	3.75	0.65	3	1.631	1.14	3	OAT	species	larvae	Y	51	>50	H	crustacean	2.6
205	50	Watson	2018	Global Change Biology	79.83	12	6	80.12	7.06	6	OA	species	egg	N	12	>10-50	H	fish	0.43
206	50	Watson	2018	Global Change Biology	2.51	1.5	6	2.57	1.72	6	OA	species	larvae	N	12	>10-50	H	fish	3.6
207	50	Watson	2018	Global Change Biology	79.83	12	6	72.62	6	6	Temp	species	egg	N	12	>10-50	H	fish	0.43
208	50	Watson	2018	Global Change Biology	2.51	1.5	6	1.18	0.67	6	Temp	species	larvae	N	12	>10-50	H	fish	3.6
209	50	Watson	2018	Global Change Biology	79.83	12	6	73.34	5.65	6	OAT	species	egg	N	12	>10-50	H	fish	0.43
210	50	Watson	2018	Biology	2.51	1.5	6	1.28	0.39	6	OAT	species	larvae	N	12	>10-50	H	fish	3.6

211	51	Wolfe	2013	Cahiers De Biologie Marine	96.7	3.3	4	98.3	1.5	4 OA	species	juvenile	Y	10 >5-10	H	echinoids	2
212	51	Wolfe	2013	Cahiers De Biologie Marine	96.7	3.3	4	98.5	1.8	4 Temp	species	juvenile	Y	10 >5-10	H	echinoids	2
213	51	Wolfe	2013	Cahiers De Biologie Marine	96.7	3.3	4	97.6	4.8	4 OAT	species	juvenile	Y	10 >5-10	H	echinoids	2
214	52	Zhang	2014	Marine Pollution Bulletin	93.77	2.72	3	90.27	1.56	3 OA	species	adult	Y	1.21 1 to 5	H	mollusc	0.4
215	52	Zhang	2014	Marine Pollution Bulletin	88	7.6	3	83.2	9.2	3 OA	species	adult	Y	1.21 1 to 5	H	mollusc	0.4
216	52	Zhang	2014	Marine Pollution Bulletin	93.77	2.72	3	100	0.001	3 Temp	species	adult	Y	1.21 1 to 5	H	mollusc	0.4
217	52	Zhang	2014	Marine Pollution Bulletin	88	7.6	3	81.2	7.2	3 Temp	species	adult	Y	1.21 1 to 5	H	mollusc	0.4
218	52	Zhang	2014	Marine Pollution Bulletin	93.77	2.72	3	85.99	8.56	3 OAT	species	adult	Y	1.21 1 to 5	H	mollusc	0.4
219	52	Zhang	2014	Marine Pollution Bulletin	88	7.6	3	78.8	4.8	3 OAT	species	adult	Y	1.21 1 to 5	H	mollusc	0.4
220	53	Zhang	2016	Ices Journal of Marine Science	94.02	4.21	3	94.97	6.06	3 OA	species	adult	Y	1.21 1 to 5	H	mollusc	4.4
221	53	Zhang	2016	Ices Journal of Marine Science	94.02	4.21	3	92.04	6.68	3 Temp	species	adult	Y	1.21 1 to 5	H	mollusc	4.4
222	53	Zhang	2016	Ices Journal of Marine Science	94.02	4.21	3	89.94	4.91	3 OAT	species	adult	Y	1.21 1 to 5	H	mollusc	4.4

obs: observations; m1: mean of the control; sd1: standard deviation of the control; n1: control sample size; m2: mean of the treatment; sd2: standard deviation of the treatment; n2: treatment sample size; Ecol.Level: ecological level; L.stage: life stage; L.span: life span; L.span1: life span by categories; Exp: exposure time to treatments; OA: ocean acidification; Temp: elevated temperature; OAT: combination of ocean acidification and elevated temperature; N: non-califier; Y: calcifier; H: heterotroph; A: autotroph.

Code S1. R code for growth meta-analysis

```
#####GROWTH CODE
####Install metafor package

install.packages("metafor")
library(metafor)

####Setting working directory
###For Uni desktop
setwd("\\\\UOFA/USERS$/users1/a1685211/Desktop/Articulos/Data_MetaAnalysis/Graphs/Metafor/ResultsNEW/Growth/GrowthF")

###########Importing Data in R
growth<-read.csv("GrowthF.csv", header = TRUE)
summary(growth)
str(growth)

######Calculating effect sizes
datg<- escalc(measure="SMD", m1i=m2, m2i=m1, sd1i=sd2, sd2i=sd1, n1i=n2, n2i=n1, data=growth,
options(max.print = 6500))
datg

##### Fail-safe N
fsn(yi, vi, data=datg, type="Rosenthal", alpha=.05)

fsn(yi, vi, data=datg, type="Rosenberg", alpha=.05)

####TEST HETEROGENEITY WITHIN STUDY VARIANCE and BETWEEN STUDIES
##overall effect by fitting an intercept-only model
growtha<- rma.mv(yi, vi, data=datg, random = list( ~1|obs, ~1|study), tdist=TRUE)

##two-level model without within-study variance
growthb<- rma.mv(yi, vi, data=datg, random = list( ~1|obs, ~1|study), sigma2=c(0,NA), tdist=TRUE)

##two-level model without between-study variance
growthc<- rma.mv(yi, vi, data=datg, random = list( ~1|obs, ~1|study), sigma2=c(NA,0), tdist=TRUE)

anova(growtha, growthb) ###Likelihood-ratio-test to determine significance of the within-study variance
anova(growtha, growthc) ###Likelihood-ratio-test to determine significance of the between-study variance

####LIKELIHOOD RATIO TEST, CHANGE METHOD TO "ML"
grow1<- rma.mv(yi, vi, mods = ~Treatment-1, data=datg, random = list(~1|study,  ~1|obs), method="ML")

grow2<- rma.mv(yi, vi, data=datg, random = list(~1|study,  ~1|obs), method="ML")

anova(grow1, grow2)

# Determining how the total variance is distributed over the
# three levels of the meta-analytic model;
# Print the results in percentages on screen.
n <- length(datg$v)
list.inverse.variances <- 1 / (datg$v)
sum.inverse.variances <- sum(list.inverse.variances)
squared.sum.inverse.variances <- (sum.inverse.variances) ^ 2
list.inverse.variances.square <- 1 / (datg$v^2)
sum.inverse.variances.square <-
  sum(list.inverse.variances.square)
numerator <- (n - 1) * sum.inverse.variances
denominator <- squared.sum.inverse.variances -
  sum.inverse.variances.square
estimated.sampling.variance <- numerator / denominator
```

```
I2_1 <- (estimated.sampling.variance) / (grow2$sigma2[1]
                        + grow2$sigma2[2] + estimated.sampling.variance)
I2_2 <- (grow2$sigma2[1]) / (grow2$sigma2[1]
                    + grow2$sigma2[2] + estimated.sampling.variance)
I2_3 <- (grow2$sigma2[2]) / (grow2$sigma2[1]
                    + grow2$sigma2[2] + estimated.sampling.variance)
amountvariancelevel1 <- I2_1 * 100
amountvariancelevel2 <- I2_2 * 100
amountvariancelevel3 <- I2_3 * 100
amountvariancelevel1 ###within study sampling variance
amountvariancelevel2  ###differences between effect sizes within studies
amountvariancelevel3  ###between study variance

######################Selection of most parsimonious model####################
##install packages ggplot2 and MuMIn

library(ggplot2)

install.packages("MuMIn")
library(MuMIn)
eval(metafor:::.MuMIn)

###Run full model with all the predictors
fullgrow <- rma.mv(yi, vi, mods =  ~Treatment-1 + L.stage + log(L.span) + taxa + Calcifier + Kingdom +
log(exposure) , data=datg, random = list(~1|study, ~1|obs), method = "ML")

###Generates a model selection table ranked by AICc
res <- dredge(fullgrow, trace=2)
###Summarizes model selection table to the most parsimonious models (delta <= 2)
res2<-subset(res, delta <= 2, recalc.weights=FALSE)

importance(res)

#####THIS METHOD GIVES SAME RESULT AS ABOVE (IMPORTANCE OF PREDICTORS) BUT
ALLOWS US TO CREATE A TABLE AND SUBSEQUENT GRAPH
# Save results for all models: all.models, top8.models
all.models = res
top8.models = res[1:8, ]
# Create Multimodel Inference Coeffient Table and save: multimodel.coef
multimodel.coef = summary(MuMIn::model.avg(res, revised.var = TRUE))
multimodel.coef = multimodel.coef$coefmat.full

# Create importance table and save: predictor.importance
predictor.importance = data.frame(model = names(importance(res)), importance = as.numeric(importance(res)))

# Print out results
cat("\n", "Multimodel Inference: Final Results", "--------------------------", sep = "\n")
cat("\n", "- Number of fitted models:", nrow(all.models))
cat("\n", "- Full formula:", as.character(form))
cat("\n", "- Coefficient significance test:", test)
if (interaction == TRUE) {
  cat("\n", "- Interactions modeled: yes")
} else {
  cat("\n", "- Interactions modeled: no")
}
cat("\n", "- Evaluation criterion:", eval.criterion, "\n")
cat("\n", "Best 8 Models", "--------------------------", "\n", sep = "\n")
print(top8.models)
cat("\n", "Multimodel Inference Coefficients", "--------------------------", "\n", sep = "\n")
print(multimodel.coef)
```

```
cat("\n", "Predictor Importance", "--------------------------", "\n", sep = "\n")
print(predictor.importance)

# Print graph of predictors importance
ggpredictor = ggplot(predictor.importance, aes(x = reorder(model, importance), y = importance)) +
  geom_bar(stat = "identity") + coord_flip() + geom_hline(yintercept = 0.8, color = "blue") + theme_minimal() +
  theme(axis.title.y = element_blank()) + ylab("Predictor Importance")
suppressWarnings(suppressMessages(plot(ggpredictor)))

####Random effects meta-regression of the most parsimonious model (Calcifier + Nutrition model)

###First run NULL MODEL (no moderators or categories)
grow2<- rma.mv(yi, vi, data=datg, random = list(~1|study,  ~1|obs), method="ML")

#######Calcifier + Nutrition mode
growCK<-rma.mv(yi, vi, mods = ~Calcifier-1 + NutMod, data=datg, random = list(~1|study,  ~1|obs),
tdist=TRUE, test="knha")

##Estimate R^2
1-(var(resid(growCK)) / var(resid(grow2)))

##########CONTRAST MATRIX TO GET THE ESTIMATES FOR EACH OF THE MODERATORS
##########AND THEN TO GET THE CI

###install packages first
install.packages("multcomp")
library(multcomp)

#####Use the Calcification mode + Nutrition mode model named "growCK"
###Get estimates for each of the moderators
summary(glht(growCK, linfct=rbind(c(1,0,+1), c(0,1,+1))), test=adjusted("none"))

####Estimate CI
confint(glht(growCK, linfct=rbind(c(1,0,+1), c(0,1,+1)), df=df.residual(growCK)), calpha=univariate_calpha())
```

Code S2. R code for survival meta-analysis

```
####SURVIVAL CODE
####Install metafor package

install.packages("metafor")
library(metafor)


####Setting working directory
###For Uni desktop
setwd("\\\\UOFA/USERS$/users1/a1685211/Desktop/Articulos/Data_MetaAnalysis/Graphs/Metafor/ResultsNEW/Survival/SurvivalE")

########### Importing Data in R
survi<-read.csv("SurvivalE2.csv", header = TRUE)
summary(survi)
str(survi)

######Calculating effect sizes
datsvl <- escalc(measure="D2ORN", m1i=m2, m2i=m1, sd1i=sd2, sd2i=sd1, n1i=n2, n2i=n1, data=survi,
options(max.print = 6500))
datsvl

##### Fail-safe N
fsn(yi, vi, data=datsvl, type="Rosenthal", alpha=.05)

fsn(yi, vi, data=datsvl, type="Rosenberg", alpha=.05)

####TEST HETEROGENEITY WITHIN STUDY VARIANCE and BETWEEN STUDIES
##overall effect by fitting an intercept-only model
surva<- rma.mv(yi, vi, data=datsvl, random = list( ~1|obs, ~1|study), tdist=TRUE)

##two-level model without within-study variance
survb<- rma.mv(yi, vi, data=datsvl, random = list( ~1|obs, ~1|study), sigma2=c(0,NA), tdist=TRUE)

##two-level model without between-study variance
survc<- rma.mv(yi, vi, data=datsvl, random = list( ~1|obs, ~1|study), sigma2=c(NA,0), tdist=TRUE)

anova(surva, survb) ###Likelihood-ratio-test to determine significance of the within-study variance

anova(surva, survc) ###Likelihood-ratio-test to determine significance of the between-study variance

####LIKELIHOOD RATIO TEST, CHANGE METHOD TO "ML"
surv1l<- rma.mv(yi, vi, mods = ~Treatment-1, data=datsvl, random = list(~1|study,  ~1|obs), method="ML")

surv2l<- rma.mv(yi, vi, data=datsvl, random = list(~1|study,  ~1|obs), method="ML")

anova(surv1l, surv2l)

# Determining how the total variance is distributed over the
# three levels of the meta-analytic model;
# Print the results in percentages on screen.
n <- length(datsvl$v)
(list.inverse.variances <- 1 / (datsvl$v))
sum.inverse.variances <- sum(list.inverse.variances)
squared.sum.inverse.variances <- (sum.inverse.variances) ^ 2
list.inverse.variances.square <- 1 / (datsvl$v^2)
sum.inverse.variances.square <-
  sum(list.inverse.variances.square)
numerator <- (n - 1) * sum.inverse.variances
denominator <- squared.sum.inverse.variances -
```

```
sum.inverse.variances.square
estimated.sampling.variance <- numerator / denominator
I2_1 <- (estimated.sampling.variance) / (surv2l$sigma2[1]
                              + surv2l$sigma2[2] + estimated.sampling.variance)
I2_2 <- (surv2l$sigma2[1]) / (surv2l$sigma2[1]
                        + surv2l$sigma2[2] + estimated.sampling.variance)
I2_3 <- (surv2l$sigma2[2]) / (surv2l$sigma2[1]
                        + surv2l$sigma2[2] + estimated.sampling.variance)

amountvariancelevel1 <- I2_1 * 100
amountvariancelevel2 <- I2_2 * 100
amountvariancelevel3 <- I2_3 * 100
amountvariancelevel1 ###within study sampling variance
amountvariancelevel2  ###differences between effect sizes within studies
amountvariancelevel3  ###between study variance

######################Selection of most parsimonious model####################
##install packages ggplot2 and MuMIn

library(ggplot2)

install.packages("MuMIn")
library(MuMIn)
eval(metafor:::.MuMIn)

###Run full model with all the predictors
fullsurv <- rma.mv(yi, vi, mods =  ~Treatment-1 + L.stage + log(L.span) + taxa + Calcifier + Kingdom +
log(exposure) , data=datsvl, random = list(~1|study, ~1|obs), method = "ML")

###Generates a model selection table ranked by AICc
res <- dredge(fullsurv, trace=2)
###Summarizes model selection table to the most parsimonious models (delta <= 2)
res2<-subset(res, delta <= 2, recalc.weights=FALSE)

importance(res)


#####THIS METHOD GIVES SAME RESULT AS ABOVE (IMPORTANCE OF PREDICTORS) BUT
ALLOWS US TO CREATE A TABLE AND SUBSEQUENT GRAPH
# Save results for all models: all.models, top5.models
all.models = res
top5.models = res[1:5, ]
# Create Multimodel Inference Coeffient Table and save: multimodel.coef
multimodel.coef = summary(MuMIn::model.avg(res, revised.var = TRUE))
multimodel.coef = multimodel.coef$coefmat.full


# Create importance table and save: predictor.importance
predictor.importance = data.frame(model = names(importance(res)), importance = as.numeric(importance(res)))

# Print out results
cat("\n", "Multimodel Inference: Final Results", "--------------------------", sep = "\n")
cat("\n", "- Number of fitted models:", nrow(all.models))
cat("\n", "- Full formula:", as.character(form))
cat("\n", "- Coefficient significance test:", test)
if (interaction == TRUE) {
  cat("\n", "- Interactions modeled: yes")
} else {
  cat("\n", "- Interactions modeled: no")
}
```

```
cat("\n", "- Evaluation criterion:", eval.criterion, "\n")
cat("\n", "Best 5 Models", "--------------------------", "\n", sep = "\n")
print(top5.models)
cat("\n", "Multimodel Inference Coefficients", "--------------------------", "\n", sep = "\n")
print(multimodel.coef)
cat("\n", "Predictor Importance", "--------------------------", "\n", sep = "\n")
print(predictor.importance)
```

 # Print graph of predictors importance

```
ggpredictor = ggplot(predictor.importance, aes(x = reorder(model, importance), y = importance)) +
  geom_bar(stat = "identity") + coord_flip() + geom_hline(yintercept = 0.8, color = "blue") + theme_minimal() +
  theme(axis.title.y = element_blank()) + ylab("Predictor Importance")
suppressWarnings(suppressMessages(plot(ggpredictor)))
```

####Random effects meta-regression of the most parsimonious model (Treatment + Life stage)

####First run NULL MODEL (no moderators or categories)

```
survnull<- rma.mv(yi, vi, data=datsvl, random = list(~1|study,  ~1|obs), tdist=TRUE, test="knha")
```

#####TReatment + Life stage

```
survTLs<-rma.mv(yi, vi, mods = ~Treatment-1 + L.stage, data=datsvl, random = list(~1|study,  ~1|obs),
tdist=TRUE, test="knha")
```

###Estimate R^2

```
1-(var(resid(survTLs)) / var(resid(survnull)))
```

#####CONTRAST MATRIX TO GET THE ESTIMATES FOR EACH OF THE MODERATORS
########AND THEN TO GET THE CI

###install packages first

```
install.packages("multcomp")
library(multcomp)
```

#####Use the TReatment + Life stage model named "survTLs"
###Get estimates for each of the moderators

```
summary(glht(survTLs, linfct=rbind(c(1,0,0,+1,0,0), c(1,0,0,0,+1,0), c(1,0,0,0,0,+1),
                          c(0,1,0,+1,0,0), c(0,1,0,0,+1,0), c(0,1,0,0,0,+1),
                          c(0,0,1,+1,0,0), c(0,0,1,0,+1,0), c(0,0,1,0,0,+1))), test=adjusted("none"))
```

####Estimate CI

```
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                          c(0,1,0,+1,0,0), c(0,1,0,0,+1,0), c(0,1,0,0,0,+1),
                        c(0,0,1,+1,0,0), c(0,0,1,0,+1,0), c(0,0,1,0,0,+1)), df=df.residual(survTLs)),
                    calpha=univariate_calpha())
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Chapter V: Phenotypic responses in fish behaviour narrow as climate ramps up

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ii. permission is granted for the candidate in include the publication in the thesis; and

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Abstract

Natural selection alters the distribution of phenotypes as animals adjust their behaviour and physiology in response to environmental change. We have little understanding of the magnitude and direction of environmental filtering of phenotypes, as trait selection under future conditions is challenging to study. The expression of trait variability provides us with a crucial understanding of how populations might adapt or acclimate to future climate. Here we test whether climate stressors drive shifts in the frequency distribution of behavioural and physiological phenotypes within populations of 17 fish species, studied at natural climate change analogues (CO_2 vents and warming hotspots) and in the laboratory (mesocosms and aquaria). We discovered that fish from natural populations (4 out of 6 species) narrowed their phenotypic distribution under ocean acidification towards behaviourally bolder individuals, representing loss of shyer phenotypes. In contrast, ocean warming drove a loss of bolder phenotypes (2 out of 11 species) as well as a gain (2 out of 11 species) in natural and laboratory conditions. Furthermore, the phenotypic variance within species populations was reduced at natural CO_2 vents and warming hotspots compared to control conditions, but this pattern was not observed within laboratory systems. Fishes that experienced bolder behaviour at these natural ecosystems generally showed increased densities in the wild. Yet, neither shifts in phenotype nor its reduced distribution affected body condition as most individuals across all 17 species were able to maintain physiological homeostasis (measured through 5 different traits). Boldness is a highly heritable trait that is related to both loss of fitness (i.e. increased mortality risk) and gain in fitness (i.e. increased resource acquisition, growth, reproduction). Hence, climate conditions that mediate the relative occurrence of shy and bold phenotypes may reshape the strength of species interactions and consequently alter population and community dynamics in a future ocean.

Introduction

The increasing emissions of anthropogenic CO_2 into the atmosphere are rapidly changing the physico-chemical conditions of the world's oceans by increasing their acidity and surface temperatures (Caldeira and Wickett, 2003; IPCC, 2013). Ocean acidification and warming are set to challenge marine life by modifying their physiology and behaviour

(Nagelkerken and Connell, 2015) leading to altered biodiversity and ecosystem health (Bellard et al., 2012; Nagelkerken et al., 2017; Wittmann and Pörtner, 2013; Connell et al. 2018). Organisms may be able to persist environmental change by shifting their ranges, (epi)genetic adaptation, and adaptive phenotypic plasticity (Nunney, 2016; Souza, 2018). The persistence of sessile organisms with limited dispersal capacity will depend more heavily on phenotypic plasticity, as they cannot move towards more favourable environments under global change (Vallardes et al., 2007; Reed et al., 2011; Leung et al., 2020). Phenotypic plasticity is the capacity of a single genotype to express multiple phenotypes in response to environmental stimuli (Scheiner, 1993; Pigliucci, 2005; Souza et al., 2018) allowing organisms to cope with environmental change (Bonamour et al., 2019). Phenotypic plasticity increases population persistence and can be adaptive by improving an individual's fitness to altered conditions (Schmid and Guillaume, 2017; Bonamour et al., 2019). Alternatively, plasticity can be maladaptive if fitness is reduced, or neutral if there is no effect on fitness (Ghalambor et al., 2007). We currently do not know how phenotypic plasticity might allow marine vertebrates to acclimate under climate change, and whether this is sufficient to allow their populations to persist under future conditions.

Plastic responses in an individual's morphological, physiological and behavioural traits are a fundamental source of variation in a population (Henn et al., 2018; Gibert and Brassil, 2014; Matesanz et al., 2012; Sultan and Spencer, 2002). In natural systems, selection fluctuates in space and time (Buskirk, 2017) and favours specific phenotypes over others, i.e. those that are better pre-adapted to the novel conditions (Edelaar et al., 2017). A single phenotype cannot maintain fitness in a wide range of environments; therefore, selection in heterogeneous environments will favour plasticity which promotes diversification of traits (Reed et al., 2011; Lafuente and Beldade, 2019). Species populations can undergo three patterns of natural selection. The first one is directional selection where selection acts towards a single phenotypic extreme, shifting the distribution to one end (Kingsolver and Pfenning, 2007). When selection acts in one direction and there is a lack of phenotypic variation, the vulnerability of these populations increases (Assis et al., 2016). A second mode of selection is stabilizing selection, where fitness increases for individuals closest to the mean value, as the extremes of the trait are selected against (Kingsolver and Pfenning, 2007). A third mode of selection is disruptive selection, where

there is selection against mean trait values, and the highest levels of fitness are found at the extremes of the trait values (Kingsolver and Pfenning, 2007).

Species responses to climate change are typically expressed as the mean value of their traits, disregarding the fact that population variation in phenotypes can modify the patterns of species interactions and natural selection (Gibert and Brassil, 2014; Start, 2019). Understanding the changes in the direction, frequency, or variability of the frequency distribution of phenotypes can indicate whether a population will be able to persist in a future climate. Whether a specific phenotype will be selected depends on the adaptive capacity of specific phenotypic traits to the changing environment. Whilst abiotic conditions influence the selection of species or populations with particular traits and phenotypes that aid them to establish, persist, and reproduce (environmental filtering), biotic interactions can also be a significant contributor (Kraft et al., 2015; Lozada-Gobilard et al., 2019). Phenotype selection can alter demographic parameters that alter population size. Populations that undergo alterations in size and phenotypic distribution will result in altered interactions with other species populations that may either be stable or undergoing changes as well (Donelson et al., 2019). Consequently, modified species interactions will ultimately alter the structure of community in fluctuating environments (Nagelkerken and Munday, 2016).

We here test how the phenotypic distribution of different behaviours and physiologies within populations of various fish species adjusts to future climate, simulated under natural and laboratory conditions. We used natural volcanic CO_2 vents to test for effects of elevated CO_2, and natural climate-warming regions to test for the effects of elevated temperature. Laboratory evaluations of future climate effects were performed using mesocosm and aquarium systems. A wide range of behavioural and physiological traits in 17 fish species were quantified to study resultant changes in trait frequency distributions within species populations. We reveal that only risk-taking behaviours were consistently affected in species populations, with little to no changes in their physiological homeostasis. Assessing which phenotypes predominate in a changing ocean provides an understanding of their potential persistence or vulnerability under global change.

Materials and methods

Natural systems

Natural CO_2 seeps

This study was conducted on a temperate rocky reef at White Island, a volcanic island in Bay of Plenty, New Zealand. Sample sites were located along the north-eastern coast of the island and consisted of two independent vent sites (north and south) and two independent controls sites (north and south) (see Fig. S1 in Connell et al., 2018). The two vents sites represented future CO_2 enriched oceans for the year 2100 (RCP 8.5 "business-as-usual" projections, Bopp et al., 2013) without confounding differences in water temperature, were located at 6-8 m water depth, and had a dimension of ~24 × 20 m each. The control sites represented current ambient pH levels and were situated ~25 m away from the vent sites. Studies undertaken over multiple time points showed that the seawater chemistry (pH, pCO_2 values) are relatively consistent over time at the study sites (Nagelkerken et al., 2016, 2017). Salinity and temperature levels did not differ between vent and control sites. Vents were characterized by a benthic community dominated by turf algae (<10 cm in height), and the control sites comprised a mosaic of kelp (*Ecklonia radiata*), turf macroalgae, and hard-substratum sea urchin barrens devoid of vegetation (Connell et al., 2018).

Seawater chemistry

Seawater physico-chemical parameters were sampled *in situ* near the bottom where the experiments were performed. Water samples were collected during May 2013, November 2013, February 2015, March 2016, February 2017, and February 2018. Temperature and pH were recorded using a Hobo Pendant and a Mettler Toledo pH meter respectively. Salinity was measured with a SR6 refractometer (Vital Sine). Total alkalinity (TA) water samples were collected for the years 2013 and 2015 and 2017, and were fixed with mercuric chloride and preserve in Duran glass bottles (Schott) for further analysis (Dickson et al. 2007), in accordance with standard procedures for ocean CO_2 measures. Alkalinity measures were not taken for the year 2016, instead values from the years 2013 and 2015 were used to estimated pCO_2 (see Nagelkerken et al., 2017). TA was measured using a potentiometric titrator (888 Titrando, Metrohm, Switzerland). Seawater CO_2 levels were

estimated using values of temperature, salinity, pH_{NBS}, and TA from the sampled sites (Table S1). The program CO2SYS (Pierrot et al., 2006) for Excel with constants K1 and K2 from Mehrbach et al. (1973) refit by Dickson and Millero (1987) was used to calculate seawater pCO_2 (µatm). Values for standards were maintained within 1% accuracy from certified reference material from A. Dickson (Scripps Institution of Oceanography).

Anti-predator behaviour

Antipredator behaviour was evaluated for the most common site-attached species of fish at the study site: common triplefin *Forsterygion lapillum*, crested blenny *Parablennius laticlavius*, Yaldwin's triplefin *Notoclinops yaldwyni*, blue-eyed triplefin *Notoclinops segmentatus*, variable triplefin *Forsterygion varium,* and the scaly damselfish *Parma alboscapularis*.

Antipredator responses were quantified by simulating the approach of a potential threat to the fish while recording their escape behaviour, and recording the distance at which fish initiated a flight response (startle distance). This simulated attack involved the use of a cubical frame made of white PVC pipes, with a GoPro camera attached to the top (see Fig. S3 in Nagelkerken et al., 2016). The top of the frame had an attached black iron rod that extended ~60 cm forward from the camera. At the end of the iron rod a metal ruler (30 cm) was attached in a downward direction to allow the bottom half of the ruler to appear in the camera's field of view. All recordings were taken at a speed of 30 frames per second.

For each trial a random individual fish was selected to initiate an escape response by lowering the tip of the ruler vertically towards its head until the fish escaped (Nagelkerken et al., 2015). This mimics the escape response of fish from natural predators (Nagelkerken et al. 2017). The threat approach and escape path were fully captured by the camera, representing the fish fast start response (Domenici and Blake, 1997; Figueroa et al., 2009). The response of the fish (flight initiation response) consisted of a set of movements that commenced with the individual directing its eyes toward the approaching ruler, followed by a fast, single continuous jump with a few tail flips when the ruler approached too close, and finally settling back several centimetres away onto the substratum.

Only fish that escaped in a plane parallel to the camera (i.e. upward or sideward, not toward or away from the camera) were used to measure escape distance. Escape behaviour was recorded for 25 individuals per CO_2 treatment for the common triple fin, crested blenny, Yaldwin's triplefin, blue-eyed triplefin, and variable triple fin fishes in 2016. Due to the lower natural densities of the blue-eyed triplefin the number of individuals were reduced to 15 at control and 5 at vents. For the year 2013, 73 individuals per treatment of the common triplefin were recorded, and for 2017, 25 individuals per treatment were recorded for the scaly damselfish. Recordings were analysed using VLC media player 2.0.1, where the distance at which the fish initiated its escape response from the approaching ruler was quantified. The moment at which an individual started its jump until it landed back on the substratum was defined as the fish escape response.

Startle distance values were converted in the graphs (for distribution, fig. 1A-E, 1J-K, S1A-I, and variability, fig. 3A-B) so that larger values represented greater boldness. This was performed by subtracting each of the values (starting with the smallest) from the greatest value within a species so that the x-axis was shifted in an opposite direction.

Fish sampling and tissue collection

The muscle tissues of fish were sampled in years 2017, 2018, and 2019. Fish were collected with a hand net and euthanized using the *iki jime* technique (Barker et al., 2002). Small pieces of muscle tissue of each individual were stored in RNAlater for further biomarker analyses whilst the remainder of the fish was stored on ethanol. Fish individual weight and length were also recorded.

Samples in 2017 were collected for the common triplefin *Forsterygion lapillum* and consisted of 84 individuals for control sites and 127 for the vents; only gonads and livers were measured for these individuals. For the year 2018, the common triplefin (10 individuals at control, 10 individuals at vents), the crested blenny (9 individuals at control, 10 individuals at vents), the blue-eyed triplefin (13 individuals at control, 10 individuals at vents), and the Yaldwin's triplefin (13 individuals at control, 10 individuals at vents) were collected. In 2019, samples were taken for the same species of fish as in 2018, and consisted of 10 individuals per treatment for each fish species. Experiments were

performed under animal ethics approval numbers S-2015-222 and S-2015-019, and according to the University's animal ethics guidelines.

Natural warming hotspots

The study sites were located along the coast of Southeast Australia, which is considered a hotspot for ocean warming (Poloczanska et al., 2007; Figueroa and Booth, 2010), where a latitudinal temperature gradient occurs (spatial increase towards lower latitudes) with accelerated warming occurring at the higher latitudes (temporal increase with time) (Figueroa and Booth, 2010). Fish were sampled at different locations across this latitude to represent colder or warmer sites: South West Rocks and Port Stephens (warm region); Sydney (either a warm or cold region, depending on the fish affinity); and Bass Point, Narooma, and Merimbula (cold region). Antipredator behaviour was tested, using the same methodology and device as at the natural CO_2 vents, for juveniles of five fish species: the coral reef-associated species *Acanthurus nigrofuscus* (brown tang), *Acanthurus triostegus* (convict tang), and *Abudefduf vaigiensis* (Indo-Pacific sergeant), and the temperate species *Atypichthys strigatus* (mado) and *Microcanthus strigatus* (stripey). The former three species are range-extending coral-reef fishes (Booth et al., 2018).

Sample collections of muscle tissue were performed for four species: *Acanthurus triostegus*, *Abudefduf vaigiensis*, *Atypichthys strigatus*, and *Microcanthus strigatus*. Fish were collected using a hand net with an anaesthetic mixture (clove oil and 100% ethanol, 1:3 ratio) in the summer of 2018. Fish were collected by hand net and euthanized using the *iki jime* technique. Muscle tissue was collected immediately after and stored in RNAlater for further physiological analyses. Experiments were performed under The University of Adelaide Animal Ethics Committee approval S-2017-002.

Laboratory systems

Mesocosm experimental design

Juvenile fishes were collected using a seine net along different coastal sites in the northern part of the Spencer Gulf and the eastern coast of the Gulf St. Vincent, South Australia from September to October 2016. Three pelagic species, small mouthed hardyhead, gold spot

mullet, yellow-eyed mullet (*Atherinosoma microstoma*, *Liza argentea*, and *Aldrichetta forsteri*, respectively), and four benthic species, southern longfin goby, blue weed whiting, smooth toad fish, congollis (*Favonigobius lateralis*, *Haletta semifasciata*, *Tetractenos glaber*, and *Pseudaphritis urvillii*) were selected for the study. Upon collection, fish were acclimated under ambient temperature and pH levels to tank conditions (73 l bins) for three weeks. Subsequently, fish were transferred to outdoor circular mesocosms (1800 l capacity) where they were kept for one week. After the acclimation period, future climate conditions were simulated in a factorial design. A total of 12 mesocosms maintained four treatments (control, ocean acidification, elevated temperature, and the combined ocean acidification and elevated temperature), each with three replicates. Seven individuals from each species were added together into each mesocosm, with the exception of hardyheads for which a total of 14 individuals were added per mesocosm. Initially, the hardyheads were considered as two species, the small mouthed hardyhead (*Atherinosoma microstoma*) and elongated hardyhead (*Atherinosoma elongatum*). After physiological examination they were considered as small mouthed hardyheads due to their single developed gonad and tooth patches on the tongue (Ivantsoff and Crowley, 1996; Ye et al., 2015).

Seawater temperature in the mesocosms varied in relation to air temperature, but the elevated temperature treatment was set at 1.2 °C above air temperature. This temperature was controlled using submersible titanium heaters with a programmed temperature controller (Weipro 500 W). Heaters were placed inside each elevated-temperature mesocosm as well as in the header tank that distributed warmed seawater to all elevated temperature mesocosms. Ocean acidification mesocosms were provided with pre-treated seawater using a header tank where pure CO_2 was bubbled into the seawater. Additionally, each ocean acidification mesocosm was provided with enriched CO_2 levels using a Pegas 4000 MF gas mixer. Control seawater pCO_2 was maintained at an average of 370 μatm, and 500 μatm for ocean acidification treatments. Temperature and pH were measured 2–3 times a day in each mesocosm using a 913 Metrohm pH meter and a Mettler Toledo SG2 SevenGo meter. Total alkalinity was measured weekly using potentiometric titrator (888Titrando, Metrohm, Switzerland). CO2SYS (Pierrot et al., 2006) for Excel with constants from Mehrbach et al. (1973) refit by Dickson and Millero (1987) (Table S2) was

used to calculate seawater pCO_2 (µatm). Seawater inflow of each mesocosm had a rate of 2 l min^{-1}, corresponding to a full replenishment every 15 hrs.

Fishes were fed with a mixture of blended sardines, shrimps and squids *ad libitum* on a daily basis. After a 2-month period of exposure to the climate treatments, the mesocosm project was terminated. Individual weight and total length were measured for each fish at the start and end of the mesocosm experiment. The southern longfin gobies (*Favonigobius lateralis*) and the small mouthed hardyheads (*Atherinosoma microstoma*) were then transferred to an indoor temperature-controlled aquarium. The remained fish species were euthanized with the *iki jime* technique and kept frozen for further analyses. All fish species were part of the mesocosm behavioural experiments, but only the southern logfin gobies and the small mouthed hardyheads were included for further behavioural analyses in aquarim conditions.

Mesocosm behavioural experiments

A set of behavioural responses were evaluated for the fish species in response to the various climate treatments. Fish activity levels, bite rate, boldness, and species interactions were tested after 40 days of exposure to the treatments. A 50 ml transparent vial with apertures on the sides and covered with mesh was placed in the middle of the mesocosm tank. The vial contained 25 live adult brine shrimps (*Artemia salina*) as visual cues, and a mixture of food (3 g of blood worms and 1.5 g of blended sardines, shrimp and squid) as olfactory cues. Fish behaviour was recorded from the top of the tank for 7 min using a GoPro™ Hero4 Silver camera attached to a PVC frame. Recordings were analysed using VLC media player 2.1.3. A frame was overlayed onto the computer screen and divided the field of view in eight areas. The behaviour of individual fish was recorded individually from the time it entered until it left the field of view. Each time a fish entered the field of view it was considered a new individual. Activity level was measured as the percentage of time the fish spent swimming. Bite rate was estimated as the number of bites the fish took at the food vial per minute. Boldness was quantified as the percentage time a fish spent in the areas closest (arena area) to the vial. Due to the difficulty off differentiating between gold spot mullet and yellow-eyed mullet in the video analysis, they were categorized into one group as mullets.

Aquarium experimental design

Fishes relocated to the aquarium room were held in 40 l tanks for an additional 3.2 months. The quality of the seawater was maintained similar to the conditions of the mesocosms, but fish were kept separated by species. The 40 l tanks were placed inside 300 l water baths where temperature was controlled with submersible titanium heaters with programmed temperature controllers (Weipro 500 W). The average temperature of the seawater in the tanks was 20.5 °C for present-day conditions and 21.8 °C (+1.3 °C difference) under future climate conditions. Seawater pCO_2 was regulated by placing two air stones in each tank, one supplying ambient air (average pCO_2: 529 µatm; pH: 7.95) and the second one supplied CO_2-enriched air (average pCO_2: 825 µatm; pH: 7.76; 0.2 pH units difference compared to controls) using a Pegas 4000 MF gas mixer. Control pCO_2 seawater was maintained by only supplying ambient air to the respective tanks. Temperature and pH were measured every day using a 913 Metrohm pH meter, while salinity was measured using a StarterPen conductivity meter (IC-ST10C-C). Total alkalinity values were estimated by Gran titration from 40 ml samples. Seawater samples were measured after one week of transfer to the aquarium; after one month, samples were taken weekly during three consecutive weeks. Seawater alkalinity samples were processed on the same day of collection. Mean pCO_2 of seawater was calculated using CO2SYS for Excel (Pierrot et al., 2006) with constants from (Mehrbach et al.1973) refit by (Dickson and Millero, 1987) (Table S3). Seawater changes were performed daily to remove food waste (after feeding the fish), with pre-treated seawater from their respective treatment. Tanks containing southern longfin gobies had a sandy bottom and harboured shelters made from PVC pipes. Each tank contained seven southern longfin gobies. Control (C) and warming (W) treatments had two replicate tanks, while ocean acidification (OA) and the combined ocean acidification and warming (OAW) had three replicate tanks. Hardyhead treatments had two replicate tanks each, harbouring 14 fish per tank, and all tanks harboured PVC pipes for shelter. Fishes were fed daily *ad libitum* with the same diet as in the mesocosm. Fish individual weights and total lengths were measured at the end of the aquarium experiment. Fishes were euthanized using the *iki jime* technique after a total 5.2 months of treatment exposure (mesocosm + aquarium) and immediately frozen in liquid nitrogen and stored at -80 °C until further analyses.

Aquarium behavioural experiments

After 3.7 months of treatment exposure (combined mesocosm and aquarium conditions) fish activity levels and bite rates were tested inside the 40 l aquarium tanks. A 50 ml vial with the same characteristics as in the mesocosm experiments was placed in the middle of the tank. The vial contained the same visual (brine shrimps) and olfactory cues (food mixture) described in the mesocosm experiments. Fish behaviour was recorded remotely from the top of the tank for 7 min, using either a Canon Legria HF-R406 or a Canon Legria HFM52 camera attached to a metal frame. Behaviour was then analysed from the videos using VLC media player 2.1.3 with a grid of eight squares overlapping the tank arena. Activity levels were evaluated as the number of lines crossed by the fish per minute (Munday et al., 2013), while bite rate was quantified as the number of bites at the food vial per minute. Boldness was quantified as the percentage time a fish spent in the areas closest (arena area) to the vial. Due to some poorly focused videos, we were able to evaluate 6 min of the recordings for southern longfin gobies and 5 min for hardyheads. Experiments were performed under The University of Adelaide Animal Ethics Committee approval #S-2016-165.

Physiological proxies

Physiological indicators were tested within both natural and laboratory systems (aquarium fish only). Because biomarkers, RNA/DNA ratios, and behaviour respond almost immediately to treatment effects, and because fish spent 3.2 months in the aquarium before tissue sampling, these measurements relate to the effects of the aquarium treatment conditions rather than those of the mesocosm.

Stress responses and condition of the fishes were evaluated by assessing different indicators: total antioxidant capacity (TAC), lipid peroxidation or oxidative damage (MDA), RNA/DNA ratio, gonadosomatic index (GSI), hepatosomatic index (HSI), Fulton's condition index, and somatic growth.

Fish muscle tissue (~25 mg for laboratory, ~4 mg for vents, and ~4.8 mg for natural warming natural systems) was used for the RNA/DNA ratio analyses. The *D7001 ZR-Duet™ DNA/RNA MiniPrep Kit* was used for DNA and RNA extraction. RNA samples

were treated with the *E1010 DNase I Set (250 U) w/ DNA Digestion Buffer* to avoid contamination from DNA into RNA samples. A Quantus Fluorometer was used for quantification of the DNA and RNA samples. To adjust the quantified value to the weight of the sample, we obtained the total weight of DNA or RNA sample and divided this by the weight of the tissue sample:

$$\frac{RNA}{DNA} = \frac{\left\{\left[\text{Quantus value}\left(\frac{\text{ng}}{\mu\text{l}}\right) / \text{Volume}\ (\mu\text{l})\right] * \text{Weight of sample}\ (\text{mg})\right\}}{\left\{\left[\text{Quantus value}\left(\frac{\text{ng}}{\mu\text{l}}\right) / \text{Volume}\ (\mu\text{l})\right] * \text{Weight of sample}\ (\text{mg})\right\}}$$

Fish muscle tissue (~100 mg, ~15 mg for vents and natural warming systems) was also used to prepare a 10% tissue homogenate in an ice bath, and subsequently used to assess total antioxidant capacity (TAC) and malondialdehyde concentration (MDA, indicative of oxidative damage). Coomassie blue staining method was used to quantified the protein concentration in the 10% tissue homogenate. Assay kits purchased from Nanjing Jiancheng Bioengineering Institute, China, were used to evaluate TAC (CAT no: A015-1) and MDA concentration (CAT no: A003-1), following the manufacturer's manuals.

The energy reserves of aquarium fishes were calculated based on the hepatosomatic index (HSI). The HSI was calculated based on the wet weight of the liver and of the entire fish:

$$HSI = (\text{wet liver weight/total body wet weight}) \times 100$$

Liver wet weight was used to estimate the reproductive investment of fishes from the natural systems.

Body condition was calculated for each fish individually using the Fulton's condition factor (K-factor):

$$K = 100 \times \text{wet weight/standard length}^3$$

For the vents systems condition was only estimated for the common triplefin (2017 samples). Mesocosm and aquarium fish condition was tested at the end of each experiment.

Statistical analyses

We constructed frequency-distribution plots for all the behavioural and physiological responses in order to visualize the distribution of phenotypes across controls vs treatments. We used a two-sample Kolmogorov-Smirnov test, using the KS-test function in R-Studio v.3.6.0, to test if the control data came from population distributions of the same shape as the climate treatments.

To test for species variability between control and natural sites or treatments, we estimated the standard deviation (SD) of each tested species for both the control and climate treatments. Subsequently, for each system (aquarium, mesocosm, CO_2 vents, and natural warming locations) the SD of the species phenotypic response was tested between control and treatments using a T-test with the *t.test* function in R-Studio v.3.6.0. This test was only performed for boldness as this was the only behaviour that was affected in most species. Additionally, the mean, median, and standard deviation of the population response for boldness of each species were tested between controls and climate treatments. Fish densities was also measured for each species in the natural systems (CO_2 vents and warming systems) by visually counting the number of individuals per unit area within belt transects (Nagelkerken et al., 2017, Ferreira et al., 2018).

We calculated the ratio of density change by dividing the density of fishes at naturally elevated CO_2 or elevated temperature by the density at controls, respectively. Similarly, we estimated the ratio of change in boldness (i.e. mean startle distance at CO_2 vents or warming systems divided by that at the controls). We tested the relationship between the change in fish density and change in startle distance using least squares linear regression and calculated the R^2 of the fitted regression line. We tested for outliers using Cook's distance (Cook and Weisbert, 1984).

Results

Elevated CO_2 drove an increase in frequency of occurrence of bold individuals relative to present-day conditions. This pattern was consistent for natural CO_2 vents (four out of six species, Figs. 1A-E, S1A-B) and laboratory aquarium conditions (one out of two species,

Fig. 1F, S1C-F). For all these observations, zero to very few shy individuals remained under elevated CO_2 conditions. This pattern was not observed for species from mesocosm systems, where boldness distribution was either similar between elevated CO_2 and control conditions (five out of six species, Figs. 1H-I, S1D-F), or was reduced under elevated CO_2 (one species, Fig. 1G).

Fish exposed to warmer environments in natural and laboratory systems presented three main responses in the distribution of their boldness phenotypes. First, in cases where their distributions shifted towards an increased frequency of occurrence of bold individuals combined with a reduced frequency of shy phenotypes (one out of five species at natural warming systems; Figs. 1J, S1G-I, and one out of two species in aquarium systems; Figs. 1F, S1C). Second, in cases where the width of the boldness distribution curves was reduced, we observed a loss of both shy and bold individuals (one out of five species at natural warming systems; Fig. 1K), and consequently a peak of phenotypes with medium boldness values. Third, where there was an increase in the frequency of occurrence of shy individuals and a reduced frequency of bolder individuals (two out of six species in mesocosms, Figs. 1H, I). Fish exposed to the combination of elevated CO_2 and warming in aquaria and mesocosms generally showed a distribution similar to that of the controls (Figs. S1, S2), or were positioned in between that of elevated temperature and elevated CO_2 in isolation (Fig. 1F).

For natural systems, within-species phenotypic variance for boldness (Table 1) was lower at CO_2 vents ($p = 0.049$, Fig. 2A) and natural warming hotspots ($p = 0.024$, Fig. 2B) compared to controls (control ambient CO_2 and colder water temperature, respectively), but this reduction was not observed under any of the laboratory conditions (mesocosm or aquarium, Figs. 2C, D).

There was a significant linear relationship between boldness at CO_2 vents sites and the density of the fish ($R^2=0.866$, $p=0.007$, Fig. 3A; Table S5), only when the detected outlier was removed from the analysis (see Table S4 for results with complete data set). For natural warming sites, increased boldness resulted in increased densities for 3 out of 5 species, but no significant linear relationship was found (Tables S4, S5). The frequency distribution of phenotypes of other behaviours (activity levels and feeding rate, Figs. S2, S3) and of various physiological proxies (body condition index, total cellular antioxidant

capacity, cellular oxidative damage, RNA/DNA tissue ratios, and liver weight or hepatosomatic index; Figs. S4–S8) generally did not differ between control and treatment conditions (temperature or elevated CO_2 or their combination), either in natural or laboratory systems. There were a few exceptions to this observation, but these did not present any consistent patterns (Figs. S2-4).

Discussion

We reveal that risk-taking phenotypes (bolder individuals) increased in relative abundance, as opposed to the other seven phenotypes, within both natural and laboratory simulated ocean acidification. This increase coincided with a reduction in population-level phenotypic variance for boldness in naturally disturbed environments. At least five out of twelve fish species experienced a shift in their trait distribution towards bolder phenotypes when exposed to elevated CO_2, with a consequent loss of shy individuals. When faced with elevated temperature, however, species showed a dual response comprising losses as well as gains of bold phenotypes. Likewise, laboratory studies based on short-term exposures have shown increases (Munday et al., 2010; Biro et al., 2010) and decreases (Hamilton et al., 2013, Rossi et al., 2015) in boldness under ocean acidification and ocean warming. In contrast, the frequency distribution of phenotypic traits related to feeding and physiology was similar under future climate and control conditions across all study systems, with the exception of a few species. These results suggest that environmental filtering of phenotypes occurs under ocean acidification and warming, but is more readily observed in wild populations that were exposed to climate stressors for the majority of their life.

Populations with a greater proportion of bold individuals occurred in localities of ocean warming and acidification. Rather than suffer poorer body condition, individuals within these populations were more densely packed within natural CO_2 or warmed systems. Bold individuals are often more active, dominant, and successful in acquiring food and other resources than their shyer counterparts (Ariyomo and Watt, 2012). Bolder individuals often show positive somatic growth, although their risk of predation increases at the same time (Smith and Blumstein, 2008). The natural CO_2 vent sites used in this study had reduced densities of predators compared to control sites (Nagelkerken et al., 2016, 2017),

providing a potential survival advantage to bolder fishes under elevated CO_2. The scarcity of predators at CO_2 vents and the increase in food resources could have aided individuals in maintaining their physiological homeostasis (Thomsen et al., 2013; Ramajo et al., 2016; Gobler et al., 2018). Organisms need to adjust their behaviour to changes in the environment, and these behavioural adjustments influence the strength of species interactions (Wong and Candolin, 2015). Hence, under elevated CO_2 an increase in bolder phenotypes could confer the species with greater growth or reproductive success, and a competitive advantage for resources over species that do not show such shifts in boldness, ultimately increasing the population size of species that show positive phenotypic adjustments to ocean acidification.

Wild populations under present-day conditions had greater variability in boldness phenotypes compared to those subjected to elevated CO_2 or elevated temperature, although this was not observed in laboratory systems. In nature, species interactions and environmental factors can pose selective pressure on phenotypic traits (Sobral et al. 2013). When facing environmental change, the degree of phenotypic variation affects the viability of a population, as a wider range of available phenotypes are more likely to hold a particular plastic response needed in novel or changing environments (Brown et al., 2007; Ariyomo and Watt, 2012). As a result, narrowing phenotypic variability will negatively influence populations at an evolutionary and ecological scale (Ariyomo and Watt, 2012), which will have consequences for population selection during environmental disturbances. As such, populations where a phenotypic trait is favoured in the environment will face greater risk of decline if natural conditions change, either by climate-related or human stressors.

Risk-taking behaviour was the only trait that was consistently altered in its frequency distribution across climate change stressors and across a variety of species. At naturally elevated CO_2 vents risk-taking phenotypes were distributed toward bolder behaviours. Over generations, if a trait in a population is favoured towards one end of the phenotypic distribution, directional selection can occur (Breed and Moore, 2012), resulting in a decrease in population variance, and a change in the mean value of the trait (Kingsolver and Pfenning 2007, Sanjack et al, 2018). Selection of a phenotype will only lead to evolutionary changes if the trait is heritable (Kingsolver and Pfenning 2007).

Boldness is known to be a highly heritable trait (Ferrari et al. 2016), and therefore environments where climatic stressors are continuously facilitating bolder phenotypes, might experience selection in favour of this trait when individual fitness is enhanced. Phenotypic variability in a population allows for the initial selection of a particular trait that provides an advantage within the new conditions, but when the most advantageous traits in the environment are selected they can become common in the population and reduce phenotypic variability.

Selection towards a larger trait value or a change in its frequency distribution can also modify the patterns of species interactions and natural selection (Start, 2019), irrespective of its heritability. Thus, due to the different effects that climate change exerts on fish species and the narrowing of risk-taking phenotypic variation, the strength of interactions in the community can be altered in a future climate scenario. Differences in behavioural responses across species can change the strength and nature of their interactions, such as predation and competition (Wong and Candolin, 2015), given that behavioural responses of one species can be linked to the ecological and selective environment of other species (Wolf and Weissing, 2012). Consequently, differential shifts in the distribution of bold phenotypes across species under changing environments could have an indirect impact on the structure of species communities, through reductions of less dominant species.

Understanding how phenotypic plasticity alters species adjustments to climate change is key to recognising their capacity to acclimate and persist under future environments. We demonstrate that global change can modify and narrow the distribution of bold phenotypes in fishes, particularly under ocean acidification. Future changes in climate can put populations under selective pressure. Consequently, altered distributions of shy and bold behavioural phenotypes can modify the interaction between species, strengthening the dominance of some species over others, and opening a pathway towards more homogenised communities.

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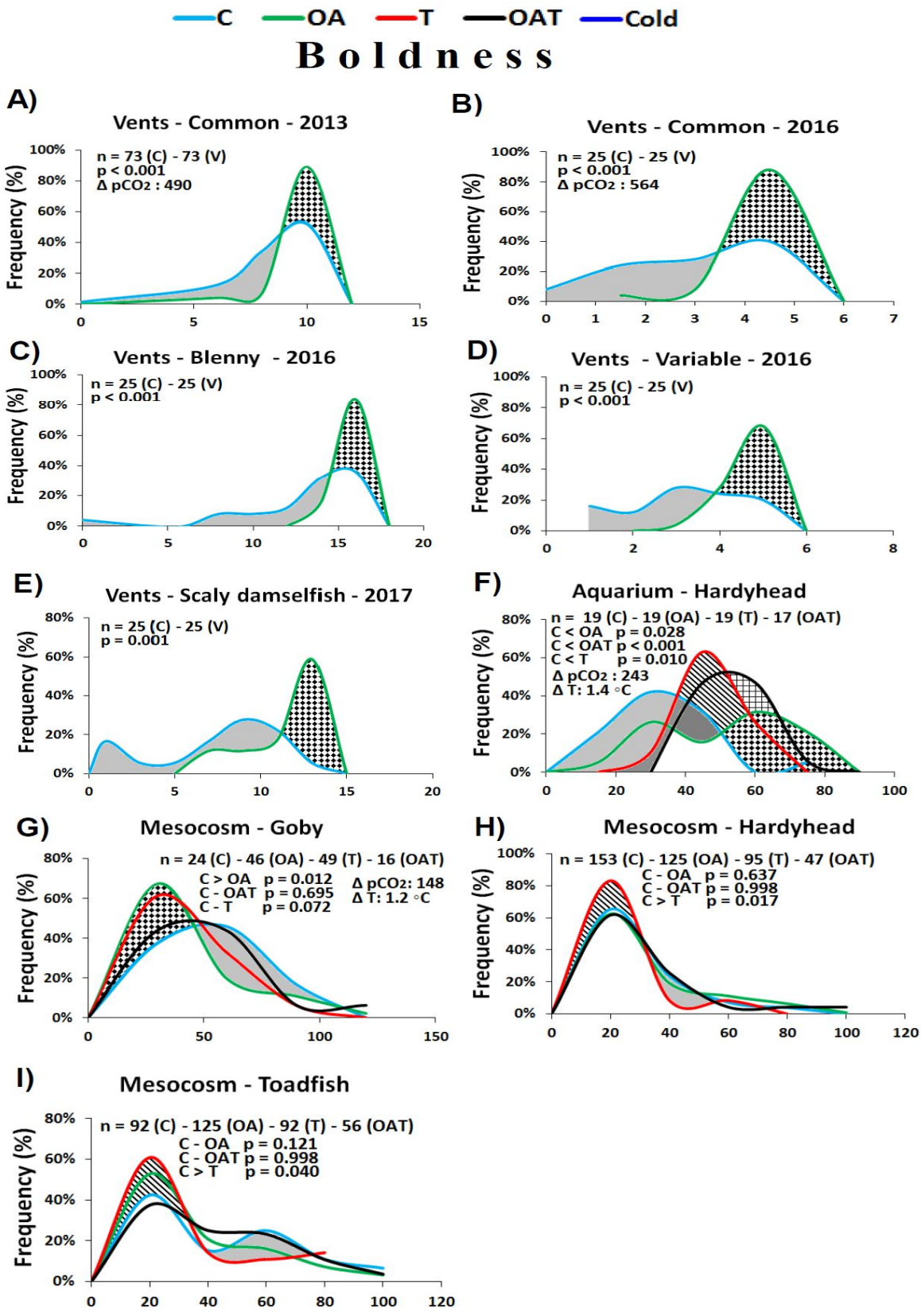
Table 1. Mean, median, and standard deviation (SD) of boldness* for all fish species.

	Control				OA				T				OAT			
Vents	**Mean**	**Median**	**SD**	**N**	**Mean**	**Median**	**SD**	**N**	**Mean**	**Median**	**SD**	**N**	**Mean**	**Median**	**SD**	**N**
Common triplefin 2013 (*Forsterygion lapillum*)	2.1	1.8	1.8	73	1.0	0.6	1.1	73								
Common triplefin 2016 (*Forsterygion lapillum*)	2.3	2.0	1.4	25	0.8	0.5	0.9	25								
Crested blenny 2016 (Parablennius laticlavius)	3.8	2.8	3.6	25	1.0	1.0	0.9	25								
Variable triplefin 2016 (*Forsterygion varium*)	2.3	2.1	1.3	25	0.6	0.3	0.7	25								
Scaly damselfish 2017 (*Parma alboscapularis*)	6.7	5.5	3.6	25	2.2	1.5	2.5	25								
Blue eyed triplefin 2016 (*Notoclinops segmentatus*)	1.1	0.9	0.8	15	0.8	0.9	0.5	5								
Yaldwin triplefin 2016 (*Notoclinops yaldwyni*)	2.2	1.7	1.5	25	2.0	1.5	1.6	25								
Aquarium																
Goby (*Favonigobius lateralis*)	35.8	26.4	40.5	8	34.1	42.8	24.8	11	33.9	25.2	29.9	12	51.8	47.7	16.7	12
Hardyhead (*Atherinosoma microstoma*)	25.2	24.0	16.8	19	41.7	46.7	17.3	19	38.1	40.0	8.8	19	45.0	46.7	9.0	17
Mesocosm																
Goby (*Favonigobius lateralis*)	36.2	40.0	23.6	24	24.6	18.8	28.0	46	21.7	19.8	23.0	49	31.9	34.6	28.2	16
Hardyhead (*Atherinosoma microstoma*)	13.7	0.0	19.4	153	16.9	0.0	22.6	125	6.8	0.0	14.9	95	17.2	0.0	26.1	47
Toadfish (*Tetractenos glaber*)	31.2	28.7	29.2	92	21.8	14.3	25.2	125	20.4	0.0	25.7	92	30.1	0.0	25.8	56
Congolli (*Pseudaphritis urvillii*)	0.0	0.0	NA	1	27.2	0.0	38.2	7	38.2	0.0	34.6	7	35.7	44.7	34.7	23
Mullet (*Liza argentea* and *Aldrichetta forsteri*)	9.9	0.0	17.3	100	11.9	0.0	19.6	70	8.8	0.0	17.2	10	6.1	0.0	11.2	107
Whiting (*Haletta semifasciata*)	9.5	0.0	23.3	6	10.0	10.0	14.1	2	0.0	0.0	0.0	3	25.0	25.0	25.0	3
Natural warming																
Brown tang (*Acanthurus nigrofuscus*)	7.8	7.7	1.6	12					5.1	4.5	1.2	9				
Convict tang (*Acanthurus triostegus*)	7.3	6.5	3.7	11					5.1	5.0	1.9	14				
Indo-Pacific sergeant (*Abudefduf vaigiensis*)	5.7	5.5	2.8	26					5.3	5.5	2.1	21				
Mado (*Atypichthys strigatus*)	5.0	4.5	2.2	17					6.0	6.0	0.6	10				
Stripey (*Microcanthus strigatus*)	4.6	4.0	2.7	21					4.7	4.4	2.0	18				

OA: ocean acidification; T: elevated temperature; OAT: combination of ocean acidification and elevated temperature. N: number of individuals for each experiment, but for mesocosms the N represents the number of events. *Boldness at CO_2 vents and natural warming hotspots are measured as startle distance to an approaching threat, with shorter distance representing bolder phenotypes.


C
OA
T
OAT
Cold
Boldness
A)
Vents - Common - 2013
n = 73 (C) - 73 (V)
p < 0.001
Δ pCO2 : 490
B)
Vents - Common - 2016
n = 25 (C) - 25 (V)
p < 0.001
Δ pCO2 : 564
C)
Vents - Blenny - 2016
n = 25 (C) - 25 (V)
p < 0.001
D)
Vents - Variable - 2016
n = 25 (C) - 25 (V)
p < 0.001
E)
Vents - Scaly damselfish - 2017
n = 25 (C) - 25 (V)
p = 0.001
F)
Aquarium - Hardyhead
n = 19 (C) - 19 (OA) - 19 (T) - 17 (OAT)
C < OA p = 0.028
C < OAT p < 0.001
C < T p = 0.010
Δ pCO2 : 243
Δ T: 1.4 ◦C
G)
Mesocosm - Goby
n = 24 (C) - 46 (OA) - 49 (T) - 16 (OAT)
C > OA p = 0.012
C - OAT p = 0.695
C - T p = 0.072
Δ pCO2: 148
Δ T: 1.2 ◦C
H)
Mesocosm - Hardyhead
n = 153 (C) - 125 (OA) - 95 (T) - 47 (OAT)
C - OA p = 0.637
C - OAT p = 0.998
C > T p = 0.017
I)
Mesocosm - Toadfish
n = 92 (C) - 125 (OA) - 92 (T) - 56 (OAT)
C - OA p = 0.121
C - OAT p = 0.998
C > T p = 0.040
Frequency (%)

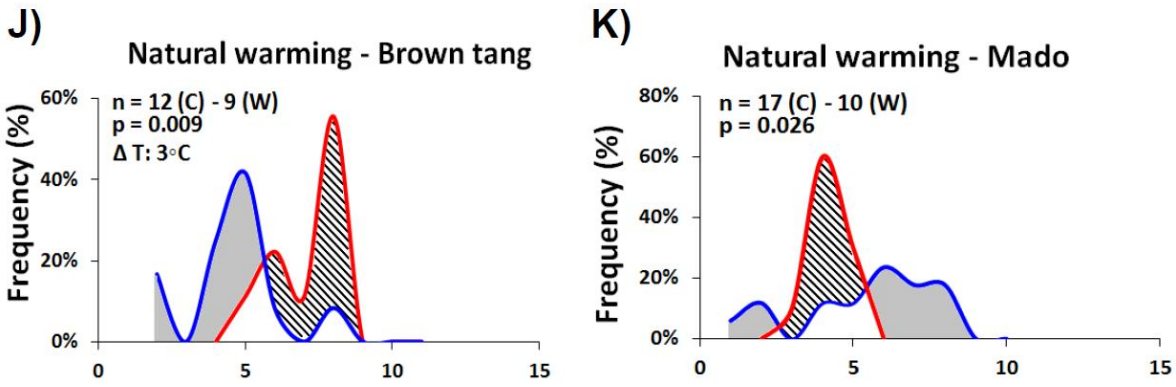


Figure 1. Boldness frequency distributions of fish from natural CO_2 vent systems (a–e), aquaria (f), mesocosms (g–i), and natural warming hotspots (j–k). Only graphs showing significant differences among distributions are presented; see Supplementary material for all other graphs. Coloured areas indicate loss or gain of phenotypes. Grey shade: control and cold (at natural warming sites); diamond pattern: elevated CO_2; diagonal lines: elevated temperature; area with squares: combined elevated CO_2 and temperature. C: control, OA: ocean acidification, T: elevated temperature, OAT: combined elevated CO_2 and elevated temperature. Natural warming, C: cold, W: warming. n = number of individuals; p = p-value; Δ = difference between control (or colder seawaters in natural systems) and the climate stressor (temperature or pCO_2). See Table 1 for full scientific and common species names.

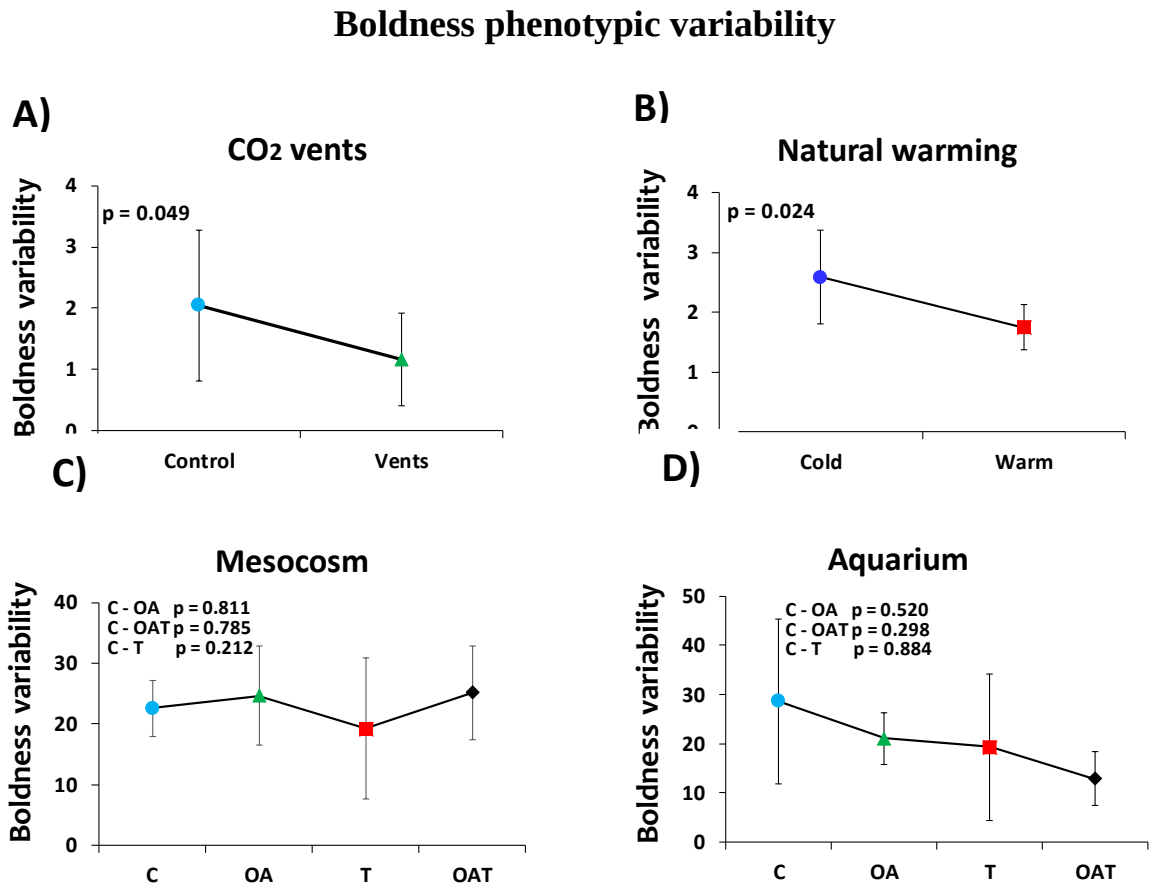


Figure 2. Change in mean variability (1 SD) of boldness phenotypes within species at controls and treatments for: A) natural CO_2 vents, B) natural warming hotspots, C) mesocosms, and D) aquaria. C: control; OA: ocean acidification, T: elevated temperature; OAT: combination of ocean acidification and temperature. Error bars represent standard deviation.

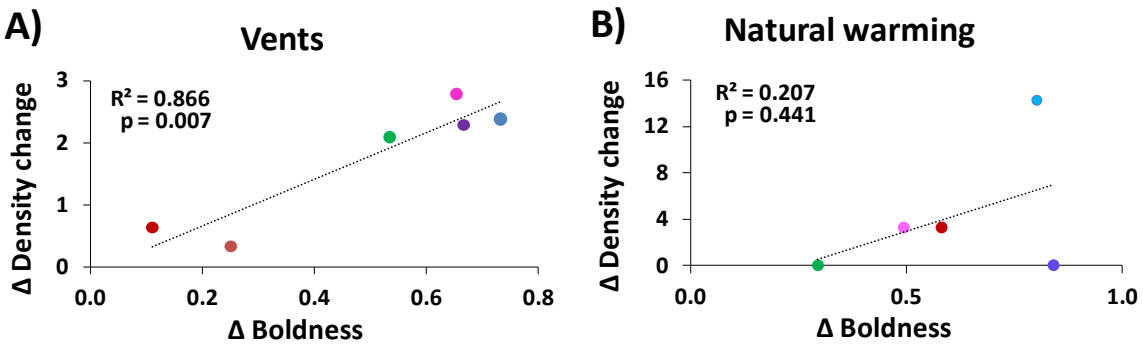


Figure 3. Increases in fish densities in the wild as a function of increased fish boldness for natural analogues of climate stressors. A) volcanic CO_2 vents (one outlier removed); B) natural warming hotspots. Each dot represents a different species. Fitted regression lines with associated R^2-values and p-values are shown (see also Tables S4, S5 for statistical outputs).

Supplementary information

There were exceptions where phenotypes related to behaviour and physiological proxies presented significant differences between controls and treatments (elevated temperature or elevated CO_2). For activity levels of aquarium fish, there were two species that shifted their distribution towards greater activity levels, one species in all of the aquarium treatments (Fig. S2E), and the second species only under the combination of elevated CO_2 and temperature (OAT, Fig. S2D) in the aquarium. At the natural warming systems, three out of five species increased their activity levels with warmer temperatures (Figs. S2M, N, O), and one out of five increased its feeding rate (Fig. S3O). Additionally, one mesocosm species presented a small significant distribution shift towards reduction in their condition index (under elevated temperature, Fig. S4J), one aquarium species towards an increased condition under the combination of elevated CO_2 and temperature (Fig. S4C). At the natural warming systems, one species (Fig. S4L) had a significant increase in its condition under warmer temperatures, and one species had a reduced condition at warmer sites (Fig. S4M).

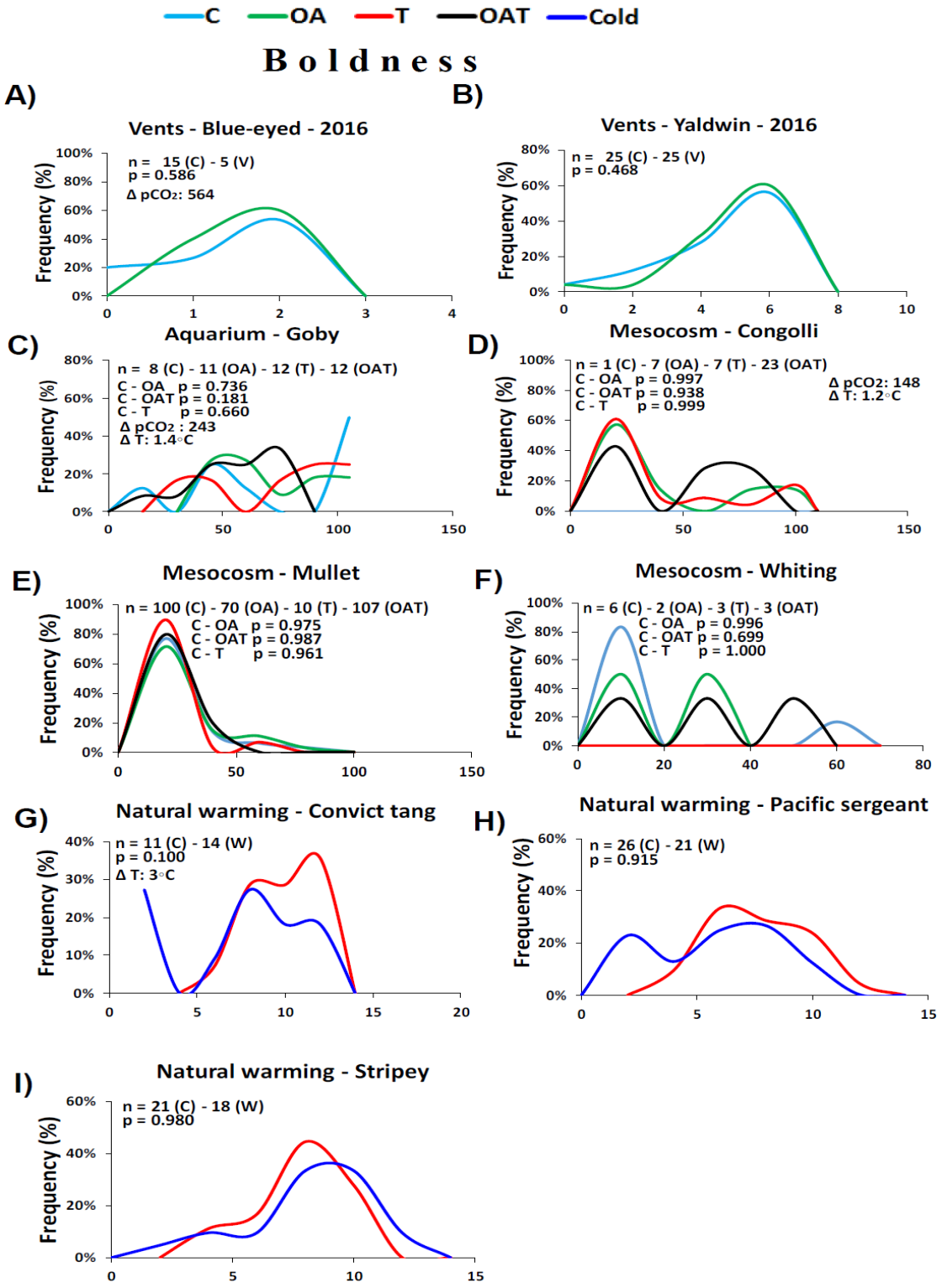
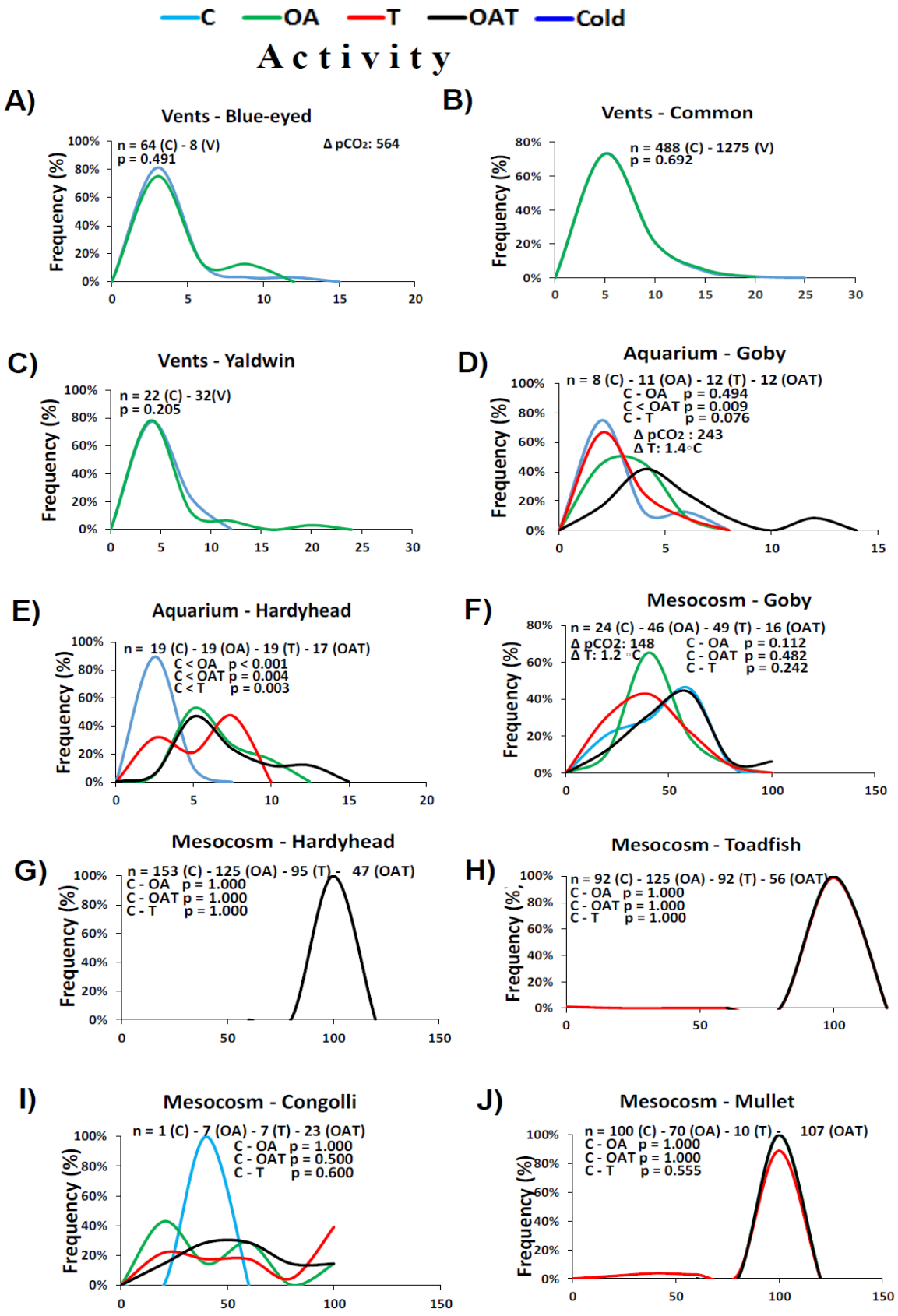


Figure S1. Boldness frequency distributions of fish from natural CO_2 vent systems (A-B), aquaria (C), mesocosms (D-F), and natural warming hotspots (G-I). Only values showing

non-significant differences are presented. C: control, OA: ocean acidification, T: elevated temperature, OAT: combined elevated CO_2 and elevated temperature. Natural warming, C: cold, W: warming. n = number of individuals; p = p-value; Δ = difference between control (or colder seawaters in natural systems) and the climate stressor (temperature or pCO_2).


C
OA
T
OAT
Cold
Activity
A)
Vents - Blue-eyed
n = 64 (C) - 8 (V)
p = 0.491
Δ pCO2: 564
B)
Vents - Common
n = 488 (C) - 1275 (V)
p = 0.692
C)
Vents - Yaldwin
n = 22 (C) - 32(V)
p = 0.205
D)
Aquarium - Goby
n = 8 (C) - 11 (OA) - 12 (T) - 12 (OAT)
C - OA p = 0.494
C < OAT p = 0.009
C - T p = 0.076
Δ pCO2 : 243
Δ T: 1.4◦C
E)
Aquarium - Hardyhead
n = 19 (C) - 19 (OA) - 19 (T) - 17 (OAT)
C < OA p < 0.001
C < OAT p = 0.004
C < T p = 0.003
F)
Mesocosm - Goby
n = 24 (C) - 46 (OA) - 49 (T) - 16 (OAT)
Δ pCO2: 148
Δ T: 1.2 ◦C
C - OA p = 0.112
C - OAT p = 0.482
C - T p = 0.242
G)
Mesocosm - Hardyhead
n = 153 (C) - 125 (OA) - 95 (T) - 47 (OAT)
C - OA p = 1.000
C - OAT p = 1.000
C - T p = 1.000
H)
Mesocosm - Toadfish
n = 92 (C) - 125 (OA) - 92 (T) - 56 (OAT)
C - OA p = 1.000
C - OAT p = 1.000
C - T p = 1.000
I)
Mesocosm - Congolli
n = 1 (C) - 7 (OA) - 7 (T) - 23 (OAT)
C - OA p = 1.000
C - OAT p = 0.500
C - T p = 0.600
J)
Mesocosm - Mullet
n = 100 (C) - 70 (OA) - 10 (T) - 107 (OAT)
C - OA p = 1.000
C - OAT p = 1.000
C - T p = 0.555
Frequency (%)

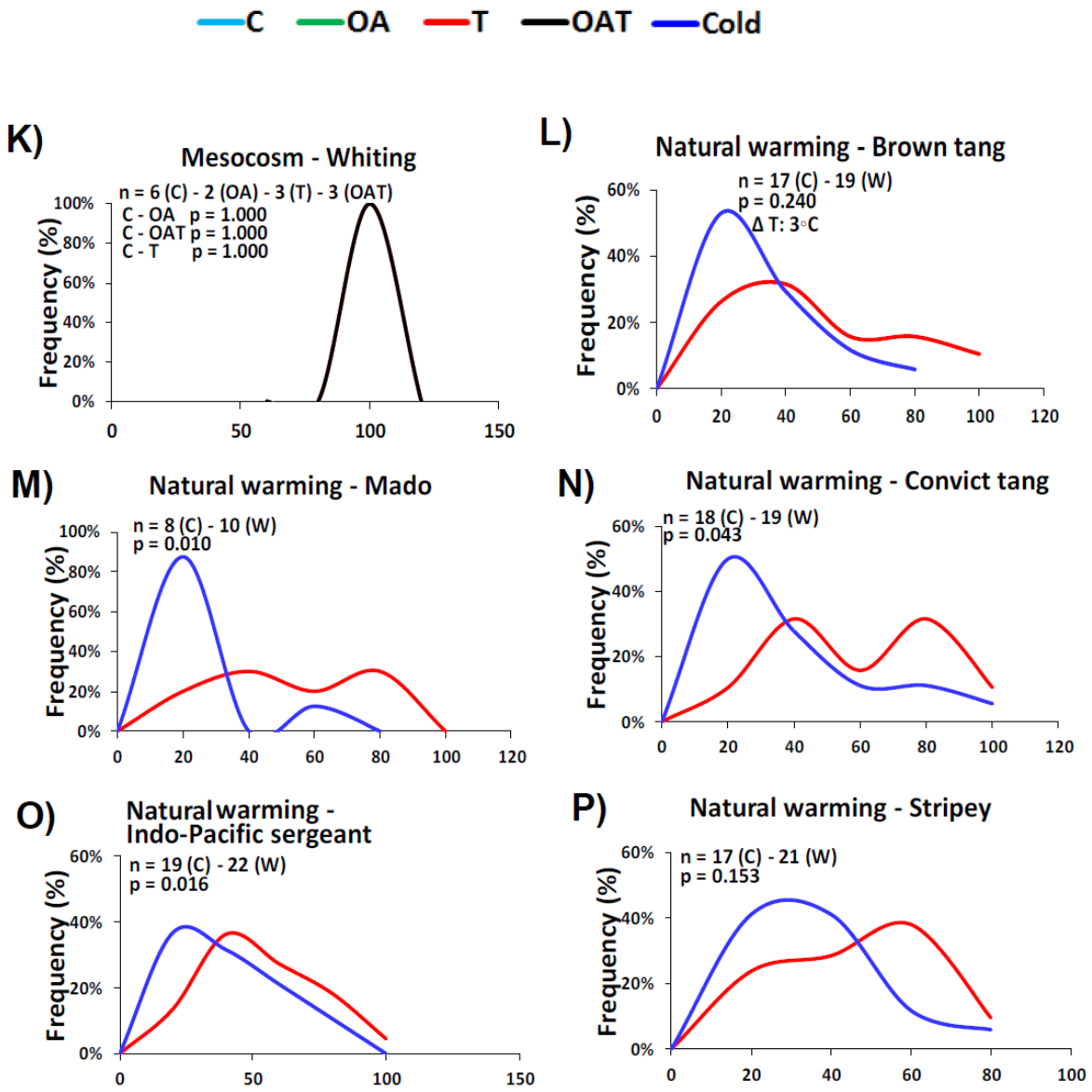
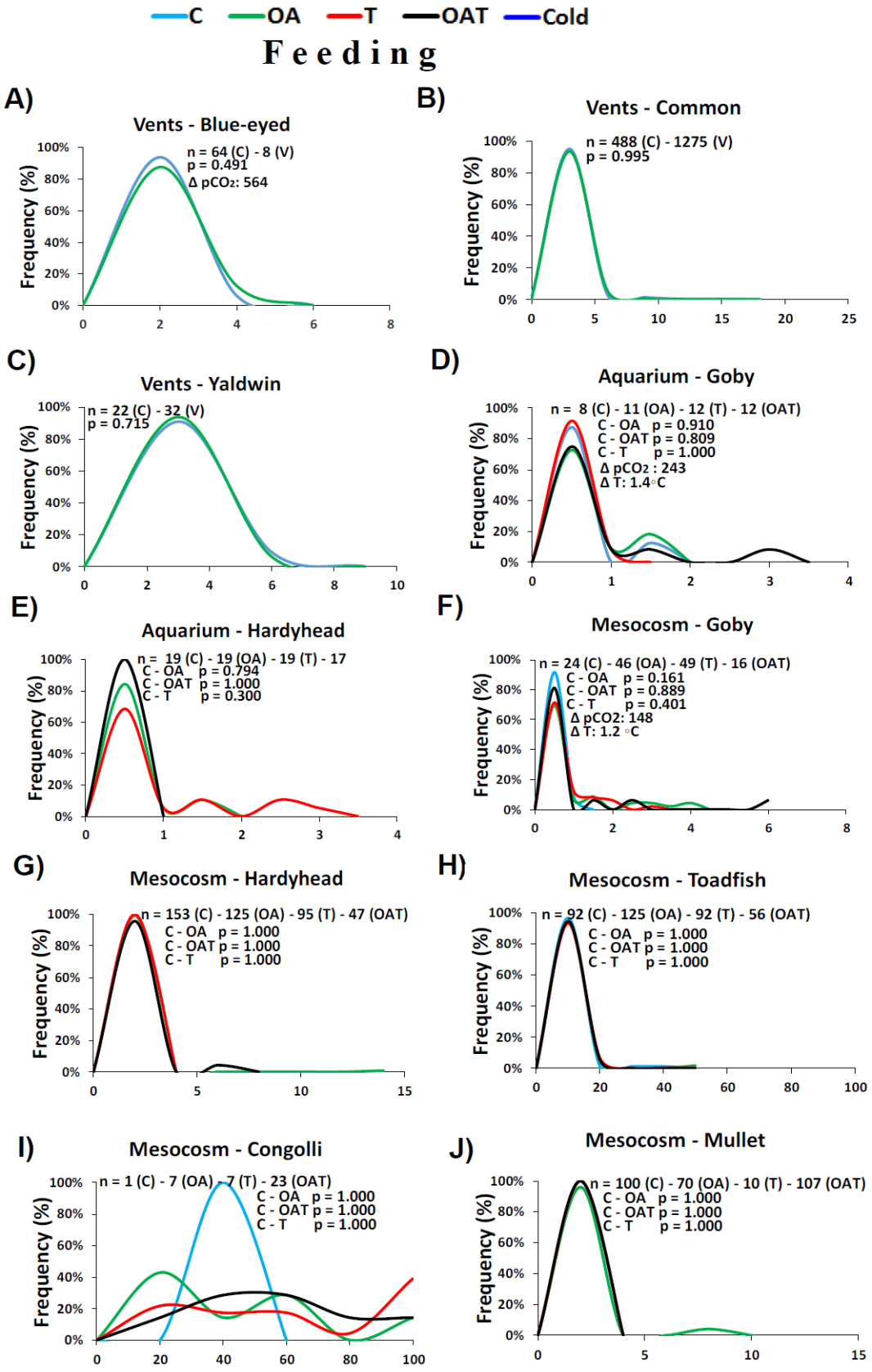


Figure S2. Activity frequency distributions of fish from natural CO_2 vent systems (A-C), aquaria (D-E), mesocosms (F-K), and natural warming systems (N-P). C: control, OA: ocean acidification, T: elevated temperature, OAT: combined elevated CO_2 and elevated temperature. Natural warming, C: cold, W: warming. n = number of individuals; p = p-value; Δ = difference between control (or colder seawaters in natural systems) and the climate stressor (temperature or pCO_2).


C
OA
T
OAT
Cold
Feeding
A)
Vents - Blue-eyed
n = 64 (C) - 8 (V)
p = 0.491
Δ pCO2: 564
B)
Vents - Common
n = 488 (C) - 1275 (V)
p = 0.995
C)
Vents - Yaldwin
n = 22 (C) - 32 (V)
p = 0.715
D)
Aquarium - Goby
n = 8 (C) - 11 (OA) - 12 (T) - 12 (OAT)
C - OA p = 0.910
C - OAT p = 0.809
C - T p = 1.000
Δ pCO2 : 243
Δ T: 1.4◦C
E)
Aquarium - Hardyhead
n = 19 (C) - 19 (OA) - 19 (T) - 17
C - OA p = 0.794
C - OAT p = 1.000
C - T p = 0.300
F)
Mesocosm - Goby
n = 24 (C) - 46 (OA) - 49 (T) - 16 (OAT)
C - OA p = 0.161
C - OAT p = 0.889
C - T p = 0.401
Δ pCO2: 148
Δ T: 1.2 ◦C
G)
Mesocosm - Hardyhead
n = 153 (C) - 125 (OA) - 95 (T) - 47 (OAT)
C - OA p = 1.000
C - OAT p = 1.000
C - T p = 1.000
H)
Mesocosm - Toadfish
n = 92 (C) - 125 (OA) - 92 (T) - 56 (OAT)
C - OA p = 1.000
C - OAT p = 1.000
C - T p = 1.000
I)
Mesocosm - Congolli
n = 1 (C) - 7 (OA) - 7 (T) - 23 (OAT)
C - OA p = 1.000
C - OAT p = 1.000
C - T p = 1.000
J)
Mesocosm - Mullet
n = 100 (C) - 70 (OA) - 10 (T) - 107 (OAT)
C - OA p = 1.000
C - OAT p = 1.000
C - T p = 1.000
Frequency (%)

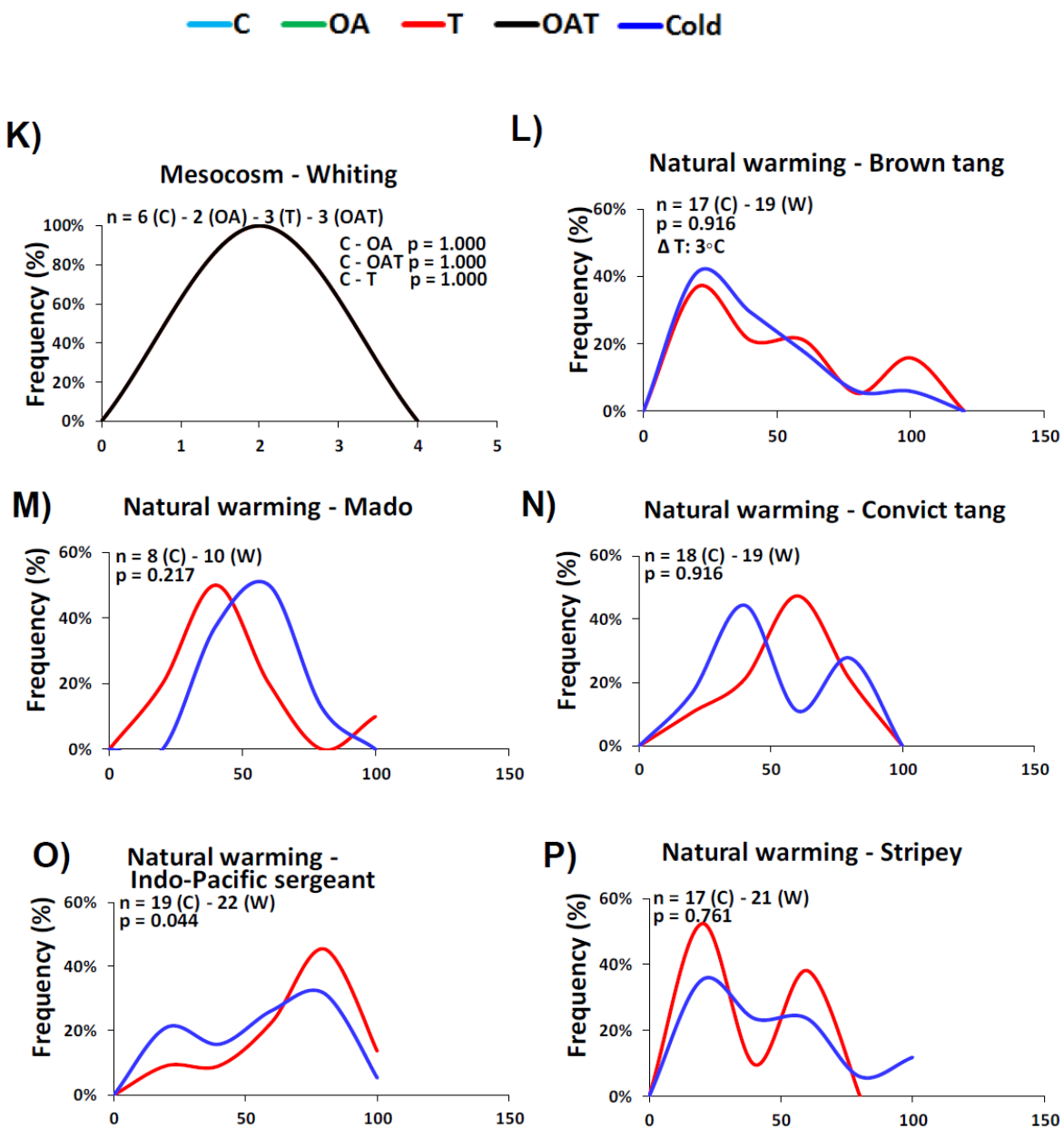
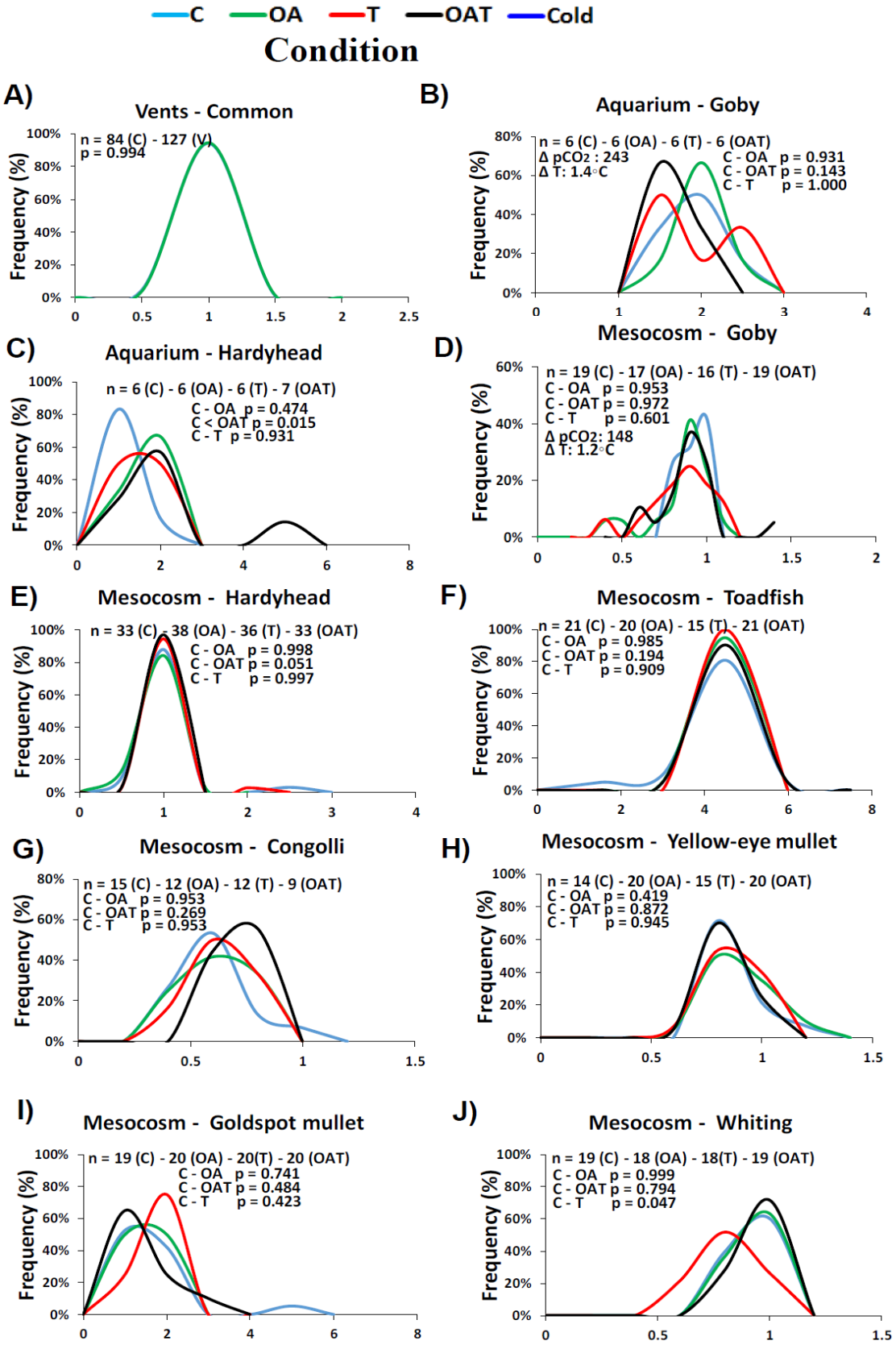


Figure S3. Feeding frequency distributions of fish from natural CO_2 vent systems (A-C), aquaria (D-E), mesocosms (F-K), and natural warming systems (N-P). C: control, OA: ocean acidification, T: elevated temperature, OAT: combined elevated CO_2 and elevated temperature. Natural warming, C: cold, W: warming. n = number of individuals; p = p-value; Δ = difference between control (or colder seawaters in natural systems) and the climate stressor (temperature or pCO_2).


C
OA
T
OAT
Cold
Condition
A)
Vents - Common
n = 84 (C) - 127 (V)
p = 0.994
B)
Aquarium - Goby
n = 6 (C) - 6 (OA) - 6 (T) - 6 (OAT)
Δ pCO2 : 243
Δ T: 1.4◦C
C - OA p = 0.931
C - OAT p = 0.143
C - T p = 1.000
C)
Aquarium - Hardyhead
n = 6 (C) - 6 (OA) - 6 (T) - 7 (OAT)
C - OA p = 0.474
C < OAT p = 0.015
C - T p = 0.931
D)
Mesocosm - Goby
n = 19 (C) - 17 (OA) - 16 (T) - 19 (OAT)
C - OA p = 0.953
C - OAT p = 0.972
C - T p = 0.601
Δ pCO2: 148
Δ T: 1.2◦C
E)
Mesocosm - Hardyhead
n = 33 (C) - 38 (OA) - 36 (T) - 33 (OAT)
C - OA p = 0.998
C - OAT p = 0.051
C - T p = 0.997
F)
Mesocosm - Toadfish
n = 21 (C) - 20 (OA) - 15 (T) - 21 (OAT)
C - OA p = 0.985
C - OAT p = 0.194
C - T p = 0.909
G)
Mesocosm - Congolli
n = 15 (C) - 12 (OA) - 12 (T) - 9 (OAT)
C - OA p = 0.953
C - OAT p = 0.269
C - T p = 0.953
H)
Mesocosm - Yellow-eye mullet
n = 14 (C) - 20 (OA) - 15 (T) - 20 (OAT)
C - OA p = 0.419
C - OAT p = 0.872
C - T p = 0.945
I)
Mesocosm - Goldspot mullet
n = 19 (C) - 20 (OA) - 20(T) - 20 (OAT)
C - OA p = 0.741
C - OAT p = 0.484
C - T p = 0.423
J)
Mesocosm - Whiting
n = 19 (C) - 18 (OA) - 18(T) - 19 (OAT)
C - OA p = 0.999
C - OAT p = 0.794
C - T p = 0.047
Frequency (%)

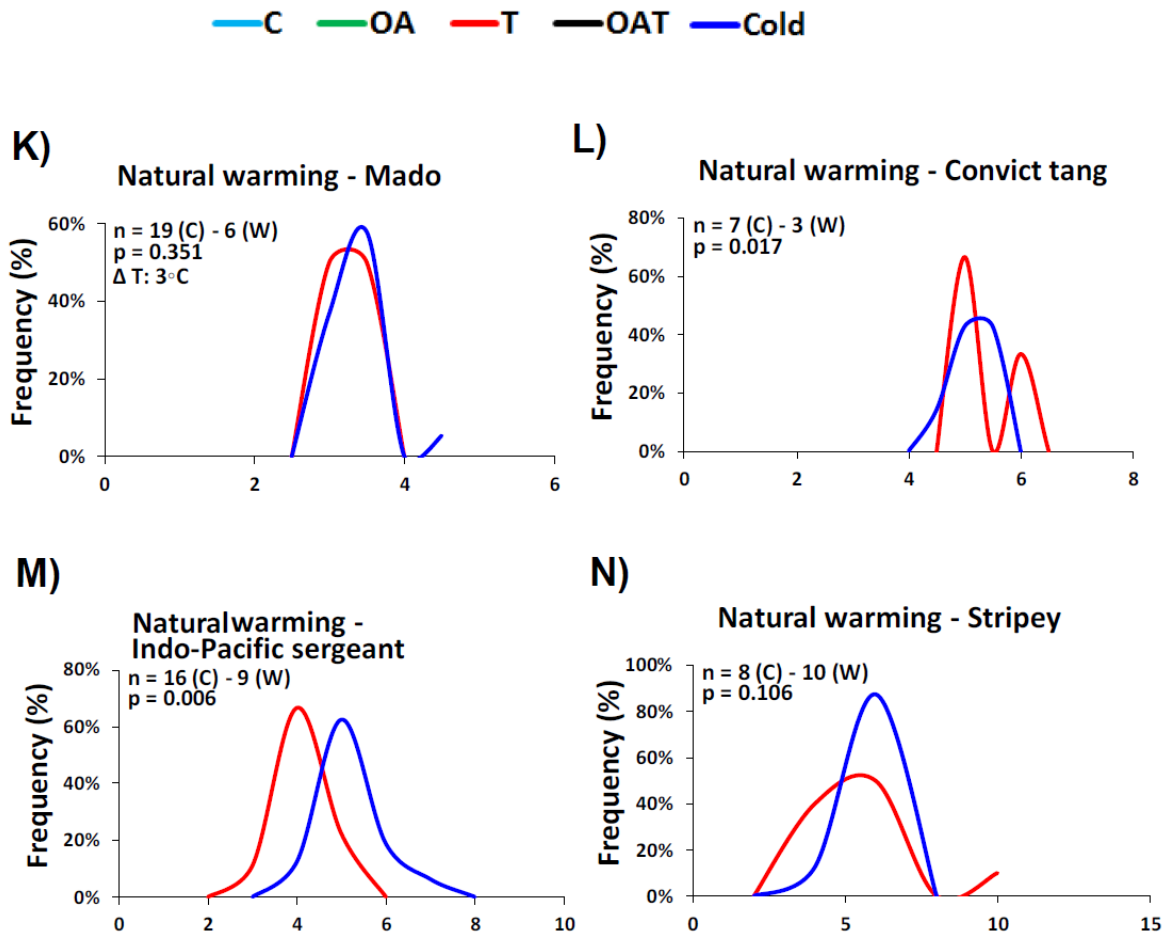


Figure S4. Fulton condition index frequency distributions of fish from natural CO_2 vent systems (A), aquaria (B-C), mesocosms (D-J), and natural warming systems (K-N). C: control, OA: ocean acidification, T: elevated temperature, OAT: combined elevated CO_2 and elevated temperature. Natural warming, C: cold, W: warming. n = number of individuals; p = p-value; Δ = difference between control (or colder seawaters in natural systems) and the climate stressor (temperature or pCO_2).

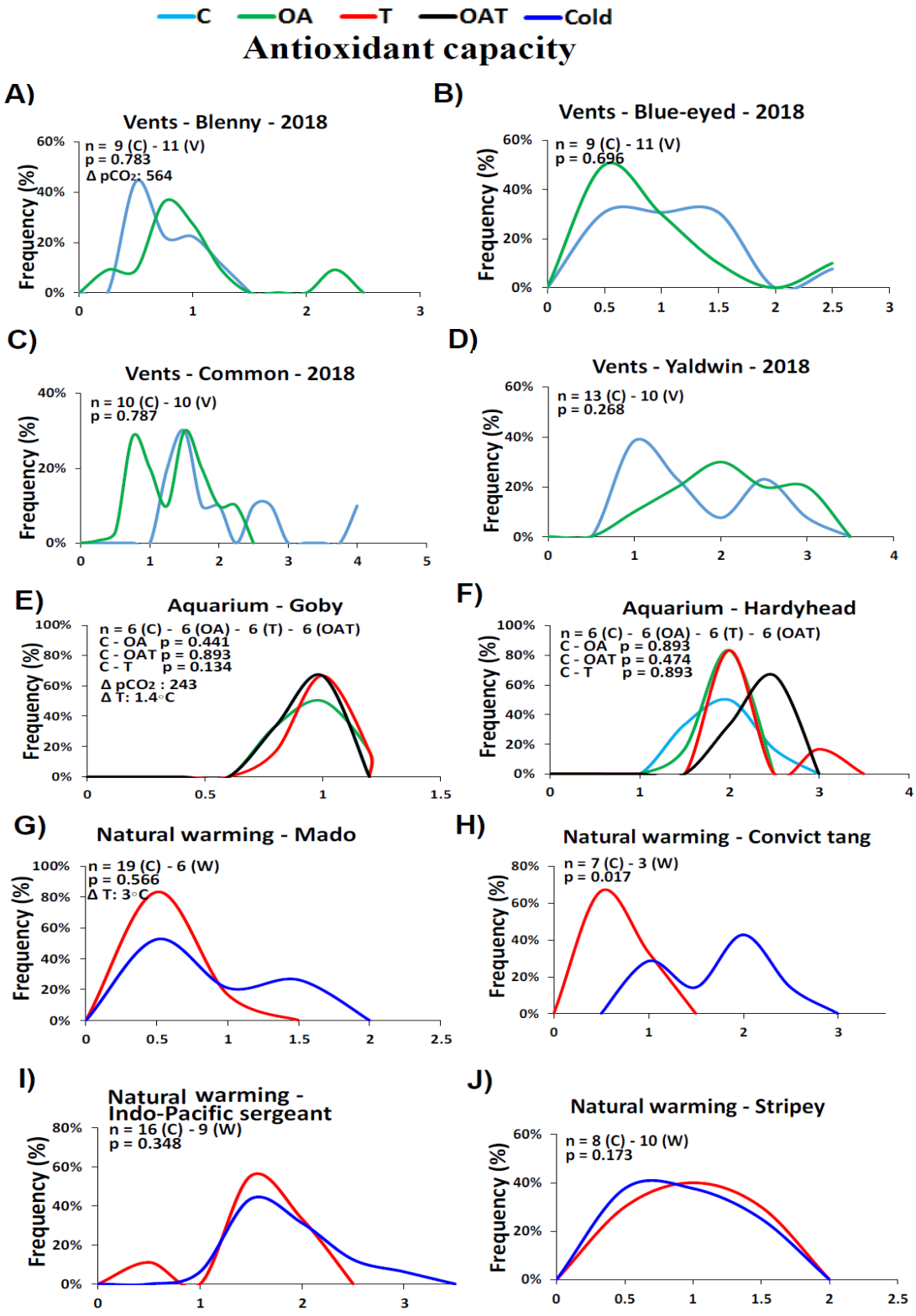


Figure S5. Total antioxidant capacity frequency distributions of fish from natural CO_2 vent systems (A-D), aquaria (E-F), and natural warming systems (G-J). C: control, OA: ocean

acidification, T: elevated temperature, OAT: combined elevated CO_2 and elevated temperature. Natural warming, C: cold, W: warming. n = number of individuals; p = p-value; Δ = difference between control (or colder seawaters in natural systems) and the climate stressor (temperature or pCO_2).

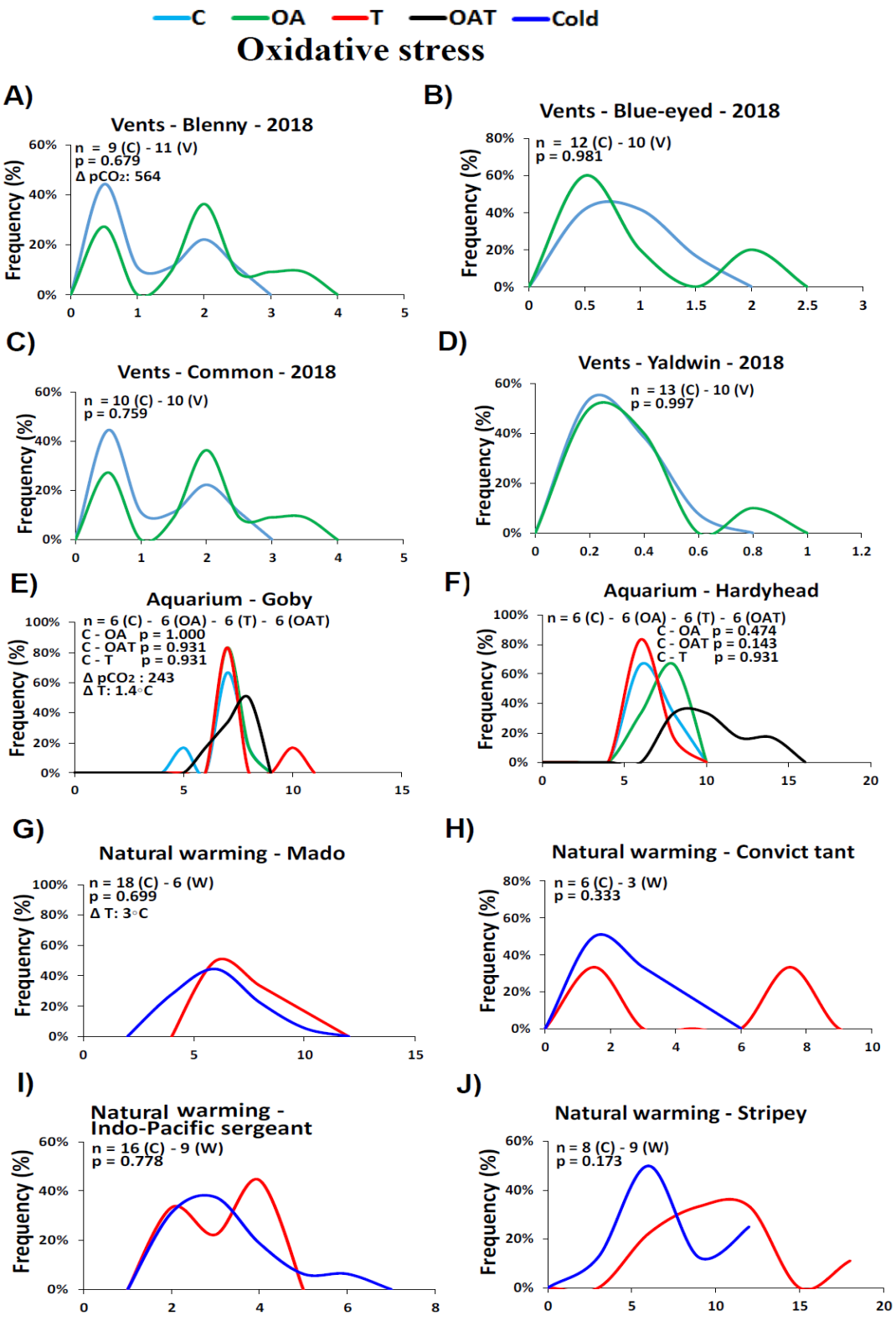

C
OA
T
OAT
Cold
Oxidative stress
A)
Vents - Blenny - 2018
n = 9 (C) - 11 (V)
p = 0.679
Δ pCO2: 564
B)
Vents - Blue-eyed - 2018
n = 12 (C) - 10 (V)
p = 0.981
C)
Vents - Common - 2018
n = 10 (C) - 10 (V)
p = 0.759
D)
Vents - Yaldwin - 2018
n = 13 (C) - 10 (V)
p = 0.997
E)
Aquarium - Goby
n = 6 (C) - 6 (OA) - 6 (T) - 6 (OAT)
C - OA p = 1.000
C - OAT p = 0.931
C - T p = 0.931
Δ pCO2 : 243
Δ T: 1.4◦C
F)
Aquarium - Hardyhead
n = 6 (C) - 6 (OA) - 6 (T) - 6 (OAT)
C - OA p = 0.474
C - OAT p = 0.143
C - T p = 0.931
G)
Natural warming - Mado
n = 18 (C) - 6 (W)
p = 0.699
Δ T: 3◦C
H)
Natural warming - Convict tant
n = 6 (C) - 3 (W)
p = 0.333
I)
Natural warming - Indo-Pacific sergeant
n = 16 (C) - 9 (W)
p = 0.778
J)
Natural warming - Stripey
n = 8 (C) - 9 (W)
p = 0.173
Frequency (%)

Figure S6. Oxidative stress frequency distributions of fish from natural CO_2 vent systems (A-D), aquaria (E-F), and natural warming systems (G-J). C: control, OA: ocean acidification, T: elevated temperature, OAT: combined elevated CO_2 and elevated temperature. Natural warming, C: cold, W: warming. n = number of individuals; p = p-value; Δ = difference between control (or colder seawaters in natural systems) and the climate stressor (temperature or pCO_2).

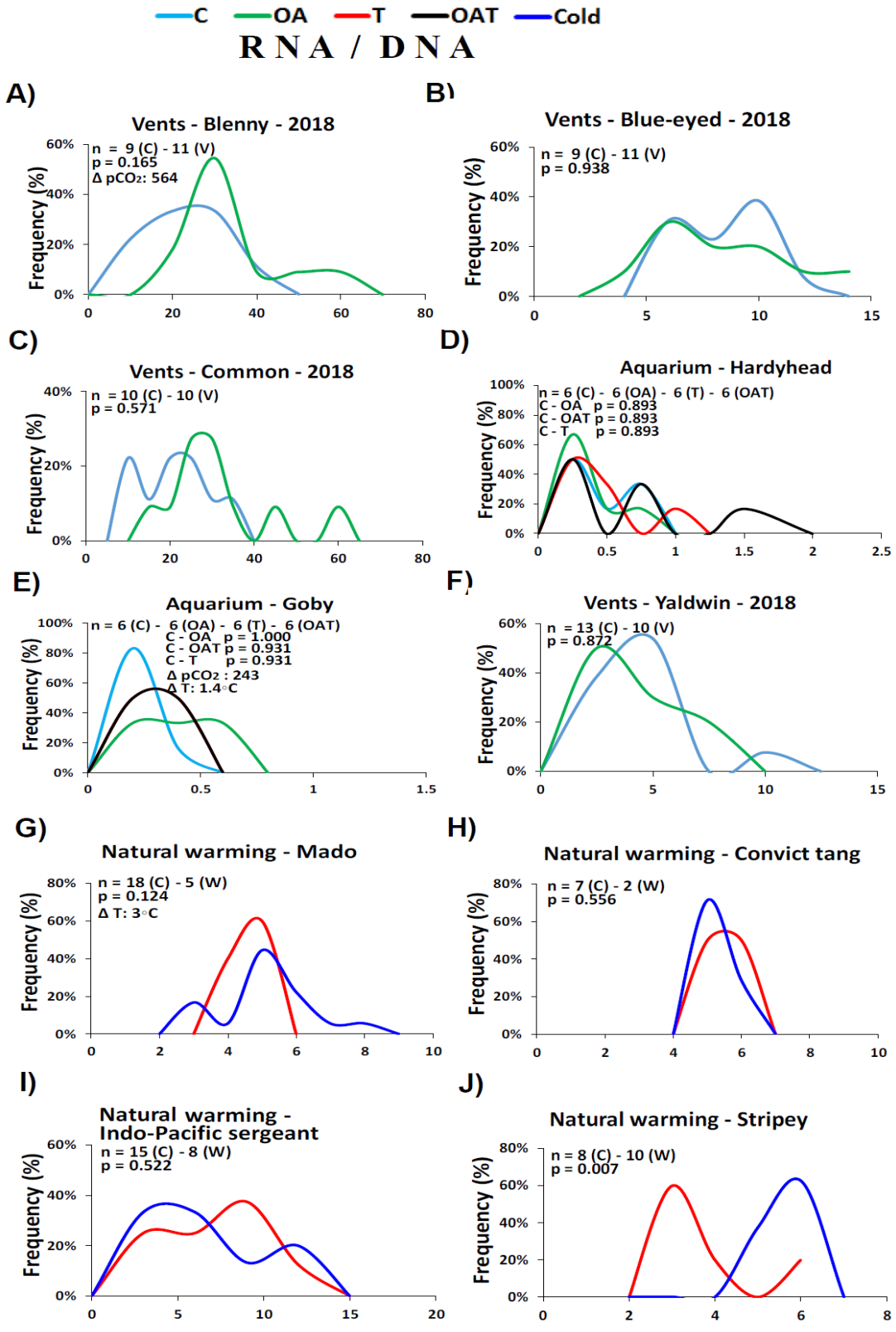

C
OA
T
OAT
Cold
RNA / DNA
A)
Vents - Blenny - 2018
n = 9 (C) - 11 (V)
p = 0.165
Δ pCO2: 564
B)
Vents - Blue-eyed - 2018
n = 9 (C) - 11 (V)
p = 0.938
C)
Vents - Common - 2018
n = 10 (C) - 10 (V)
p = 0.571
D)
Aquarium - Hardyhead
n = 6 (C) - 6 (OA) - 6 (T) - 6 (OAT)
C - OA p = 0.893
C - OAT p = 0.893
C - T p = 0.893
E)
Aquarium - Goby
n = 6 (C) - 6 (OA) - 6 (T) - 6 (OAT)
C - OA p = 1.000
C - OAT p = 0.931
C - T p = 0.931
Δ pCO2 : 243
Δ T: 1.4◦C
F)
Vents - Yaldwin - 2018
n = 13 (C) - 10 (V)
p = 0.872
G)
Natural warming - Mado
n = 18 (C) - 5 (W)
p = 0.124
Δ T: 3◦C
H)
Natural warming - Convict tang
n = 7 (C) - 2 (W)
p = 0.556
I)
Natural warming - Indo-Pacific sergeant
n = 15 (C) - 8 (W)
p = 0.522
J)
Natural warming - Stripey
n = 8 (C) - 10 (W)
p = 0.007
Frequency (%)

Figure S7. RNA/DNA frequency distributions of fish from natural CO_2 vent systems (A-D), aquaria (E-F), and natural warming systems (G-J). C: control, OA: ocean acidification, T: elevated temperature, OAT: combined elevated CO_2 and elevated temperature. Natural warming, C: cold, W: warming. n = number of individuals; p = p-value; Δ = difference between control (or colder seawaters in natural systems) and the climate stressor (temperature or pCO_2).

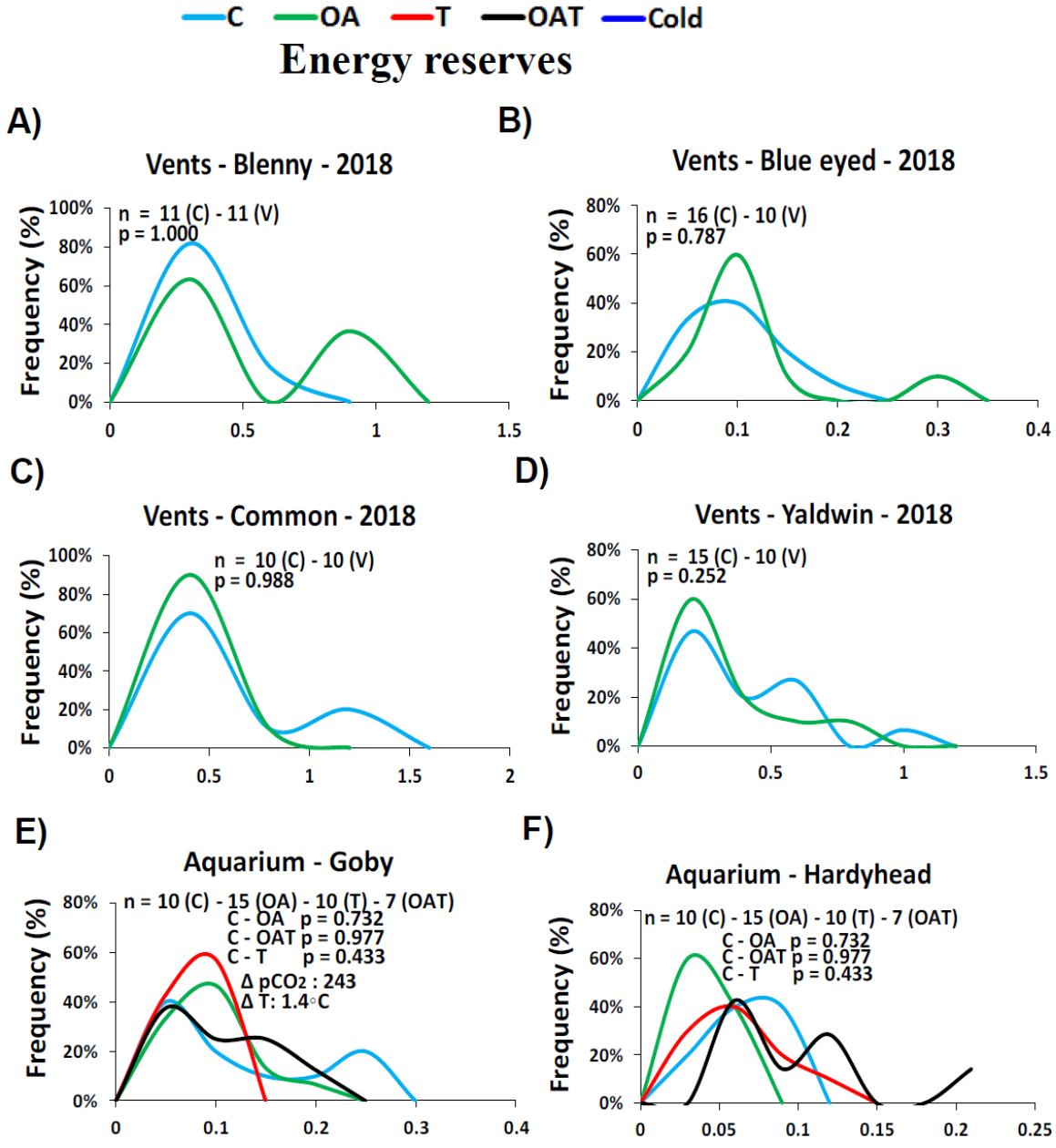


Figure S8. Energy reserves frequency distributions of fish from natural CO_2 vent systems (A-D, measured as liver weight), and aquarium (E-F, measured as hepatosomatic index). C: control, OA: ocean acidification, T: elevated temperature, OAT: combined elevated CO_2 and elevated temperature. Natural warming, C: cold, W: warming. n = number of individuals; p = p-value; Δ = difference between control (or colder seawaters in natural systems) and the climate stressor (temperature or pCO_2).

Table S1. Mean (± SE) values of seawater chemistry parameters at White Island. Samples were taken over multiple days, during daytime, close to the bottom, and in the same areas as where the fish surveys were performed. pCO_2 values were calculated using CO2SYS. SW = salt water. The first column of N represents that for T, pH, and pCO_2, while the second column of N represents that for TA.

Site	Zone	Temperature (◦C)	pH (NBS)	pCO_2 (µatm)	N	TA (mmol/kg SW)	N
May	Control	19.5 ± 0.5	8.05 ± 0.01	399.0 ± 8.7	2	2333.0 ± 2.0	2
2013	Elevated	19	7.72 ± 0.01	988.6	1	2329	1
Nov.	Control	17.6 ± 0.1	8.06 ± 0.02	538.8 ± 32.3	21	2295.8 ± 10.7	4
2013	Elevated	17.9 ± 0.1	7.86 ± 0.02	929.7 ± 54.1	33	2287.3 ± 12.1	4
Feb.	Control	21.3 ± 0.1	8.14 ± 0.01	418.8 ± 12.5	30	2244.8 ± 1.2	4
2015	Elevated	21.4 ± 0.0	7.84 ± 0.01	948.1 ± 29.0	30	2242.3 ± 2.5	6
Mar.	Control	21.0 ± 0.1	8.11 ± 0.01	474.7 ± 14.9	27	mean of 2013	0
2016	Elevated	21.3 ± 0.1	7.82 ± 0.02	1038.9 ± 113.3	27	mean of 2015	0
Feb.	Control	20.1 ± 0.1	8.08 ± 0.01	503 ± 9	12	2263 ± 5	6
2017	Elevated	20.1 ± 0.1	7.82 ± 0.04	1049 ± 122	20	2255 ± 5	5
Feb.	Control	23.2 ± 0.1	8.03 ± 0.02	628 ± 29	12		
2018	Elevated	23.2 ± 0.1	7.84 ± 0.04	1066 ± 112	12		

Table S2. Mean (± SE) values of seawater chemistry parameters in the 1,800 L outdoor mesocosm tanks (temperature, salinity, pH, total alkalinity, pH, and pCO_2). pCO_2 values were estimated using CO2SYS. SW = seawater. OA = Ocean acidification; W = warming; OAW = combination of ocean acidification and warming.

Treatment	Temperature (°C)	Salinity	pH	Total alkalinity (mmol/kgSW)	pCO_2 (µatm)
Control	19.6 (±0.53)	36	8.2 (±0.02)	2431.7 (±4.5)	352 (±19.0)
OA	19.7 (±0.51)	36	8.1 (±0.01)	2415.7 (±5.2)	505 (±19.5)
W	20.7 (±0.45)	36	8.2 (±0.02)	2431.5 (±5.2)	377 (±22.4)

OAW	21.0 (±0.45)	36	8.1 (±0.02)	2429.5 (±5.2)	519 (±22.4)

Table S3. Mean (± SE) values of seawater chemistry parameters in the 40 L laboratory tanks (temperature, salinity, pH, total alkalinity, pH, and pCO_2) for both fish species. pCO_2 values were estimated using CO2SYS. SW = seawater. OA = Ocean acidification; W = warming; OAW = combination of ocean acidification and warming.

Species	Treatment	Temperature (°C)	Salinity	pH	Total alkalinity (mmol/kgSW)	pCO_2 (µatm)
Goby	Control	20.6 (±0.06)	35.4 (±0.07)	7.9 (±0.01)	2099.4 (±110.4)	515 (±38.1)
	OA	20.6 (±0.04)	35.5 (±0.05)	7.7 (±0.01)	2012.6 (±55.0)	842 (±64.8)
	W	21.8 (±0.04)	36.1 (±0.08)	8.0 (±0.01)	2188.2 (±120.2)	554 (±35.2)
	OAW	21.9 (±0.03)	38.7 (±1.80)	7.7 (±0.01)	2066.8 (±42.1)	926 (±70.7)
Hardyhead	Control	20.4 (±0.04)	37.0 (±0.10)	8.0 (±0.01)	2194.7 (±30.7)	536 (±45.5)
	OA	20.3 (±0.04)	37.2 (±0.08)	7.8 (±0.01)	2178.8 (±41.4)	798 (±63.9)
	W	21.8 (±0.05)	36.5 (±0.09)	8.0 (±0.01)	2191.7 (±75.8)	510 (±46.2)
	OAW	21.7 (±0.05)	37.0 (±0.10)	7.8 (±0.01)	2214.5 (±67.8)	734 (±54.0)

Table S4. Results from regression test for startle distance and fish density at CO_2 natural vents and warming hotspots for the full dataset (including outliers).

	Estimate	S.E.	t value	*p*	R^2	Adjusted R^2	*F*
Vents systems							
Intercept	2.6685	0.8729	3.057	0.0282			
Vents	-2.3812	1.6527	-1.441	0.2092	0.2934	0.2934	2.076
Warming systems							
Intercept	14.79	12.31	1.202	0.316			
Warming	-11.85	13.39	-0.885	0.441	0.2069	-0.05747	0.7826

Table S5. Results from regression test for startle distance and fish density at natural CO_2 vents (1 outlier) and warming hotspots (2 outliers) with outliers removed.

	Estimate	S.E.	t value	*p*	R^2	Adjusted R^2	*F*
Vents systems							
Intercept	3.6562	0.4116	8.884	0.0009			
Vents	-3.7312	0.7353	-5.075	***0.0071***	0.8656	0.8319	25.75
Warming systems							
Intercept	14.891	4.033	3.692	0.168			
Warming	-12.181	3.843	-3.169	0.195	0.9095	0.8189	10.04

Bold and cursive numbers indicate significant results

Chapter VI: General discussion

General Discussion

The effect of long-term exposure to environmental stressors is rarely assessed in marine organisms, particularly their behaviour and fitness. Short-term and immediate reactions are most frequently studied given that these responses tend to be immediate. The aim of this thesis was to evaluate the sensitivity of marine species, fish in particular, and their potential to acclimate to the effects of ocean acidification and ocean warming. This thesis contributes with new knowledge by evidencing the distinct mechanisms that species use to cope with changing environments. In addition, I reveal how the response of some species to novel conditions can confer them with greater competitive advantage by the benefit of the adjustments made in their physiology, behaviour and ultimately into their phenotypes.

I assessed how fish adjust to and cope with ocean acidification and ocean warming by testing their acclimation capacity, adjustments to physiological functions, behavioural alterations, and phenotypic plasticity at different stages of their life. To determine the effects of early life exposure to climate change, responses of the embryonic phase was compared between ambient and elevated CO_2 concentrations in a reciprocal design. The exposure to acidified conditions during the embryonic stage impeded fish behaviour by increasing their anxiety levels and this was not restored when transplanted into present day conditions (Chapter 2). The undeveloped acid-base mechanisms in early life stages might explain their higher sensitivity to elevated CO_2 levels compared to adults (Bauman et al., 2012; Munday et al., 2016). Additionally, neurotransmitter receptors in fish can be impaired by CO_2 and alter behaviour (Nilsson et al., 2012; Forsgren et al., 2013). The vulnerability of early life stages was also assessed with a meta-analysis (Chapter 4) where I found that eggs and larvae had decreased survival, compared to juveniles and adults, to simulated climate change. Other meta-analyses have reported early life stages as the most vulnerable to environmental variability (Kroeker et al., 2013; Harvey et al., 2013; Pandori et al., 2019). The smaller size of eggs and larvae, and their less developed organs compared to adults contributes to their sensitivity towards environmental stressors (Byrne, 2011; Przeslawski et al., 2015; Marshal et al., 2016). High mortality rates of early life stages will directly alter fish populations, as they will mediate the abundance of fish stocks (Baumann et al., 2012). By including the embryonic stage in this thesis I was able to detect an

irreversible carry-over effect from ocean acidification onto juvenile stages. Analysing species only from their larvae or juvenile stages could hide the real direction of response to stressors, which will obstruct making accurate predictions of species future persistence to environmental fluctuations.

The adaptive responses of two species of fish to multiple climate stressors (temperature, CO_2, and their combination) were assessed over six months of development: from juvenile to their adult stages. These experiments focused on relating behavioural adjustments to cellular indicators and fitness traits (Chapter 3). I found that all fishes were able to maintain their homeostasis as shown by unaltered fitness traits (energy reserves, reproductive investment and growth). Only fish with cellular defences and oxidative status that were unaffected by ocean acidification and its combination with temperature, presented higher growth rates as their feeding behaviour increased. By contrast, fish whose cellular defences were negatively affected could only prevent oxidative stress if there was an increase in their feeding behaviour, otherwise they experienced oxidative stress. It is important to note that the maintenance of their fitness traits could have been modulated by the food provisioning during the experimental period. Fish oxidative levels can increase as a response to stressful conditions such as absence of food sources (Pascual et al., 2003; Zheng et al., 2016) and modify their behavioural responses (Wang et al., 2019). In conditions where fish have to spend more energy foraging or are unable to acquire sufficient food, alterations in the responses between physiology and behaviour could take place. Analysing the pathways of adaptive responses from physiology to behaviour provides a better understanding into species adaptability to stressful environments (Leung et al. 2019a). Species that are able to resist or even benefit from novel conditions will have a competitive advantage that will allow them to dominate ecological interactions in changing environments.

Variability in species responses to changing climate are likely given their varying physiological requirements. In Chapter 4, predictive variables were assessed in a meta-analysis that tested which variables had a greater effect on marine species growth and survival. I found that the effects of climate change on growth and survival are mostly modulated by calcification mode and treatment (temperature, acidification or a combination of both), respectively. However, the variability explained by these factors only represented

a small percentage. The low predictive score of the variables included in the analyses can be explained by the high number of taxa included in the analysis. Some taxonomic groups will present more variability in their species-specific responses than others as it is unlikely to find the same responses across species (Harley et al., 2017). Identifying which groups will be more sensitive to climate change stressor is essential as species-specific responses can re-shape the structure of populations.

Comparisons between wild populations and aquarium populations may reveal insights into how traits adjust to changing climate. Hence, I compared the responses of various fish species in laboratory and natural conditions. Including natural systems provides a more realistic scenario of organisms' responses. In natural conditions, individuals face a diversity of selective pressures, from food limitation, to competition for resources and shelter (Sobral et al. 2013; Crozier and Hutchings, 2014). The frequency distribution of behavioural and physiological phenotypic responses were assessed in small aquaria and large mesocosms (laboratory systems) and in natural systems (CO_2 vents and natural gradients of warming; Chapter 5). A general pattern was discovered where risk taking behaviours were mostly affected across species irrespective of the stressor (CO_2 vents or warming sites) or study system (natural vs laboratory). A shift towards bolder phenotypes was found in various species facing elevated CO_2 levels, while species exposed to increased temperatures presented losses as well as gains of bold phenotypes. Changes in environmental conditions are known to alter behaviours (Biro et al., 2010). Experimental assessments have demonstrated that ocean acidification and warming exert distinct responses in risk-taking behaviours by increasing (Munday et al., 2010; Biro et al., 2010) or reducing (Hamilton et al., 2014, Rossi et al., 2015) their boldness. In spite of the altered responses of fish in their risk-taking behaviours, most species were able to maintain their physiological homeostasis. The physiological traits that were evaluated presented no changes compared to control conditions. Moreover, when I tested for the variability of bold behaviours, natural systems presented a reduced variability compared to laboratory environments. The different biotic and abiotic factors that interact in a natural environment act as sources of selective pressure, leading to reduced variability of phenotypes within a trait (Sobral et al., 2013). By contrast, in laboratory set ups (Chapter 3 and Chapter 5) the daily provision of food and lack of predators eroded the sources of environmental pressure.

Phenotypic variation in a population can function as a response to variations in the environment (Carja and Plotkin, 2019; Botero et al., 2015). If variation is reduced, the persistence of a population can be at risk when facing novel conditions as the optimal phenotypic trait may no longer be available in the population (Ariyomo and Watt, 2012). The differences in species phenotypical responses and their variability will be regulated by the biotic and abiotic factors in the environment (Chevin and Hoffman, 2017), and the positive or negative responses that they exert will be critical for their future persistence.

Species will cope with environmental fluctuations by using a variety of strategies that require the regulation of their physiology and behaviour. These adjustments will vary between species and can be dependent on their sensitivities during their different life stages, in particular during the egg and larval phases. Differences at the intra-specific level will also shape the responses of populations to environmental alterations, by shifts in the mean and distribution of their phenotypes and changes in their phenotypic variation. The distinct coping mechanisms of species can facilitate the maintenance of an optimal fitness during stressful events, and increase their likelihood of persistence. The unequal responses among species to environmental change, whether positive or negative, strong or weak, are likely to contribute to the re-structuring of communities by modifying species interactions.

Future directions

A variety of mechanisms used by fish to cope with ocean warming and acidification were revealed in my thesis. I have shown the within-generational fish responses to climatic stressors from cellular to population level; however, additional processes that also influence species resilience or resistance were not addressed here. As discussed in Chapter 2, aside from direct effects of elevated CO_2 on embryos, non-genetic parental effects could also impact the responses of fish life stages. Different studies have shown non-genetic transgenerational effects where fish can either acclimate (Donelson et al., 2012; Millet et al., 2012) or not (Allan et al., 2014; Welch et al., 2014) to environmental stressors. Most recently, genetic-based transgenerational acclimation was described by Ryu et al. (2018) in a tropical fish species, where the epigenetic regulations of acclimation are described. It will be useful to test whether successive generations acquire stronger mechanisms, non-genetic

and genetic acclimation, to adjust and possibly adapt. In a similar way, the phenotypic responses of fish were only assessed within a generation in Chapter 5. Testing the physiology, behaviour and metabolic responses of species and the distribution of their phenotypes across multiple generations will also help understand the predictive value of shorter-term experiments.

Another approach that appears worth including in future studies is assessing species responses to distinct food ratios. Food has been shown to have a fundamental effect on performance of individuals (Leung et al. 2019b). The maintenance of growth (Chapter 3) and homeostasis (Chapter 5) under laboratory conditions may have been mediated by the daily provision of unlimited food. Some studies have evaluated the effects of different food levels under elevated temperature, but the results are variable. Some studies have found negative effects on reproduction (Donelson et al., 2010) or no effect on behaviour (McMahon et al., 2018) with reduced food ratios for fish exposed to elevated temperature and CO_2, respectively. The studies that have examined food ratios have been limited to tropical species, hence the incorporation of a wider range of fish from different latitudes may be useful, especially if temperature drives energetic demands (Boltaña et al., 2017, Kang et al., 2019). In Chapter 4, I showed that climate change stressors will affect growth in organisms depending on their calcifying mode. Some calcifying groups have shown resistance to ocean acidification (Ramajo et al., 2016). *Mytilus edulis* for instance, has been found to prevent corrosion of its shell inner layer (Melzner et al., 2011), and increase its growth and calcification (Thomsen et al., 2013) when food is abundant. Thus, the negative effects of ocean acidification on growth and calcification could be buffered, but this process has a high energetic demand and requires the supply of abundant food sources (Wood et al., 2008; Thomsen et al., 2013; Ramajo et al., 2016). Thus, including different functional groups will help evaluate which physiological processes and species will be mostly impaired by food limitation.

Conclusion

This thesis has shown how various mechanisms can be adjusted to allow animals to cope with ocean acidification and warming. Early life stages appear particularly sensitive to changing climate and the future acclimation potential of vulnerable species will, therefore,

also depend on transgenerational responses. Behavioural responses are noticeably important over short-scales. They can be linked to physiological alterations through a feedback of regulatory mechanisms. A noticeable feature of my research was the large amount of variability in response among species. Even where acclimation occurs, it may not always be sufficiently large or quick to enable a species to maintain its performance. Such species-specific variation is a characteristic of biology and likely to drive change in strength and type of interactions among species. Where such interactions are disproportionately strong within a community of species, they have the potential to alter the function of ecosystems.

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