Conserving threatened species during rapid environmental change: using biological responses to inform management strategies of giant clams

Sue-Ann Watson1,2,* and Mei Lin Neo3,4

1 Biodiversity and Geosciences Program, Museum of Tropical Queensland, Queensland Museum Network, 70-102 Flinders Street, Townsville, Queensland, 4810, Australia
2 Australian Research Council Centre of Excellence for Coral Reef Studies, James Cook University, 1 James Cook Drive, Townsville, Queensland, 4811, Australia
3 Tropical Marine Science Institute, National University of Singapore, 18 Kent Ridge Road, Singapore 119227, Singapore
4 Department of Biological Sciences, National University of Singapore, 16 Science Drive 4, Singapore 117558, Singapore

*Corresponding author: Biodiversity and Geosciences Program, Museum of Tropical Queensland, Queensland Museum Network, Townsville, Queensland, Australia. Email: sueann.watson@jcu.edu.au

Giant clams are threatened by overexploitation for human consumption, their valuable shells and the aquarium trade. Consequently, these iconic coral reef megafauna are extinct in some former areas of their range and are included in the International Union for Conservation of Nature (IUCN) Red List of Threatened Species and Convention on International Trade in Endangered Species of Wild Fauna and Flora. Now, giant clams are also threatened by rapid environmental change from both a suite of local and regional scale stressors and global change, including climate change, global warming, marine heatwaves and ocean acidification. The interplay between local- to regional-scale and global-scale drivers is likely to cause an array of lethal and sub-lethal effects on giant clams, potentially limiting their depth distribution on coral reefs and decreasing suitable habitat area within natural ranges of species. Global change stressors, pervasive both in unprotected and protected areas, threaten to diminish conservation efforts to date. International efforts urgently need to reduce carbon dioxide emissions to avoid lethal and sub-lethal effects of global change on giant clams. Meanwhile, knowledge of giant clam physiological and ecological responses to local–regional and global stressors could play a critical role in conservation strategies of these threatened species through rapid environmental change. Further work on how biological responses translate into habitat requirements as global change progresses, selective breeding for resilience, the capacity for rapid adaptive responses of the giant clam holobiont and valuing tourism potential, including recognizing giant clams as a flagship species for coral reefs, may help improve the prospects of these charismatic megafauna over the coming decades.

Key words: climate change, CO₂, ocean acidification, light, Tridacna, Hippopus

Editor: Dr. Steven Cooke

Received 10 March 2021; Revised 26 July 2021; Editorial Decision 26 September 2021; Accepted 22 October 2021

Cite as: Watson S-A, Neo ML (2021) Conserving threatened species during rapid environmental change: using biological responses to inform management strategies of giant clams. Conserv Physiol 9(1): coab082; doi:10.1093/conphys/coab082.
Introduction

Since the onset of the Industrial Revolution about 250 years ago, human-induced global change has influenced all of Earth’s bioregions. Climate change, causing global climate destabilization, is being realized through increases in temperature, heatwaves and associated phenomena, such as ocean acidification—where carbon dioxide (CO$_2$) reacts with seawater lowering the pH of the oceans. Global change has accelerated rapidly, particularly in the past 50 years, and we are tracking the worst-case emissions scenario—the business-as-usual Representative Concentration Pathway (RCP) 8.5 (Collins et al., 2013). This recent epoch of change is causing major ecosystem losses and a biodiversity crisis on Earth, with many species threatened or lost already in the sixth mass extinction. We are inevitably losing species before they can be described, let alone understood.

Rapid global change in the marine realm has contributed to consecutive global ocean heating events in the past decade (Bureau of Meteorology, 2020). These events have led to major coral reef bleaching around the world, including some of the world’s most pristine and protected reefs, such as the northern Great Barrier Reef (Hughes et al., 2017; Hughes et al., 2018). Worldwide, coral reef ecosystems are in decline (IPBES, 2019); however, it is these ecosystems that play host to major groups of marine megafauna* including (i) bony fishes, (ii) sea birds, (iii) giant clams, (iv) squids and octopuses, (v) sharks and rays, (vi) whales and sea cows and (vii) sea turtles (Pimiento et al., 2020). (*Note that the definitions of megafauna vary among ecosystems, with size-based threshold definitions often used to define megafauna appropriate to each ecosystem (Moleón et al., 2020). In benthic marine ecosystems, length-based definitions are typically used for invertebrates, where megafauna can include animals such as sea stars, crabs and worms (Moleón et al., 2020). Here we consider giant clams as megafauna, although we acknowledge most giant clam species do not attain sizes greater than the c. 45 kg mass threshold (Estes et al., 2016) traditionally used to define animals, typically mammals (Roberts et al., 2001), as megafauna.)

Many of these megafaunal groups are already threatened by human overexploitation. Now global change not only threatens the coral reef ecosystems in which these megafauna live, but also directly affects megafaunal individuals through physiological responses to stressors such as elevated temperature. Giant clams, for example, contain symbiotic microalgae within their tissues, like reef-building corals do, and are thus susceptible to bleaching from elevated sea surface temperatures (SSTs) (see below). A recent analysis identified the giant clam (Tridacna gigas) as one of the top five marine megafauna species threatened globally, based on a functional trait and extinction risk assessment (Pimiento et al., 2020).

Giant clams

Giant clams (Bivalvia: Cardiidae: Tridacninae) are large marine bivalves inhabiting coral reefs across the Indo-Pacific, with 12 recognized species in two genera (Hippopus and Tridacna) (Tan et al., 2021; Fig. 1a). The largest of them all is T. gigas (also known as the true giant clam), a species that can weigh over 250 kg and measure over 1.3 m long (Rosewater, 1965), producing the biggest shell in the world. These charismatic bivalves are also characterized by their longevity (i.e. predicted maximum life span of 100 years), late reproductive maturity (i.e. 7–10 years for females), mostly sessile habit after settlement and dependence on photosynthesis (Yamaguchi, 1977; Lucas, 1994; Ungvari et al., 2013).

Within coral reef ecosystems, giant clams are known to make important contributions such as enhancing the net primary productivity of coral reefs by mixotrophy, nutrient recycling, provisioning of nurseries and shelters for other reef animals and serving as reservoirs of viable symbionts (Neo et al., 2015; Umeki et al., 2020). Giant clam calcification also contributes to carbonate budgets and is estimated to contribute 0.7–9.0% of the mean calcium carbonate budget of Red Sea coral reef communities (Rossbach et al., 2021). The provision of structural refugia in particular scores bivalves, including giant clams, highly for their functional importance on coral reefs (Wolfe et al., 2020). Worldwide, the giant clam (T. gigas) is one of the top three functionally unique marine megafauna species, along with the dugong and green sea turtle (Pimiento et al., 2020).

Giant clams are also significant coastal resources for humans and have been consumed for their meat for millennia. In Pacific Island countries and territories, giant clams are the main invertebrate harvested (~28% catch) by gleaning and free diving (Bell et al., 2011). Giant clams are also used as materials for their strong calcified shells (Lyons et al., 2011), and more recently as reef pets in the ornamental aquarium trade (Mies et al., 2017). Giant clams are recognized as iconic creatures in coral reef tourism and feature as the only invertebrate among the eight iconic creatures of the Great Barrier Reef, Australia (Barrier Reef Australia, 2021) (Fig. 1b).

‘Solar-powered’ animals: benefits and vulnerability

Multicellular animals that have captured single-celled algae within their tissues include corals and giant clams. This ‘solar-power’ capability arises from photosynthesis by tiny algal protists—endosymbiotic dinoflagellates from the family Symbiodiniaceae, also known as zooxanthellae—within their bodies, providing the animal host with an additional energy source other than the ingestion of food items.
Giant clams can thus obtain nutrients via two pathways: photosynthesis and filter-feeding. These mixotrophic bivalves depend heavily on their endosymbionts to acquire the bulk of their carbon and nitrogen requirements for growth and metabolism (Klumpp and Griffiths, 1994; Hawkins and Klumpp, 1995), even though they possess the functional gills and digestive systems typical of heterotrophic bivalves. In giant clams, the reliance on phototrophy increases with body size. For example, small *T. gigas* individuals (shell length, ~43 mm) obtain 65% of their carbon from filter-feeding, compared to 34% for larger individuals (shell length, ~167 mm) (Klumpp et al., 1992), and this trend continues as individuals grow (e.g. Klumpp and Griffiths, 1994). Indeed, at normal depths and light levels, phototrophy alone may provide most, if not all, of the carbon requirements in giant clam species (*T. gigas*: Fisher et al., 1985; Klumpp et al., 1992; *T. mbalavuana* and *T. derasa*: Klumpp and Lucas, 1994), and *T. squamosa* juveniles can survive for 10+ months with light as the sole energy source (Fitt and Trench, 1981). The combination of phototrophy and heterotrophy is thought to explain why giant clams have rapid growth rates and likely allows them to grow to large body sizes compared to other bivalves (Klumpp and Griffiths, 1994). However, this heavy reliance on phototrophy to meet their energy needs, especially with increasing body size, makes giant clams more sensitive and thus vulnerable to increased SSTs caused by global warming (e.g. Andréfouët et al., 2013; Van Wynsberge and Andréfouët, 2017; Van Wynsberge et al., 2018).

At local and regional scales, giant clams face other human-induced pressures such as overfishing, habitat degradation and coastal urbanization (Neo et al., 2017; Neo, 2020;
Fig. 1c), which reduce densities of populations across their ranges in the wild. Consequently, stock depletion impedes their reproductive success in nature as giant clams rely on synchronized broadcast spawning among conspecific individuals (Lucas, 1988). As these threats still persist today, the number of viable spawning individuals is rapidly dwindling and populations face imminent declines due to poor reproductive success (Gwyther and Munro, 1981).

‘Traditional’ conservation solutions

Giant clams are protected species under Appendix II of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES), which consists of species that are not necessarily currently threatened with extinction but may become so unless trade is closely controlled. Of the 12 recognized giant clam species, only 9 have been assessed and listed in the International Union for Conservation of Nature (IUCN) Red List of Threatened Species: T. gigas, T. derasa, T. rosewateri and T. mbalaana are listed as Vulnerable and Hippopus hippopus, H. porcellamus, T. maxima, T. squamosa and T. crocea are listed as Lower Risk (Wells et al., 1983; Wells, 1997). At local and regional scales, several countries have specific laws to protect their giant clam stocks (see Neo, 2020). While these measures are in-place to safeguard these threatened bivalves from overexploitation, there are several shortcomings. Due diligence on the enforcement of CITES is largely dependent on whether trading countries are signatories to the CITES Treaty, and there is an urgent need to update the IUCN Red Listings to reflect the contemporary status of each giant clam species (Neo, 2020). For example, the recently rediscovered species (T. squamosina, T. noae and T. elongatissima) have yet to be assessed, and due to lack of current knowledge about their biology and abundance, they will likely be classified as ‘Data deficient’.

Breeding programmes have existed since the late 1980s to help restock over-exploited wild populations of giant clams (e.g. Gomez and Mingoa-Licuanan, 2006; Moorhead, 2018). Gametes are collected from broodstock and subsequent larvae reared in laboratory-style facilities with juveniles grown out in land- and/or ocean-based aquaculture settings. This mariculture (seawater aquaculture) of giant clams has been a feasible technique to mass produce individuals for restocking rare species or extirpated populations in several regions, such as the Pacific Islands, Southeast Asia and Japan (e.g. Heslinga et al., 1984; Gomez and Mingoa-Licuanan, 2006; Kurihara et al., 2012; Neo and Todd, 2012). Despite the extensive application of mariculture and restocking in numerous countries, the rates of success of these initiatives are neither well studied nor well documented (Teitelbaum and Friedman, 2008; Moorhead, 2018). Some of the possible challenges that clam breeders face are operations related such as recurring high mortality rates, coupled with high running costs and labour-intensive rearing. Also, hatchery-bred clams, spawned from an inherently sub-sampled population (broodstock), are likely to be less genetically diverse (Benzie and Williams, 1996), which could increase their vulnerability to diseases and/or environmental change stressors.

New conservation considerations in a rapidly changing world

In recent years, we are recognizing that giant clams are not only threatened by overexploitation by humans, but are also threatened by a suite of environmental change drivers including (i) global change stressors, such as climate change, global warming and ocean acidification, and (ii) local and regional stressors from agriculture and urbanization, such as turbidity and sedimentation. Of the global pressures on marine life, pollution and climate change continue to occur at peak pressures (Duarte et al., 2020). Crucially, the effects of local to global environmental stressors not only act in isolation, but also in concert, with potentially unknown synergistic effects occurring within the complex coastal environments that giant clams inhabit.

Global-scale environmental stressors

Ocean warming

During the past 40 years, the Indo-Pacific warm pool, where SSTs are permanently over 28°C, has expanded nearly two-fold in area covering much of the Indo-Pacific region (Roxy et al., 2019) and affecting large areas of the range of giant clams. The highest temperatures occur within the centre of giant clam diversity in an area around the Coral Triangle—a region considered the global centre of marine biodiversity in the Indonesian-Philippines and Far Southwestern Pacific bioregions.

Heat stress in the marine environment is generally measured by SST metrics, such as degree heating weeks (DHW, where SST anomalies over the 1985–1993 baseline are summed). DHW are often used to indicate the likelihood of coral bleaching (although see McClanahan et al., 2019 for a comparison of conventional and new SST metrics). Global heat stress since the year 2015 has been substantial, affecting large areas of the Indo-Pacific. Further projected heat stress from continued global warming will affect large areas of the range of all giant clam species (Fig. 2a). In Fig. 2a, projected marine heat stress is indicated by the onset of 8 DHW per year under RCP8.5. We acknowledge that although SST metrics, such as DHW, are generally used for corals, they could act as proxies for bleaching in giant clams, and the development and use of heat stress metrics for giant clams is an area worth future research.

Elevated temperatures cause a range of physiological effects in giant clams including decreases in photosynthetic activity, changes in respiration rate (Bliedberg et al., 2000) and effects on symbiont photosynthetic yield and density
Figure 2: (a) Projected heat stress caused by global warming and (b) reduced saturation state of seawater with respect to aragonite (caused by ocean acidification) will affect areas within the ranges of all giant clam species. Abbreviations for giant clam species: T.si, T. squamosina; T.e, T. elongatissima; T.r, T. rosewateri; H.p, H. porcellanus; T.d, T. derasa; T.mb, T. mabalavua; T.c, T. crocea; T.g, T. gigas; T.n, T. noae; H.h, H. hippocus; T.m, T. maxima; T.s, T. squamosa. Base map data from van Hooidonk et al. (2014) reproduced with permission from Ruben van Hooidonk (National Oceanic and Atmospheric Administration Coral Reef Conservation Program and the University of Miami).

(Brahmi et al., 2019) and enzyme activities (Zhou et al., 2019). Like corals, giant clams bleach in response to high temperatures and high light intensities (Buck et al., 2002), with documented cases of bleaching in giant clams in the wild from high temperatures (e.g. Addessi, 2001; Andréfouët et al., 2018; Apte et al., 2019). Elevated seawater temperature also changes fatty acid composition in T. maxima (Dubousquet et al., 2016), affects embryonic and larval development (in T. gigas) (Enricuso et al., 2019) and leads to oxidative stress and collapse of the clam-algae symbiosis (in T. crocea) (Zhou et al., 2019). A review of French Polynesian giant clam populations concluded that abnormal weather conditions linked to climate change, climate anomalies and global warming occurred in all documented cases of mass mortality of giant clams (Van Wynsberge and Andréfouët, 2017), highlighting the dominance of temperature as the primary environmental stressor involved in giant clam mass mortalities.

Ocean acidification

CO₂ from the atmosphere is absorbed by the oceans where it reacts with seawater and lowers pH in a process called ocean acidification. This process has caused a decline in the saturation state of seawater with respect to calcium carbonate polymorphs including aragonite (Jiang et al., 2015)—a more soluble polymorph compared to calcite and the main form of calcium carbonate in giant clam shells (Moir, 1990). Marine animals that produce calcium carbonate shells and exoskeletons are thus particularly vulnerable to ocean acidification. For giant clams, which produce such large shells and are thus very heavily calcified, ocean acidification could be particularly
problematic. Projected continued reductions in aragonite saturation state will be experienced by all giant clam species across their ranges (Fig. 2b). Lower seawater saturation state occurs in an opposite latitudinal gradient to ocean warming, meaning there is no safe haven for coral reef species at low or high latitudes from the combined impacts of warming and acidification (van Hooitdonk et al., 2014).

In giant clams, ocean acidification leads to reduced survival (Watson et al., 2012a; Watson, 2015) and growth (Watson, 2015; Kurihara and Shikota, 2018; Brahmi et al., 2019). The effect of ocean acidification on giant clams can also depend on temperature (Watson et al., 2012a) and light availability (Watson, 2015) demonstrating interactions among stressors in the marine environment.

For animals with symbiotic microalgae, increased CO₂ availability could lead to enhanced primary production of energy. However, although elevated CO₂ increased endosymbiont density in the giant clam T. crocea, endosymbiont productivity did not change, which suggests productivity per endosymbiont decreased at elevated CO₂, and thus negative effects of CO₂ were not countered by any potential increases in photosynthesis (Kurihara and Shikota, 2018). Ocean acidification also leads to altered behaviour in invertebrates (Manriquez et al., 2013; Watson et al., 2014), including tropical molluscs (Watson et al., 2014, Watson et al., 2017a, Spady et al., 2014; Spady et al., 2018; Thomas et al., 2021) likely through mechanisms including disrupted functioning of ligand-gated chloride channels, such as GABA_A receptors (Watson et al., 2014, Thomas et al., 2020; Thomas et al., 2021), further increasing the vulnerability of calcareous taxa. Behavioural changes could affect settlement choices in invertebrate planktonic larval stages and antipredator responses in planktonic and settled life stages.

**Ocean deoxygenation**

Oxygen loss in the ocean, known as ocean deoxygenation or hypoxia, is emerging as a pervasive negative threat to marine life across multiple taxonomic groups (Sampaio et al., 2021; Sutherland et al., 2021). Deoxygenation is likely an increasingly important, but underestimated and under-reported, source of mortality on coral reefs (Altieri et al., 2017; Breitburg et al., 2018). While the giant clam holobiont might produce a net increase in oxygen during the day, night time respiration requires a net use of oxygen, and it is thus during dark periods that giant clams are most likely to be susceptible to hypoxic conditions. Overall, in T. squamosa, oxygen uptake exceeds total oxygen production and oxygen extraction in the dark is high relative to species without photosymbionts (Mangum and Johansen, 1982), suggesting that giant clams could be susceptible to ocean deoxygenation.

**Salinity change**

Ocean salinity is also changing as a response to global warming with higher salinity regions becoming more saline and fresher regions becoming less saline (Durack et al., 2012). Studies show some giant clam species are tolerant to hypersaline conditions (T. squamosa: Neo et al., 2013; Eckman et al., 2014), whereas others are affected by low salinities (T. gigas: Maboloc et al., 2014; Maboloc et al., 2015; Sayco et al., 2019) or low and high salinities (H. hippopus: Panggabean et al., 2009). Overall, since giant clams have some tolerance to a range of salinities (e.g. Maboloc and Villanueva, 2017), the small scale changes currently occurring in ocean salinity, within the order of ±0.1 or 0.2 units (Durack et al., 2012), are unlikely to be a direct stressor compared to other global changes.

**Local- to regional-scale environmental stressors**

**Light availability**

A range of local- to regional-scale coastal activities, such as terrestrial run-off of sediments and chemicals from agriculture and urban areas, can lead to a reduction in light availability (often measured by photosynthetically active radiation, PAR) in the water column, known as coastal ocean darkening. Since light regimes structure aquatic food webs, this water column light attenuation could be a key driver in coastal food web changes (Aksnes et al., 2009).

‘Solar-powered’ animals with symbiotic microalgae within their bodies necessarily have a strong interdependence on optimum light levels in their environment. Giant clams have a range of light levels in which they can survive and within that, optimum light levels for growth. For instance, studies have found that T. squamosa can engage in light-enhanced growth and shell formation through the increased expression of specific proteins to facilitate transport of inorganic nutrients from the clam host to its endosymbionts (Ip et al., 2017; Chew et al., 2019).

In giant clams, calcification and primary production are dependent on light and are highest at incident light levels equivalent to 3–5 m water depths (Rossbach et al., 2019a). On the other hand, too much light can induce changes in chlorophyll content or alter endosymbiont cell size and populations and can cause bleaching (Buck et al., 2002). At the other end of the scale, too little light is problematic with low light levels reducing giant clam survival (Watson, 2015; Eckman et al., 2019). The optimum light range is likely to differ among species, with some species such as T. crocea often found in very shallow water, and other species like T. mbalavuana found up to 30 m deep (Neo et al., 2017). Indeed, different depth distributions among species may be explained by their degree of mixotrophy. In the Red Sea for example, T. maxima is a strict functional photoautotroph and exhibits a shallow depth distribution (down to ~10 m, maximum 17 m), whereas T. squamosa extends its depth range (down to 42 m) by heterotrophy (Jantzen et al., 2008).
Humans have altered the flux of sediment reaching the global coastal oceans (Syvitski et al., 2005). Processes such as turbidity and sedimentation both reduce light availability and create physical disturbance when particles settle onto the mantle (photosynthetic upward facing soft tissues) of the clam. Increased seawater sediment loading results in more mantle contractions (Elfwing et al., 2001), presumably to rid the mantle of sediment; however, this activity would dramatically increase demand on the energy budget of otherwise relatively inactive giant clams. Since clams from disturbed sites with higher turbidity and nutrient loading have reduced photosynthetic activity (Elfwing et al., 2003), their ability to recoup energy stores is likely to be diminished.

Other factors

Other urbanization factors, such as pollution, also affect giant clams. A study on T. squamosa found that increased heavy metals (copper) in seawater decreased gross production:respiration ratio by about one third through decreased photosynthesis (Elfwing et al., 2001). Tourists too have the potential to affect giant clams. The presence of movement or dark silhouettes above giant clams leads to mantle contractions and/or shell contractions as a natural anti-predator response. Thus, snorkelers and divers can cause partial or full shell closure by swimming above and around clams, touching clams and by kicking up sediment from the seafloor that could land on the clam’s mantle. Tourism activities may also generate pollution, including from boats (chemical and noise pollution) and marine litter.

While these above factors tend to act on local to regional scales, they will almost certainly interact with stressors occurring on global scales, such as global warming and ocean acidification. The potential synergistic effects of multiple stressors and interactions in the natural environment remain little studied, in part because of the complexity; however, experiments investigating multiple broad-scale stressors suggest that combined stressors can result in particularly negative effects on giant clams with increased lethal and sub-lethal effects (T. squamosa Watson et al., 2012a; Watson, 2015; although compare T. maxima Brahmi et al., 2019; Armstrong et al., 2020).

**Responses to environmental change**

The responses of giant clams to environmental change may include the following: shifts in biogeographical and/or depth distributions (mid- to longer-term); changes in behaviour and/or physiology, including modifying symbiotic communities (short- to mid-term), phenotypic plasticity (mid-term), genetic adaption (longer-term); and extinction. Distribution shifts can occur in response to a changing environmental condition that occurs along a gradient (e.g. temperature with latitude and light with depth). After considering (i) distribution shifts, we explore (ii) the capacity for rapid adaptive responses to environmental change from fast to slower timeframes.

**Distribution shifts**

**Biogeographical distribution—reduced latitudinal habitat availability**

As global temperatures warm with climate change, species can take advantage of the decreasing planetary temperature gradient from equatorial to polar latitudes and shift their distribution poleward towards higher latitudes and cooler conditions (Lambers, 2015). Global warming has already caused a poleward range expansion of many terrestrial and marine species (e.g. Pecl et al., 2017). Giant clams produce pelagic larvae that are dispersed by ocean currents indicating that range expansion of giant clam species as ocean temperatures warm is possible. Range expansions of corals (Yamano et al., 2011) and coral reef-associated fishes (Booth et al., 2018) have already been observed. Most giant clam species do not need corals to survive, although wild T. crocea, the boring clam, bores into large boulder-shaped coral colonies or other calcium carbonate-based structures.

However, the saturation state of seawater with respect to calcium carbonate polymorphs such as aragonite decreases with increasing latitude. Light availability, a key metric for the success of giant clams, also decreases with latitude. Thus, the formation and persistence of giant clam shells (the production of which may represent a greater proportional cost to the total energy budget than the shells of less calcified molluscs; see Watson et al., 2012b; Watson et al., 2017b) and the ability of giant clam photosymbionts to capture light are both likely to diminish on a poleward trajectory. Consequently, a poleward shift may well be limited and overall likely to result in a reduction in available latitudinal habitat size primarily driven by a range retraction from lower latitudes. In some locations, such as the Red Sea, giant clams also face a physical poleward migration barrier. This puts species in these locations at greater risk from global change. These factors, and further critical unknowns, such as local water quality conditions and interactions with other local- to global-scale environmental drivers, mean a reliance on a poleward distribution shift for the persistence of giant clam species is likely a risky strategy. Furthermore, in sedentary animals, such as giant clams, distribution shifts will tend to occur over multiple generations and may well not keep pace over ground with global change.

**Depth distribution—reduced habitat availability within a species’ depth range**

Physiological responses of giant clams to global- and local- regional-scale stressors may influence their ecology on coral reefs, for example by altering their natural depth distribution. High SSTs and high light intensities from solar irradiation limit the upper depth distribution of giant clams (Fig. 3a). Uppermost depth distributions will move deeper because high temperature and intense light levels will bleach giant clams or...
cause other physiological stress responses (Fig. 3b). The lower depth distribution of giant clams is dictated by low light levels. Reduced light levels at the deepest depth distribution through natural light attenuation in seawater, especially in combination with other stressors such as elevated temperatures and ocean acidification that cause lethal and sub-lethal effects at low light (Watson et al., 2012a; Watson, 2015), are likely to create a shoaling effect, limiting the lower depth distribution of photosymbiotic giant clams (Fig. 3c). Increased turbidity or sediment load will further reduce light availability and thus reduce habitable depth even more. Compressed depth distributions with global change will limit giant clam habitat on reefs leading to an overall reduction in suitable habitat within their natural range.

Once giant clams recruit to the coral reef substrata, they are essentially sessile, like reef-building corals, and cannot move to find more optimal habitat should environmental conditions change. Although juvenile clams have some ability to move with their foot once they settle onto the coral reef (Soo and Todd, 2014), this movement is limited and they will soon attach themselves permanently with byssal threads or bore into the substrata (in the case of boring species). Older, and thus, larger giant clams become too heavy and are unable to change their position on reefs. Given limited or no ability to move, giant clams need stable local conditions, such as light availability through water clarity, to persist.

Modelling of available habitats using present-day and projected future physical and chemical parameters (such as depth, temperature, aragonite saturation state and light levels) could be used to estimate the effect of reduced depth distributions on the total habitat availability within a species range. This modelling approach could be used to investigate the vulnerabilities of each giant clam species since they have different depth distributions, with certain species, such as T. mbalavuana, presumably able to tolerate lower light levels naturally.

Considering depth distribution in giant clams provides an example of how physiological responses may help predict ecological patterns and inform conservation management approaches of these threatened species. The principles of this approach, as well as other aspects of the current paper, could also be applied to other sessile photosymbiotic animals, such as reef-building corals.

### Capacity for rapid adaptive responses

#### Behaviour

Although sessile beyond juvenile stages, giant clams have the ability to open and close their shell using their large adductor muscle. This immediate behavioural response to changing conditions is one way that clams can respond to environmental change (Dehaudt et al., 2019) and in a different way compared to corals. This distinct physiological advantage allows them to expose or protect their symbiotic tissues from light and predators. In low daylight conditions, giant clams can extend their mantle to maximize light capture. At night, they retract their mantle and partially close their shells, presumably to deter predators, and because there is no light for photosynthesis. During periods of elevated temperatures or very high light levels, giant clams have the option to partially close their shells and retract their mantle, providing shading

---

**Figure 3**: (a) Giant clam depth distributions are influenced by environmental conditions and are likely to be limited by (b) current and (c) continued global change. Increasing CO₂ levels cause ocean warming and acidification, which are likely to compress the upper and lower limits, respectively, of the depth distributions of giant clams, especially in combination with other factors such as reduced light availability. Giant clam symbol credit: Tracey Saxby, Integration and Application Network (ian.umces.edu/media-library).
Microorganisms associated with the giant clam holobiont

Like corals, giant clams are holobionts, harbouring a range of microorganisms within their tissues, such as algae (endosymbiotic dinoflagellates), bacteria (Rossbach et al., 2019b; Guibert et al., 2020) and, potentially, fungi and viruses as well. Associations of the host with microorganisms offer the potential for rapid adaptive responses to environmental change in corals (Torda et al., 2017), and similarly in giant clams.

While the stony corals hold their symbiotic microalgae in the endodermal cells lining the gastrovascular cavity, the microalgae endosymbionts in giant clams are found intercellularly within the siphonal mantle, specifically in the tertiary tubes of the zooxanthellal tubular system (Norton et al., 1999). This location of symbionts could offer increased protection against rapid environmental changes and possibly confer some resistance to bleaching, compared with corals. There have been instances during bleaching events where corals have either bleached or died due to heat stress but giant clams have not (Neo et al., 2017).

Studies have also found that microalgae endosymbiont distribution and diversity in giant clams can be driven by local conditions such as ambient temperature levels and temperature fluctuations (Lim et al., 2019). During the ontogeny of giant clams from juveniles to adults, the composition and densities of endosymbionts may shift, often also as a result of changing environmental conditions (Belda-Baillie et al., 2017). In addition, the diversity and community structure of Symbiodiniaceae in giant clams likely affects host traits such as growth rate, reproduction and photosynthetic efficiency (DeBoer et al., 2012). Giant clams mostly associate with Symbiodiniaceae from the genera Symbiodinium (clade A), Cladocopium (clade C) and Durusdinium (clade D) (Ikeda et al., 2017; Lim et al., 2019). Hosting multiple endosymbiont species likely enables giant clams to cope better with changing environments, as each endosymbiont species has different tolerances to temperature, irradiance and turbidity. Within the host, endosymbiont communities are not static and host-endosymbiont shuffling can occur as the holobiont acclimatizes to changing environmental conditions (Belda-Baillie et al., 1999).

Recently, different microbial communities, or ‘microbiotypes’, have been found associated with giant clams; three microbiotypes were found in a study of T. maxima individuals from French Polynesia (Guibert et al., 2020). Seawater temperature and the presence of different corals did not change the composition of Symbiodiniaceae or bacterial communities, but the giant clam microbiotype dominated by the bacterial family Vibrionaceae was linked to increased host mortality, especially in the presence of the coral Acropora cytherea, and this effect on mortality was amplified at elevated temperatures (Guibert et al., 2020).

Phenotypic plasticity and genetic adaptation

The phenotype of an organism can be modified through non-genetic processes, known as phenotypic plasticity, acclimation or acclimatization. Nongenetic processes can occur within a generation (e.g. reversible or developmental acclimation) and between generations (e.g. transgenerational acclimation) through parental provisioning, hormones and proteins and epigenetic marks (Munday, 2014). Genetic adaptation occurs between generations when chance genetic mutations produce favourable modifications. While both these processes are likely to occur in giant clams (e.g. Neo and Todd, 2011), characteristics of giant clam life history traits mean they will play out over longer timescales in comparison to many other coral reef organisms.

Giant clams are long-lived, and larvae that are produced in present-day oceans could survive until the end of the century. However, the opportunity for early life developmental acclimation in individuals will be limited to present-day conditions. Additionally, giant clams take a long time to reach reproductive maturity. They produce first male, then male and female gametes, when they reach a larger size. This means giant clam generation times are long, and reduced generation turnover time limits the potential for genetic adaption. Additionally, the selective exploitation of large giant clams from the wild will reduce the proportion of female clams. On the other hand, one positive characteristic of giant clam biology is that they can spawn millions of gametes, potentially producing high numbers of larvae and thus increasing the chances of selection acting to produce fitter individuals.

Conservation strategies through rapid environmental change

In addition to traditional breeding programmes, we should now view the conservation of giant clams through a global change lens to focus on protecting wild populations of these threatened species in the face of rapid environmental change. Conservation strategies and actions include (i) the management of local and regional conditions close to optimal while global CO₂ emissions are stabilized, (ii) adaptive population management, (iii) selective breeding of tolerant giant clam holobionts for restocking programmes in selected areas and (iv) inoculation of tolerant strains of microalgae endosymbionts in giant clam early life stages.

Management of local and regional conditions while global CO₂ emissions are stabilized

While management of global change stressors involves moving to net zero CO₂ emissions as soon as possible, and poten-
Giant clam populations can also be managed in high-traffic tourist areas. Although tourists have the potential to contribute some local-scale disturbances to certain giant clam individuals, such highly localized impacts are likely to be easily managed and, importantly, the value of tourists seeing and appreciating giant clams in nature will likely outweigh the minimal impacts of tourist operations (see Tourism potential section below). Management of giant clams in such areas will involve awareness that clams may be using more energy to cope with some physical disturbance from tourist operations. Although supplemental feeding of giant clams is applied in aquarium settings, management of increased energy usage by giant clam individuals in the ocean could involve protecting them from other stressors such as high temperatures and subsequent bleaching, particularly since they may already be under energy stress. Management actions such as the provisioning of shade structures could also be applied to help protect specific giant clam individuals during periods of high seawater temperature.

Selective breeding of tolerant holobionts for restocking programmes

Aquaculture breeding programmes often select for the best performing individuals, such as for growth or disease resistance. A recent mariculture study on *T. crocea* found that reciprocal hybrids produced from crossbreeding individuals from two geographical populations, separated by ∼600 km in distance, were more robust in terms of growth and survival than pure populations (i.e. breeding different individuals within the same geographic population) (Zhang et al., 2020). Giant clam aquaculture could therefore select for
### Table 1: Threats and conservation actions

| Region                               | Species diversity | Current threats                                                                 | Conservation actions                                                                                                                                 |
|--------------------------------------|-------------------|---------------------------------------------------------------------------------|-----------------------------------------------------------------------------------------------------------------------------------------------------|
| Red Sea and Gulf of Aden             | T.s, T.m, T.s1    | • Global warming                                                                 | • Attempts to cultivate giant clams were carried out in early 2000s (Roa-Quaoit, 2005)                                                                 |
|                                      |                   | • Ocean acidification                                                            | • Collecting wild giant clams in Saudi Arabia has been banned since early 2000s (AbuZinada et al., 2004)                                             |
|                                      |                   | • Deoxygenation?                                                                 |                                                                                                                                                    |
|                                      |                   | • Degraded habitats                                                             |                                                                                                                                                    |
|                                      |                   | • Water pollution (e.g. sewage discharges)                                      |                                                                                                                                                    |
|                                      |                   | • Unsustainable tourism                                                        |                                                                                                                                                    |
|                                      |                   | • Coastal development                                                           |                                                                                                                                                    |
|                                      |                   | • Ornamental shell trade                                                        |                                                                                                                                                    |
| Western Indian Ocean                 | T.c, T.s, T.m, T.e| • Global warming                                                                 | • Considerations to protect and aggregate remaining wild adults to facilitate spawning, breeding and releasing hatchery-reared clams in the Republic of Mauritius (Ramah et al., 2019) |
|                                      |                   | • Ocean acidification                                                            | • Considerations to leverage on mariculture for restocking/reintroduction to prevent further depletion of stocks in Lakshadweep (Apte et al., 2019)   |
|                                      |                   | • Deoxygenation?                                                                 |                                                                                                                                                    |
|                                      |                   | • Overfishing                                                                    |                                                                                                                                                    |
|                                      |                   | • Ornamental shell trade (ivory of the sea)                                     |                                                                                                                                                    |
|                                      |                   | • Sedimentation                                                                  |                                                                                                                                                    |
| Bay of Bengal and Andaman            | H.h, T.g, T.c, T.s, T.m | • Global warming                                                                 | • Restocking and/or reintroducing of giant clam species to sites where they have been extirpated (Teitelbaum and Friedman, 2008)                 |
| South China Sea                      | H.h, T.g, T.d, T.no, T.c, T.s, T.m | • Global warming                                                                 | • Selective crossbreeding individuals from geographically distinct areas to increase robustness (Zhang et al., 2020)                         |
|                                      |                   | • Ocean acidification                                                            | • Restocking and/or reintroducing of giant clam species to sites where they have been extirpated (Gomez, 2015)                                   |
|                                      |                   | • Deoxygenation?                                                                 |                                                                                                                                                    |
|                                      |                   | • Overfishing                                                                    |                                                                                                                                                    |
| Coral Triangle                       | H.h, H.p, T.g, T.d, T.no, T.c, T.s, T.m | • Global warming                                                                 | • Giant clam gardens in Samal and Tawi-Tawi, the Philippines for tourism                                                                       |
|                                      |                   | • Ocean acidification                                                            | • Restocking and/or reintroducing of giant clam species to sites where they have been extirpated (Teitelbaum and Friedman, 2008)                 |
|                                      |                   | • Deoxygenation?                                                                 |                                                                                                                                                    |
|                                      |                   | • Overfishing                                                                    |                                                                                                                                                    |
| Australia                            | H.h, T.g, T.mmb, T.d, T.no, T.c, T.s, T.m | • Global warming                                                                 | • Snorkel trails at Magnetic Island for tourism (pers. comms., R. Braley)                                                                            |
|                                      |                   | • Ocean acidification                                                            |                                                                                                                                                    |
|                                      |                   | • Deoxygenation?                                                                 |                                                                                                                                                    |
|                                      |                   | • Poor water quality (from sediments, nutrients and contaminants)                |                                                                                                                                                    |
| Pacific Ocean                        | H.h, T.g, T.mmb, T.d, T.no, T.c, T.s, T.m | • Global warming                                                                 | • Restocking and/or reintroducing of giant clam species to sites where they have been extirpated (Teitelbaum and Friedman, 2008; Moorhead, 2018) |
|                                      |                   | • Ocean acidification                                                            | • Translocating individuals to cooler sites or provisioning of shade structures during periods of high seawater temperatures (Andréfouët et al., 2013) |
|                                      |                   | • Deoxygenation?                                                                 | • Placing strict measures such as banning clam fishing for commercial use, setting minimum size limits for subsistence harvesting, imposing harvesting quotas or bag limits, restricting clam fishing to free diving only, banning use of mechanical fishing equipment (Andréfouët et al., 2013; Kinch and Teitelbaum, 2010) |
|                                      |                   | • Overfishing                                                                    |                                                                                                                                                    |
|                                      |                   | • Illegal harvesting                                                             |                                                                                                                                                    |

H.h, H. hippopus; H.p, H. porcellanus; T.g, T. gigas; T.mmb, T. mbalavuana; T.d, T. derasa; T.no, T. noae; T.c, T. crocea; T.s, T. squamosa; T.m, T. maxima; T.r, T. rosewateri; T.s1, T. squamosina; T.e, T. elongatissima
tolerant individuals for current conditions and/or by introducing stressor conditions. Broodstock or offspring could also be acclimated/grown at ‘moderate’ climate scenarios (e.g. an overalied seawater temperature of 1°C higher than ambient) to increase the resilience of individuals, or promote adaptation of the giant clam holobiont as a whole. Elevated temperature conditions could be achieved by active heating with heaters controlled by thermostats, or passive heating, for example, by using a greenhouse (Braley et al., 1992) or by the strategic removal or reduction of shade cloth coverings over areas of tank water. Shade cloth can also be used to establish shading regimes equivalent to particular seawater depths (e.g. 83% light = 1 m depth to 11% light = 28 m depth; Klumpp and Lucas, 1994), and this could promote resistance to higher or lower light levels (e.g. with turbidity) within the water column. Selective breeding is particularly amenable in giant clams, where spawning can produce many millions of larvae, so there is great potential for selection to new environmental conditions during early life. This process could produce individuals that have experienced developmental acclimation and/or transgenerational acclimation to projected future ocean conditions (e.g. elevated temperature and CO2).

Inoculation of tolerant strains of microalgae endosymbionts in early life
Breeding programmes offer symbiotic microalgae to larval giant clams just before settlement, and the uptake of these symbionts are crucial for the survival of the larvae. Since giant clam offspring do not acquire their microalgae endosymbionts from their parents, larvae at a few days old gain their symbiotic microalgae from the environment independently. It is therefore plausible to help build resilience in giant clam holobionts by offering tolerant strains of microalgal symbionts at this stage.

In general, studies have found that giant clams in the Indo-Pacific region generally associate with three genera of Symbiodiniaceae: Symbiodinium, Cladocaptorium and Durusdinium, where each genus possesses unique ecological characteristics. For instance, Symbiodinium species are most adapted to living in shallow-water environments and tolerant to high irradiance stress (Venn et al., 2008), while Durusdinium species are typically found in symbiosis with hosts living in stressful environments characterized by large diel or seasonal shifts in temperature and/or broad fluctuations in water turbidity (Tanzil et al., 2016). Concurrently, depending on the giant clam species and/or environmental conditions, specific species of dinoflagellates may be chosen for inoculation to increase the survival of giant clam larvae and juveniles.

Among giant clam species, some are faster growing than others (e.g. T. gigas grows 8–12 cm yr−1 versus T. squamosa that grows 2–4 cm yr−1; Beckvar, 1981). Symbiont type can also influence growth. Fitt (1985) found that inoculation of fast-growing symbiont species to larvae and juveniles of H. hippopus led to higher growth and survival rates. Symbiont species also differ among giant clam species and with host size; smaller giant clams host a more diverse array of symbiont genera than larger clams (Ikeda et al., 2017). Indeed, the use of small, rather than medium-sized, giant clams to inoculate juvenile (seed) giant clams with symbionts increases survival two-fold, likely because of the increased Symbiodiniaceae diversity (Yamashita et al., 2021).

On the other hand, regional environmental conditions can also determine symbiont type in giant clams. Red Sea giant clams (T. maxima and T. squamosa) exclusively host Symbiodinium symbionts, suggesting that this specific host-endosymbiont interaction could be beneficial in the relatively extreme heat and irradiance conditions characteristic of the Red Sea (Pappas et al., 2017). A greater understanding of giant clam host-endosymbiont interactions will therefore allow breeders to optimize the introduction of appropriate tolerant symbiont species to enhance survival of larvae and juveniles in mariculture. Such an approach may give young giant clams a head start in life and allow them to better cope under rapidly changing field conditions.

All the strategies above still require the reduction of global CO2 emissions and for nations to move to net zero emissions as soon as possible and potentially beyond net zero emissions. Continuing emissions on the current worst case RCP8.5 projection trajectory (Collins et al., 2013) will mean coastal oceans will not be conducive to giant clam survival in forthcoming decades. While breeding programmes can help restock certain areas and provide a supply to replace clam-depauuperated areas, there are high operational and labour costs and substantial equipment and facilities involved. Restocking programmes are not the primary solution to over-exploitation or global change, instead the challenge is to protect the remaining wild populations of giant clams and their coral reef habitats while global emissions, and thus environmental conditions, stabilize.

Tourism potential of giant clams in a changing world
As charismatic megafauna, and one of the top iconic animals to see on coral reefs, giant clams hold significant potential for ecotourism, and tapping into the aesthetic value of giant clams as a tourist attraction can provide an additional conservation incentive. They may also possess a greater tolerance to some environmental change stressors as opposed to corals, meaning tourists could still view giant clams in areas where coral is degraded. In locations such as the Great Barrier Reef in Australia and Samal and Tawi-Tawi in the Philippines, giant clams are used in snorkel trails or in giant clam gardens for tourists. Giant clams are particularly amenable to tourist viewing as they (i) are sessile, unlike the majority of other iconic coral reef megafauna, (ii) inhabit shallow depths, providing good viewing opportunities on snorkel, (iii) are conspicuous, (iv) are long-lived, and (v) can be translocated into position.
Aquacultured giant clams are well suited for translocation, ideally while small to medium sized. Giant clams can also be incorporated into citizen science programmes to enhance conservation efforts (e.g. Requilme et al., 2021). We suggest giant clams be flagship species (Soo and Todd, 2014; Neo et al., 2015) for coral reef habitats to help raise public awareness and whereby protection for other species, such as reef-building coral and coral reef inhabitants, would come with the protection of environmental conditions conducive to the survival of the charismatic ambassador species.

The Great Barrier Reef injects AUD$6.4bn (USD$5.0bn) into the Australian economy every year (Deloitte, 2017), and recognizing the monetary tourism value for threatened habitats and iconic species can serve as a strong conservation incentive in a currency that can be understood by policy makers and the general public. For example, manta rays are fished for their meat, but in Yap the lifetime value of each manta ray is estimated at ~USD$1.9 million because of the ecotourism revenue generated when tourists pay to watch manta rays (O’Malley et al., 2013). Demonstrating the enormous continuing revenue from the live animal compared to the dead animal empowers local people to make informed choices and incentivizes protecting iconic species. To date, no studies have yet valued giant clams in terms of tourism revenue, and this is potentially an area for further research, on the intersection of economics and conservation science, that could help to save wild stocks. Additional high value ecotourism programmes, where tourists are able to help hands-on with giant clam breeding and restocking activities may help offset some of the relatively high costs of these activities.

Future directions

While we show how results from studies on giant clam physiology, morphology and behaviour can begin to inform conservation strategies, more work on global change stressors is required to understand the responses of giant clams to these pervasive changes in natural ecosystems. Elevated temperatures are already affecting giant clam wild populations. Further work on responses of individuals maintained at both elevated temperatures and simulated heat stress events could help determine any bleaching thresholds and other responses among different species to assist management and conservation efforts. The effects of ocean acidification on giant clams are still relatively little studied, and consideration of emerging threats, such as ocean deoxygenation, is an area for further work. Also, the interaction of global- and local–regional scale stressors, such as ocean warming and ocean darkening or pollution, need to be understood.

For all these types of environmental change drivers, it will be important to assess a variety of biological responses, including physiology, morphology and behaviour, over various life stages to determine any life history bottlenecks. Additionally, the responses of communities within the holobiont, particularly the giant clam–Symbiodiniaceae association, as well as the response of the holobiont as a whole, will be important in assessing the overall resilience and adaptive capacity of giant clams to rapid environmental change. Transcriptomics could help unravel which genes are expressed at different environmental conditions and whether individuals or species have the capacity to upregulate critical genes to help cope with stressful conditions. Ecological modelling of biological responses of giant clams using physical and chemical data could help determine how the ranges of threatened species and populations may change over coming decades. Determining the economic value of giant clams for coral reef tourism and restocking activities could help incentivize and enhance their protection. Another opportunity to inform the conservation of these threatened species is to evaluate community assemblages using other types of information such as species richness, functional traits and phylogeny to identify species based on their functional and historical contributions. Such studies may also incorporate data on biological responses to holistically capture the species’ ecological standing within ecosystems.

Conclusion

Enhanced global efforts are urgently needed to meet net zero CO₂ emissions as soon as possible and progress to beyond net zero CO₂ emissions to give biodiversity the chance to survive the already locked-in changes to the Earth’s climate. Doing so will help to avoid lethal and sub-lethal effects of global change on threatened species, such as giant clams. In the meantime, this perspective article has (i) identified new environmental threats to giant clams, (ii) identified conservation management actions in the face of rapid environmental change, (iii) highlighted the importance of tourism in conserving giant clams and (iv) identified areas of further research on giant clams. While these actions are likely to allow the survival and appreciation of giant clams in the first half of this century, like coral reefs, their continued persistence in the world’s tropical oceans is ultimately dependent on rapid mitigation of global climate change.
Acknowledgements

We thank Benjamin Leow (National University of Singapore) for assistance with figure illustration and Ruben van Hooidonk (National Oceanic and Atmospheric Administration Coral Reef Conservation Program and the University of Miami) for permission to reproduce the heat stress and aragonite saturation state base maps.

Funding

This work was supported by Queensland Museum Network Biodiversity and Geosciences Program [to S.-A.W.], Australian Research Council Centre of Excellence for Coral Reef Studies [to S.-A.W.], Ian Potter Foundation [20130107 to S.-A.W.], Save Our Seas Foundation [273 to S.-A.W.], Malacological Society of Australia [to S.-A.W.], National Parks Board [to M.L.N.], National Research Foundation Singapore [to M.L.N.], St John’s Island National Marine Laboratory [to M.L.N.] and Pew Fellows Program in Marine Conservation at The Pew Charitable Trusts [to M.L.N.].

References

AbuZinada A, Robinson E, Nader I, Al Wetaid Y (2004) First Saudi Arabian National Report on the Convention on Biological Diversity. The National Commission for Wildlife Conservation and Development, Riyadh.

Addessi L (2001) Giant clam bleaching in the lagoon of Takapoto atoll (French Polynesia). Coral Reefs 19: 220.

Aksnes DL, Dupont N, Staby A, Fiksen O, Kaartvedt S, Aure J (2009) Conserving genetic resources of the giant clam Tridacna gigas – A future perspective. Conservation Physiology 9: 1–30.

Apte D, Narayana S, Dutta S (2019) Impact of sea surface temperature anomalies on giant clam population dynamics in Lakshadweep reefs: Inferences from a fourteen years study. Ecological Indicators 107: 105604.

Armstrong EJ, Dubouillet V, Mills SC, Stillman JH (2020) Elevated temperature, but not acidification, reduces fertilization success in the giant clam Tridacna maxima. Mar Biol 167: 8.

Barrier Reef Australia (2021) The great eight. https://www.barriereefaustralia.com/info/great8/ (date last accessed, 10 March 2021).

Beckvar N (1981) Cultivation, spawning, and growth of the giant clams Tridacna gigas, T. derasa, and T. squamosa in Palau, Caroline Islands. Aquaculture 24: 21–30.

Belda-Bailie CA, Sison M, Silvestre V, Villamor K, Monje V, Gomez ED, Bailie BK (1999) Evidence for changing symbiotic algae in juvenile tridacnids. J Exp Mar Biol Ecol 241: 207–221.

Bell J, Johnson J, Ganachaud A, Gehrke P, Hobday J, Hoegh-Guldberg O, Le Borgne R, Lehodey P, Lough J, Pickering T et al. (2011) Vulnerability of tropical pacific fisheries and aquaculture to climate change: Summary for Pacific Island countries and territories. Secretariat of the Paciﬁc Community, Noumea, New Caledonia, p. 386.

Bennie JAH, Williams ST (1996) Limitations in genetic variation of hatchery produced batches of giant clam, Tridacna gigas. Aquaculture 139: 225–241.

Bildberg E, Elfwing T, Plantman P, Tedengren M (2000) Water temperature influences on physiological behaviour in three species of giant clams (Tridacnidae). In M.K. Moosa et al. (eds) Proceedings of the 9th International Coral Reef Symposium, Bali, Indonesia, 23–27 October 2000. Jakarta: Indonesian Institute of Sciences, Jakarta: Ministry of Environment, Honolulu, Hawaii: International Society for Reef Studies, 561–565.

Booth DJ, Beretta GA, Brown L, Figueira WF (2018) Predicting success of range-expanding coral reef fish in temperate habitats using temperature-abundance relationships. Front Mar Sci 5: 31.

Brahmi C, Chapron L, Le Moullac G, Soyez C, Beliaeff B, Lazareth CE, Gaertner-Mazouni N, Vidal-Dupiol J (2019) Effects of temperature and pCO2 on the respiration, biomineralization and photosynthesis of the giant clam Tridacna maxima. bioRxiv preprint: https://doi.org/10.1101/672907.

Braley RD, Sutton D, Mingoa SSM, Southgate PC (1992) Passive greenhouse heating, recirculation, and nutrient addition for nursery phase Tridacna gigas - growth boost during winter months. Aquaculture 108: 29–50.

Breitbart D, Levin LA, Oschlies A, Gregoire M, Chavez FP, Conley DJ, Gordon V, Gilbert D, Gutierrez D, Isensee K et al. (2018) Declining oxygen in the global ocean and coastal waters. Science 359: eaam7240.

Bureau of Meteorology (2020) 2020 Marine heatwave on the Great Barrier Reef. Australian Government, p. 4.

Buck BH, Rosenthal H, Saint-Paul U (2002) Effect of increased irradiance and thermal stress on the symbiosis of Symbiodinium microadriaticum and Tridacna gigas. Aquat Living Resour 15: 107–117.

Chew SF, Koh CZY, Hiong KC, Choo CYL, Wong WP, Neo ML, Ip YK (2019) Light-enhanced expression of carbonic anhydrase 4-like supports
shell formation in the fluted giant clam *Tridacna squamosa*. Gene 683: 101–112.

Collins M, Knutti R, Arbaster J, Dufresne J-L, Fichefet T, Friedlingstein P, Gao X, Gutowski WJ, Johns T, Kninner G et al. (2013) Long-term Climate Change: Projections, Commitments and Irreversibility. In TF Stocker, D Qin, G-K Plattner, M Tignor, SK Allen, J Boschung, A Nauels, Y Xia, V Bex, PM Migeod, eds, *Climate Change 2013: The Physical Science Basis*. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.

DeBoer TS, Baker AC, Erdmann MV, Ambaryanto JPR, Barber PH (2012) Patterns of *Symbiodinium* distribution in three giant clam species across the biodiverse Bird’s Head region of Indonesia. *Mar Ecol Prog Ser* 444: 117–132.

Dehau B, Nguyen M, Vadlamudi A, Blumstein DT (2019) Giant clams discriminate threats along a risk gradient and display varying habituation rates to different stimuli. *Ethology* 125: 392–398.

Deloiti (2017) At what price? The economic, social and icon value of the Great Barrier Reef. Deloitte Access Economics, Deloitte Touche Tohmatsu, p. 92.

Duarte CM, Agusti S, Barbier E, Britten GL, Castilla JC, Gattuso JP, Fulweiler RW, Hughes TP, Knowlton N, Lovelock CE et al. (2020) Rebuilding marine life. *Nature* 580: 39–51.

Dubousquet V, Gros E, Bertaux-Lecellier V, Viguier B, Raharivelomanana P, Bertrand C, Lecellier GJ (2016) Changes in fatty acid composition in the giant clam *Tridacna maxima* in response to thermal stress. *Biol Open* 5: 1400–1407.

Durack PJ, Wijffels SE, Matear RJ (2012) Ocean salinities reveal strong global water cycle intensification during 1950 to 2000. *Science* 336: 455–458.

Eckman W, Vicentuan-Cabaitan K, Todd PA (2014) Observations on the hyposalinity tolerance of fluted giant clam (*Tridacna squamosa*, Lamarck 1819) larvae. *Nat Singapore* 7: 111–116.

Eckman W, Vicentuan K, Todd PA (2019) Effects of low light and high temperature on pediveligers of the fluted giant clam *Tridacna squamosa*. *Mar Freshw Behav Physiol* 52: 255–264.

Elfwing T, Plantman P, Tedengren M, Wijndrath E (2001) Responses to temperature, heavy metal and sediment stress by the giant clam *Tridacna squamosa*. *Mar Freshw Behav Physiol* 34: 239–248.

Elfwing T, Bildberg E, Sison M, Tedengren M (2003) A comparison between sites of growth, physiological performance and stress responses in transplanted *Tridacna gigas*. *Aquaculture* 219: 815–828.

Enricuso OB, Conaco C, Sayco SLG, Neo ML, Cabaitan PC (2019) Elevated seawater temperatures affect embryonic and larval development in the giant clam *Tridacna gigas* (Cardiidae: Tridacninae). *J Mollus Stud* 85: 66–72.

Estes JA, Heithaus M, McCauley DJ, Rasher DB, Worm B (2016) Megafaunal impacts on structure and function of ocean ecosystems. *Annu Rev Environ Resour* 41: 83–116.

Fisher CR, Fitz WK, Trench RK (1985) Photosynthesis and respiration in the giant clam *Tridacna gigas* as a function of irradiance and size. *Biol Bull* 169: 230–245.

Fitt WK (1985) Effect of different strains of the zooxanthella *Symbiodinium microadriaticum* on growth and survival of their Coelenterate and Molluscan hosts. In C Gabrie, M Harmelin, eds, *Proceedings of the 5th International Coral Reef Congress*, Tahiti, 27 May–1 June 1985. Volume 6: Miscellaneous Paper (B), pp. 131–136.

Fitt WK, Trench RK (1981) Spawning, development, and acquisition of zooxanthellae by *Tridacna squamosa* (Mollusca, Bivalvia). *Biol Bull* 161: 213–235.

Gomez ED, Mingoa-Licuanan SS (2006) Achievements and lessons learned in restocking giant clams in the Philippines. *Fish Res* 80: 46–52.

Gomez ED (2015) Rehabilitation of biological resources: coral reefs and giant clam populations need to be enhanced for a sustainable marginal sea in the Western Pacific. *J Int Wildl Law Policy* 18: 120–127.

Guibert I, Lecellier G, Torda G, Pochon X, Bertaux-Lecellier V (2020) Metabarcoding reveals distinct microbiotypes in the giant clam *Tridacna maxima*. *Microbiome* 8: 57.

Gwyther J, Munro JL (1981) Spawning induction and rearing of larvae of Tridacnid clams (Bivalvia: Tridacnidae). *Aquaculture* 24: 197–217.

Hawkins AJ, Klumpp DW (1995) Nutrition of the giant clam *Tridacna gigas* (L.). II. Relative contributions of filter-feeding and the ammonium-nitrogen acquired and recycled by symbiotic alga towards total nitrogen requirements for tissue growth and metabolism. *J Exp Mar Biol Ecol* 190: 263–290.

Heslinga GA, Perron FE, Orak O (1984) Mass culture of giant clams (F. Tridacnidae) in Palau. *Aquaculture* 39: 197–215.

Hughes TP, Kerry JT, Alvarez-Noriega M, Alvarez-Romero JG, Anderson KD, Baird AH, Babcock RC, Beger M, Bellwood DR, Berkelmans R et al. (2017) Global warming and recurrent mass bleaching of corals. *Nature* 543: 373–377.

Hughes TP, Kerry JT, Baird AH, Connolly SR, Dietzel A, Eakin CM, Heron SF, Hoey AS, Hoogenboom MO, Liu G et al. (2018) Global warming transforms coral reef assemblages. *Nature* 556: 492–496.

Ikeda S, Yamashita H, Kondo S, Inoue K, Morishima S, Koike K (2017) Zooxanthellal genetic varieties in giant clams are partially determined by species-intrinsic and growth-related characteristics. *PLoS One* 12: e0172285.

Ip YK, Koh CZY, Hiong KC, Choo CYL, Boo MV, Wong WP, Neo ML, Chew SF (2017) Carbonic anhydrase 2-like in the giant clam, *Tridacna squamosa*: characterization, localization, response to light, and possible role in the transport of inorganic carbon from the host to its symbionts. *Physiol Rep* 5: e13494.

IPBES (2019) In S Diaz, J Settele, ES Brondizio E, S., HT N., M. Guiéze, J Agard, A Arneth, P Balvanera, KA Brauman, SHM Butchart et al., eds, *Summary for policymakers of the global assessment report on...*
biodiversity and ecosystem services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services. IPBES Secretariat, Bonn, Germany, p. 56.

Jantzen C, Wild C, El-Zibdah M, Roa-Quiaoit HA, Haacke C, Richter C (2008) Photosynthetic performance of giant clams, Tridacna maxima and T. squamosa, Red Sea. Mar Biol 155: 211–221.

Jiang L-Q, Feely RA, Carter BR, Gledhill DK, Arzayus KM (2015) Climatological distribution of aragonite saturation state in the global oceans. Global Biogeochem Cycles 29: 1656–1673.

Kinj J, Teitelbaum A (2010) Proceedings of the Regional Workshop on the Management of Sustainable Fisheries for Giant Clams (Tridacnidae) and CITES Capacity Building (4–7 August 2009, Nadi, Fiji). Secretariat of the Pacific Community, Noumea, New Caledonia, p. 52.

Klumpp DW, Bayne BL, Hawkins AJ (1992) Nutrition of the giant clam Tridacna gigas (L.). I. Contribution of filter feeding and photosynthesates to respiration and growth. J Exp Mar Biol Ecol 155: 105–122.

Klumpp DW, Griffiths CL (1994) Contributions of phototrophic and heterotrophic nutrition to the metabolic and growth requirements of four species of giant clam (Tridacnidae). Mar Ecol Prog Ser 115: 103–115.

Klumpp DW, Lucas JS (1994) Nutritional ecology of the giant clams Tridacna tevoroa and T. derasa from Tonga: influence of light on filter-feeding and photosynthesis. Mar Ecol Prog Ser 107: 147–156.

Kurihara T, Yamashita H, Yamada H, Inoue K, Iwai K, Koike K (2012) Probability of symbiosis establishment by giant clams with fresh and cultured Symbiodinium isolated from various host animals. J Shellfish Res 31: 977–987.

Kurihara H, Shikota T (2018) Impact of increased seawater pCO2 on the host and symbiotic algae of juvenile giant clam Tridacna crocea. Galaxea 20: 19–28.

Lambers JHR (2015) Extinction risks from climate change. Science 348: 501–502.

Lim SSQ, Huang D, Soong K, Neo ML (2019) Diversity of endosymbiotic Symbiodiniaceae in giant clams at Dongsha Atoll, northern South China Sea. Symbiosis 78: 251–262.

Lucas JS (1988) Giant Clams: Description, Distribution, and Life History. In JW Copland, JS Lucas, eds, Giant Clams in Asia and the Pacific. ACIAR Monograph No. 9, pp. 21–32.

Lucas JS (1994) The biology, exploitation, and mariculture of giant clams (Tridacnidae). Rev Fish Sci 2: 181–223.

Lyons Y, Cheong D, Neo ML, Wong HF (2018) Managing giant clams in the South China Sea. Int J Mar Coastal Law 33: 467–494.

Maboloc EA, Mingo-Licuanan SS, Villanueva RD (2014) Effects of reduced salinity on the heterotrophic feeding of the juvenile giant clam Tridacna gigas. J Shellfish Res 33: 373–379.

Maboloc EA, Puzon JIM, Villanueva RD (2015) Stress responses of zooxanthellae in juvenile Tridacna gigas (Bivalvia, Cardiidae) exposed to reduced salinity. Hydrobiologia 762: 103–112.

Maboloc EA, Villanueva RD (2017) Effects of salinity variations on the rates of photosynthesis and respiration of the juvenile giant clam (Tridacna gigas, Bivalvia, Cardiidae). Mar Freshw Behav Physiol 50: 273–284.

Mangum CP, Johansen K (1982) The influence of symbiotic dinoflagellates on respiratory processes in the giant clam Tridacna squamosa. Pac Sci 36: 395–401.

Manriquez PH, Jara ME, Mardones ML, Navarro JM, Torres R, Lardies MA, Vargas CA, Duarte C, Widiccombe S, Salisbury J et al. (2013) Ocean acidification disrupts prey responses to predator cues but not net prey shell growth in Concholepas concholepas (Iloco). PLoS One 8: e68643.

McClanahan TR, Darling ES, Maina JM, Muthiga NA, D’Agata S, Jupiter SD, Arthur R, Wilson SK, Mangubhai S, Nand Y et al. (2019) Temperature patterns and mechanisms influencing coral bleaching during the 2016 El Niño. Nat Clim Change 9: 845–851.

Mies M, Dor P, Gütz AZ, Sumida PYG (2017) Production in giant clam aquaculture: trends and challenges. Rev Fish Sci Aquac 25: 286–296.

Moir BG (1990) Comparative-studies of fresh and aged Tridacna gigas shell - preliminary investigations of a reported technique for pre-treatment of tool material. J Archaeol Sci 17: 329–345.

Moleon M, Sanchez-Zapata JA, Donazar JA, Revilla E, Martin-Lopez B, Gutierrez-Canovas C, Getz WM, Morales-Reyes Z, Campos-Arceiz A, Crowder LB et al. (2020) Rethinking megafauna. Proc R Soc B Biol Sci 287: 20192643.

Moorhead A (2018) Giant clam aquaculture in the Pacific region: perceptions of value and impact. Dev Pract 28: 624–635.

Munday PL (2014) Transgenerational acclimation of fishes to climate change and ocean acidification. F1000Prime Reports 6: 99.

Neo ML, Todd PA (2011) Predator-induced changes in fluted giant clam (Tridacna squamosa) shell morphology. J Exp Mar Biol Ecol 397: 21–26.

Neo ML, Todd PA (2012) Giant clams (Mollusca: Bivalvia: Tridacnidae) in Singapore: history, research and conservation. Raffles B Zool 25: 67–78.

Neo ML, Todd PA, Tee SL-M, Chou LM (2013) The effects of diet, temperature and salinity on survival of larvae of the fluted giant clam, Tridacna squamosa. J Conchol 41: 369–376.

Neo ML, Eckman W, Vicentuan K, Tee SL-M, Todd PA (2015) The ecological significance of giant clams in coral reef ecosystems. Biol Conserv 181: 111–123.

Neo ML, Wabnitz CCC, Braley RD, Heslinga GA, Fauvelot C, Van Wysberghe S, Andréfouët S, Waters C, Tan AS-H, Gomez ED, et al. (2017) Chapter 4. Giant clams (Bivalvia: Cardiidae: Tridacnidae): A comprehensive update of species and their distribution, current threats and conservation status. In Hawkins SJ, Evans AJ, Dale AC, Firth LB, Hughes DJ, Smith IP, eds, Oceanography and Marine Biology: An Annual Review, Vol. 55. CRC Press, Boca Raton, FL, pp. 87–388.

Neo ML (2020) Conservation of Giant Clams (Bivalvia: Cardiidae). In MI Goldstein, DS DA, eds, Encyclopedia of the World’s Biomes Vol 4. Elsevier, pp. 527–538.
Norton JH, Shepherd MA, Long HM, Pitt WK (1992) The zooxanthellal tubular system in the giant clam. Biol Bull 183: 503–506.

O’Malley MP, Lee-Brooks K, Medd HB (2013) The global economic impact of manta ray watching tourism. PLoS One 8: e65051.

Panggabean M, Hutagalung R, Ayu E (2009) Effect of salinity and growth medium on Symbiodinium sp. isolated from giant clam. Mar Res Indonesia 34: 87–89.

Pappas MK, He S, Hardenstine RS, Kanee H, Berumen ML (2017) Genetic diversity of giant clams (Tridacna spp.) and their associated Symbiodinium in the Central Red Sea. Mar Biodivers 47: 1209–1222.

Pecl GT, Araujo MB, Bell JD, Blanchard J, Bonebrake TC, Chen IC, Clark TD, Colwell RK, Danielsen F, Evengard B et al. (2017) Biodiversity redistribution under climate change impact: on ecosystems and human well-being. Science 355: 1389.

Pimiento C, Leprieur F, Silvestro D, Lefcheck JS, Albouy C, Rasher DB, thinusIsland, WesternIndianOcean:implicationsforconservationand

Ramah S, Taleb-Hossenkhan N, Todd PA, Neo ML, Ranjeet B (2019) Drastic decline in giant clams (Bivalvia: Tridacninae) around Mauritius Island, Western Indian Ocean: implications for conservation and management. Mar Biodivers 49: 815–823.

Requilme JNC, Conaco C, Sayco SLG, Roa-Quiaioit HA, Cabaitan PC (2021) Using citizen science and survey data to determine the recruitment envelope of the giant clam, Tridacna gigas (Cardiidae: Tridacninae). Ocean Coast Manag 202: 105515.

Roa-Quiaioit HAF (2005) The ecology and culture of giant clams (Tridacnidae) in the Jordanian sector of the Gulf of Aqaba, Red Sea. PhD thesis, Bremen University.

Roberts RG, Flannery TF, Ayliffe LK, Yoshida H, Olley JM, Prideaux GJ, Laslett GM, Baynes A, Smith MA, Jones R et al. (2001) New ages for the last Australian megafauna: continent-wide extinction about 46,000 years ago. Science 292: 1888–1892.

Rosewater J (1965) The family Tridacnidae in the Indo-Pacific. Indo-Pacific Mollusca 1: 347–396.

Rossbach S, Saderne V, Anton A, Duarte CM (2019a) Light-dependent calcification in Red Sea giant clam Tridacna maxima. Biogeosciences 16: 2635–2650.

Rossbach S, Cardenas A, Perna G, Duarte CM, Voolstra C (2019b) Tissue-specific microbiomes of the Red Sea giant clam Tridacna maxima highlight differential abundance of Endozoicomonadaceae. Front Microbiol 10: 2661.

Rossbach S, Overmans S, Kaidarova A, Kosel J, Agusti S, Duarte CM (2020) Giant clams in shallow reefs: UV-resistance mechanisms of Tridacninae in the Red Sea. Coral Reefs 39: 1345–1360.

Rossbach S, Anton A, Duarte CM (2021) Drivers of the abundance of Tridacna spp. Giant clams in the red sea. Front Mar Sci 7: 592852.

Roxy MK, Dasgupta P, McPhaden MJ, Suematsu T, Zhang CD, Kim D (2019) Twofold expansion of the Indo-Pacific warm pool warps the MJO life cycle. Nature 575: 647–651.

Sampaio E, Santos C, Rosa IC, Ferreira V, Portner HO, Duarte CM, Levin LA, Rosa R (2021) Impacts of hypoxic events surpass those of future ocean warming and acidification. Nat Ecol Evol 5: 311–321.

Sayco SLG, Conaco C, Neo ML, Cabaitan PC (2019) Reduced salinities negatively impact fertilization success and early larval development of the giant clam Tridacna gigas (Cardiidae: Tridacninae). J Exp Mar Biol Ecol 516: 35–43.

Spady BL, Watson S-A, Chase TJ, Munday PL (2014) Projected near-future CO2 levels increase activity and alter defensive behaviours in the tropical squid Idiosepius pygmaeus. Biology Open 3: 1063–1070.

Spady BL, Munday PL, Watson S-A (2018) Predatory strategies and behaviours in cephalopods are altered by elevated CO2. Glob Chang Biol 24: 2585–2596.

Soo P, Todd PA (2014) The behaviour of giant clams (Bivalvia: Cardiidae: Tridacninae). Mar Biol 161: 2699–2717.

Sutherland WJ, Atkinson PW, Broad S, Brown S, Clout M, Dias MP, Dicks LV, Doran H, Fleshman E, Garratt EL et al. (2021) A 2021 horizon scan of emerging global biological conservation issues. Trends Ecol Evol 36: 87–97.

Syvitski JPM, Vorosmarty CJ, Kettner AJ, Green P (2005) Impact of humans on the flux of terrestrial sediment to the global coastal ocean. Science 308: 376–380.

Tan EYW, Quek RZB, Neo ML, Fauvelot C, Huang D (2021) Genome skimming resolves the giant clam (Bivalvia: Cardiidae: Tridacninae) tree of life. Coral Reefs (online version).

Tanzil JTI, Ng PKA, Tey YQ, Tan HYB, Tun YE, Huang D (2016) A preliminary characterisation of Symbiodinium diversity in some common corals from Singapore. COSMOS 12: 15–27.

Teitelbaum A, Friedman K (2008) Successes and failures in reintroducing giant clams in the Indo-Pacific region. SPC Trochus Info Bull 14: 19–26.

Thomas JT, Munday PL, Watson S-A (2020) Toward a mechanistic understanding of marine invertebrate behavior at elevated CO2. Front Mar Sci 7: 345.

Thomas JT, Spady BL, Munday PL, Watson S-A (2021) The role of ligand-gated chloride channels in behavioural alterations at elevated CO2 in a cephalopod. J Exp Biol 224: jeb242335.

Torda G, Donelson JM, Aranda M, Barshis DJ, Bay L, Berumen M, Bourne D, Cantin N, Foret S, Matz M et al. (2017) Rapid adaptive responses to climate change in corals. Nat Clim Change 7: 627–636.

Umeki M, Yamashita H, Suzuki G, Sato T, Ohara S, Koike K (2020) Fecal pellets of giant clams as a route for transporting Symbiodiniaceae to corals. PLoS One 15: e0243087.

Ungvari Z, Csiszar A, Sosnowska D, Philipp EE, Campbell CM, McQuary PR, Chow TT, Coelho M, Didier ES, Gelino S et al. (2013) Testing predictions of the oxidative stress hypothesis of aging using a novel invertebrate model of longevity: the giant clam (Tridacna derasa). J Gerontol A Biol Sci Med Sci 68: 359–367.
van Hooidonk R, Maynard JA, Manzello D, Planes S (2014) Opposite latitudinal gradients in projected ocean acidification and bleaching impacts on coral reefs. *Glob Chang Biol* 20: 103–112.

Van Wynsberge S, Andréfouët S (2017) The future of giant clam-dominated lagoon ecosystems facing climate change. *Curr Clim Change Rep* 3: 261–270.

Van Wynsberge S, Andréfouët S, Gaertner-Mazouni N, Remoissenet G (2018) Consequences of an uncertain mass mortality regime triggered by climate variability on giant clam population management in the Pacific Ocean. *Theor Popul Biol* 119: 37–47.

Venn AA, Loram JE, Douglas AE (2008) Photosynthetic symbioses in animals. *J Exp Bot* 59: 1069–1080.

Watson S-A (2015) Giant clams and rising CO2: light may ameliorate effects of ocean acidification on a solar-powered animal. *PLoS One* 10: e0128405.

Watson S-A, Southgate PC, Miller GM, Moorhead JA, Knauer J (2012a) Ocean acidification and warming reduce juvenile survival of the fluted giant clam, *Tridacna squamosa*. *Molluscan Res* 32: 177–180.

Watson S-A, Peck LS, Tyler PA, Southgate PC, Tan KS, Day RW, Morley SA (2012b) Marine invertebrate skeleton size varies with latitude, temperature and carbonate saturation: implications for global change and ocean acidification. *Glob Chang Biol* 18: 3026–3038.

Watson S-A, Lefevre S, McCormick MI, Domenici P, Nilsson GE, Munday PL (2014) Marine mollusc predator-escape behaviour altered by near-future carbon dioxide levels. *Proc Royal Soc B* 281: 20132377.

Watson S-A, Fields JB, Munday PL (2017a) Ocean acidification alters predator behaviour and reduces predation rate. *Biol Lett* 13: 20160797.

Watson S-A, Morley SA, Peck LS (2017b) Latitudinal trends in shell production cost from the tropics to the poles. *Sci Adv* 3: e1701362.

Wells S (1997) *Giant Clams: Status, Trade and Mariculture, and the Roles of CITES Management*. IUCN, Gland, Switzerland and Cambridge, UK

Wells SM, Pyle RM, Collins NM (1983) The *IUCN Invertebrate Red Data Book*. IUCN, Gland, Switzerland and Cambridge, UK

Wolfe K, Anthony K, Babcock RC, Bay L, Bourne D, Burrows D, Byrne M, Deaker D, Diaz-Pulido G, Frade PR et al. (2020) Priority species to support the functional integrity of coral reefs. *Oceanogr Mar Biol Annu Rev* 58: 179–318.

Yamaguchi M (1977) Conservation and cultivation of giant clams in the tropical Pacific. *Biol Conserv* 11: 13–20.

Yamano H, Sugihara K, Nomura K (2011) Rapid poleward range expansion of tropical reef corals in response to rising sea surface temperatures. *Geophys Res Lett* 38: L04601.

Yamashita H, Minami Y, Kondo S, Inoue K, Koike K (2021) Symbiodiniacean cell supply method for improvement in survival of *Tridacna squamosa* seeds. *Nippon Suisan Gakkaishi* 87: 123–131.

Zhang Y, Zhou Z, Qin Y, Li X, Ma H, Wei J, Zhou Y, Xiao S, Xiang Z, Noor Z et al. (2020) Phenotypic traits of two boring giant clam (*Tridacna crocea*) populations and their reciprocal hybrids in the South China Sea. *Aquaculture* 519: 734890.

Zhou Z, Liu Z, Wang L, Luo J, Li H (2019) Oxidative stress, apoptosis activation and symbiosis disruption in giant clam *Tridacna crocea* under high temperature. *Fish Shellfish Immun* 84: 451–457.