Molluscan Research 32(3): 177–180
http://www.mapress.com/mr/

ISSN 1323-5818
Magnolia Press

Ocean acidification and warming reduce juvenile survival of the fluted giant clam, *Tridacna squamosa*

SUE-ANN WATSON*[1], PAUL C. SOUTHGATE[2], GABRIELLE M. MILLER[1], JONATHAN A. MOORHEAD[2] & JENS KNAUER[3]
[1] ARC Centre of Excellence for Coral Reef Studies & School of Marine and Tropical Biology, James Cook University, Townsville, QLD, 4811, Australia
[2] Centre for Sustainable Tropical Fisheries and Aquaculture, School of Marine & Tropical Biology, James Cook University, Townsville, QLD, 4811, Australia
[3] Darwin Aquaculture Centre, Department of Resources, GPO Box 3000, Darwin, NT, 0801, Australia
*email: sueann.watson@my.jcu.edu.au

Abstract

Anthropogenic carbon dioxide (CO_2) emissions are causing ocean acidification and ocean warming; however, the synergistic effects of these stressors on giant clams are completely unknown. Juveniles of the fluted giant clam, *Tridacna squamosa* Lamarck, 1819, were exposed to present-day control seawater (416 µatm pCO_2) and seawater treated with CO_2 to simulate ocean conditions predicted for the next 50–100 years (622 µatm pCO_2 and 1019 µatm pCO_2). These CO_2 treatments were cross-factored with seawater temperatures of ~28.5 °C, ~30.0 °C and ~31.5 °C. The majority of mortality occurred between 40 and 60 days. Survival of juveniles decreased with increasing pCO_2 and decreased with increasing seawater temperature. The combination of the highest pCO_2 and both the moderate and highest seawater temperatures resulted in the lowest survival of <20 % indicating survival of *T. squamosa* could be reduced considerably at ocean conditions predicted to occur around the end of this century.

Additional keywords: climate change, carbon dioxide, high-CO_2, temperature, ecology, Cardiidae, Tridacninae, mollusc, bivalve, Bivalvia

Introduction

Anthropogenic emissions are increasing the concentration of carbon dioxide (CO_2) in the atmosphere resulting in global climate change. The oceans have absorbed *c*. 40 % of anthropogenic CO_2 emissions (Zeebe *et al*. 2008) and this has resulted in a 0.1 unit drop in the pH of the surface oceans (Caldeira and Wickett 2003); equivalent to a 30 % increase in acidity (Blackford and Gilbert 2007). This process, termed ocean acidification, has been shown to reduce survival (Watson *et al*. 2009), growth (Talmage and Gobler 2010) and metabolic rate (Michaelidis *et al*. 2005) of marine molluscs. The additive stressors of ocean acidification and global climate change are expected to be particularly problematic for marine life. Acidification and elevated temperatures have been shown to reduce fertilisation and development (Parker *et al*. 2009), and growth and survival (Talmage and Gobler 2011) in marine molluscs. Tropical Pacific aquaculture species, including giant clams, are considered vulnerable to climate change; however, little is known about the effects of global change stressors on many of these species (Pickering *et al*. 2011). The effects of ocean acidification and global warming on giant clams have never been tested and this knowledge gap limits the capacity to mitigate the impacts of global change on these species.

Giant clams (Cardiidae, Tridacninae) are the largest living bivalves (Rosewater 1965) and throughout life arguably have the largest exoskeleton to calcify of all marine animals. Icons of the coral reef, giant clams have suffered from harvesting for food, shell collecting and the marine ornamental trade. Consequently, four tridacnines (*Tridacna derasa* (Röding, 1798), *T. gigas* (Linnaeus, 1758), *T. rosewateri* Sirenho & Scarlato, 1991 and *T. tevoroa* Lucas, Ledua & Braley, 1990) are listed as vulnerable on the IUCN Red List of Threatened Species (Wells, 1996). This short study was designed to measure the potentially synergistic effects of increased temperature and carbon dioxide on the survival of juveniles of the fluted giant clam, *Tridacna squamosa* Lamarck, 1819.

Materials and methods

This study was conducted at James Cook University's Marine and Aquaculture Research Facility Unit. All methods and seawater parameters follow Miller *et al*. (2012). Briefly, for the elevated-CO_2 treatments, seawater was treated in 3000 l sumps with 100 % CO_2 using a pH computer (Aquamedic AT-Control, Germany). Seawater was heated with in-line heaters before delivery to individual aquaria.

Juveniles of the fluted giant clam, *Tridacna squamosa*, were spawned from wild caught parents (3 males and 1 female) and reared at the Darwin Aquaculture Centre. Juveniles were 14 months old at the start of the experiment (mean anterior-posterior measurement 28.23 ± 0.37 mm and wet weight 1.73 ± 0.05 g (±1 s.e.)) and were randomly assigned to nine different seawater treatment conditions in a 3x3 cross-factored CO_2 by temperature experimental grid design to determine the synergistic effects of elevated CO_2 and temperature on survival. Seawater treatments consisted of three different mean partial pressures of carbon dioxide (pCO_2): (1) present-day control pCO_2 416 ± 6 µatm; (2) moderate pCO_2 622 ± 8 µatm; and (3) high pCO_2 1019 ± 15 µatm (±1 s.e.) consistent with predictions of CO_2 in the atmosphere and ocean over the next 50–100 years (Meehl *et al*. 2007; Doney *et al*. 2009; Meinshausen *et al*. 2011). CO_2 treatments were cross-factored with three seawater temperatures: (1) T1 control ~28.5 °C; (2) T2 ~30.0 °C (+1.5 °C above control); and (3) T3 ~31.5 °C (+3.0 °C above control) consistent with predictions of ocean warming for the tropical Pacific (Poloczanska *et al*. 2007; Ganachaud *et al*. 2011).

Juvenile giant clams were kept in seven or eight 40 l replicate tanks for each treatment, with two to three individuals randomly assigned to each tank. A total of 16 juveniles were used in each of the nine treatments. Tanks were situated under tri-phosphor T8 linear fluorescent lights on a 13L:11D photoperiod. Photosynthetically active radiation (PAR) was measured with a LI-COR LI-250A light meter and LI-COR LI-192SA Underwater Quantum Sensor meter; mean PAR was 65.1 ± 3.5 μmol photons/m^2/second (±1 s.e.). Individuals were gradually adjusted to their treatment conditions via a drip feed that brought tanks to their required CO_2 and temperature over a 6 hour period. Seawater parameters are shown in Table 1.

TABLE 1. Seawater parameters for each of the nine treatment groups. Values reported are means (± 1 s.e.). Mean values across all pCO_2 treatments were 416 ± 6 µatm, 622 ± 8 µatm and 1019 ± 15 µatm and across all temperature treatments were 28.5 ± 0.0 °C, 29.9 ± 0.0 °C and 31.4 ± 0.0 °C.

Treatment	Temperature (°C)	Number of replicate tanks	pH_{NBS}	Total alkalinity (µmol kg^{-1} SW)	Salinity	pCO_2 (µatm)
Control pCO_2 and T1	28.4 (±0.0)	8	8.15 (±0.01)	2045 (±13)	32.5 (±0.2)	407.9 (±9.4)
Control pCO_2 and T2	29.8 (±0.0)	8	8.15 (±0.01)	2018 (±7)	32.5 (±0.2)	404.6 (±10.6)
Control pCO_2 and T3	31.2 (±0.0)	8	8.13 (±0.01)	2026 (±7)	32.5 (±0.2)	435.7 (±10.8)
Moderate pCO_2 and T1	28.5 (±0.0)	8	8.01 (±0.01)	2103 (±8)	33.0 (±0.1)	613.5 (±11.7)
Moderate pCO_2 and T2	30.1 (±0.0)	7	8.00 (±0.01)	2102 (±8)	33.0 (±0.1)	636.1 (±13.1)
Moderate pCO_2 and T3	31.5 (±0.0)	8	8.01 (±0.01)	2096 (±7)	33.0 (±0.1)	615.0 (±14.6)
High pCO_2 and T1	28.5 (±0.0)	8	7.84 (±0.01)	2171 (±7)	33.1 (±0.1)	981.1 (±24.0)
High pCO_2 and T2	29.9 (±0.0)	7	7.83 (±0.01)	2173 (±7)	33.1 (±0.1)	1014.1 (±26.5)
High pCO_2 and T3	31.5 (±0.0)	8	7.82 (±0.01)	2172 (±7)	33.1 (±0.1)	1061.1 (±28.0)

Results

Mortality varied over time during the experiment. From 0 to 20 days, survival remained high across all treatments (Figure 1). At day 40, survival in the control-CO_2 was 93–100 % compared to 80–93 % in the elevated-CO_2 treatments. The most rapid decline in survival occurred between day 40 and 60. During these 20 days, 50–100 % of all mortality occurred. Survival declined with increasing pCO_2 and temperature across all treatments with the exception of the combination of control pCO_2 at T3, which had greater survival than control pCO_2 at T2.

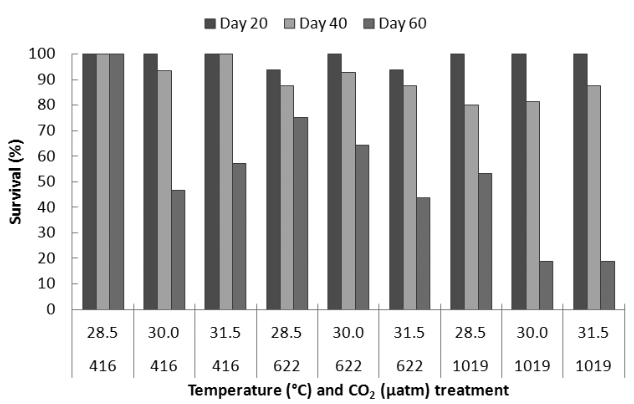

FIGURE 1. Survival of giant clam, *Tridacna squamosa*, juveniles when held under conditions of elevated CO_2 and temperature for 20, 40 and 60 days. Nominal temperatures of 28.5, 30.0 and 31.5 °C relate to the temperature treatments T1, T2 and T3, respectively.

After 60 days, survival in the control temperature and control pCO_2 group remained at 100 %; however, survival was reduced by elevated temperature to 47 % and 57 % at T2 and T3, respectively. At moderate- and high-pCO_2 conditions of 622 µatm and 1019 µatm, survival was reduced to 75 % and 53 %, respectively, at T1. The lowest survival of 19 % was recorded in the high-CO_2 treatment at T2 and T3.

Discussion

This study showed that increased ocean CO_2 and temperature are likely to reduce the survival of *Tridacna squamosa*. After two months in experimental conditions, all individuals within the control pCO_2 and temperature group survived, indicating that the causes of reduced survival were indicative of either elevated pCO_2 or temperature, or a combination of both. Particularly low survival (<20 %) occurred in the highest pCO_2 treatment at both the elevated temperatures of +1.5 °C and +3.0 °C. This indicates that juvenile *T. squamosa* may be particularly susceptible to the higher CO_2 levels predicted for the end of the century, and possibly more susceptible to relevant CO_2 increases than temperature increases.

Since more than 50 % of mortality occurred between days 40 and 60 across all treatments, a possible physiological tolerance threshold may be exceeded beyond 40 days in these elevated CO_2 and temperature conditions. As yet, we do not know the physiological processes or mechanisms behind the reduced survival observed or the effects on different life stages of *T. squamosa* or related species. Reductions in growth (Shirayama and Thornton 2005), fertilisation (Havenhand *et al*. 2008) and calcification (Langdon *et al*. 2003; Kleypas *et al*. 2006; Gazeau *et al*. 2007) have all been demonstrated in calcareous marine invertebrates. Research by Toonen *et al*. (2012) suggests that *T. squamosa* has a lower growth rate when kept in conditions of 700 to 1400 µatm pCO_2 and higher inorganic nutrients than compared to growth rates reported in the literature. Metabolic rate, photosynthesis and interactions with symbiotic zooxanthellae, shell growth, calcification and other physiological and ecological processes are likely to affect survival, growth and fitness in giant clams and these issues will be addressed in further studies in this laboratory.

Within closely related species, over evolutionary time there is considerable capacity to adapt total shell size and shape to environments where the saturation state of seawater with respect to calcium carbonate polymorphs, such as calcite or aragonite, is lower and where calcification is thus expected to be more costly (Watson *et al*. 2012). This suggests that if we can slow the rate of change in our oceans, species may be able to adapt gradually to changing conditions. However, giant clams may live for several decades or longer (Lucas, 1988) so that giant clams born into present-day oceans could live long enough to experience ocean conditions late this century. Unlike animals with shorter generation times such as many coral reef fishes, which have some capacity for transgenerational acclimation to changing ocean pCO_2 (Miller *et al*. 2012), giant clams, although highly fecund, have longer times to maturity than many coral reef fishes, and may have a reduced ability for acclimation and adaptation over the next 100 years. Thus effects of ocean acidification and climate change on *T. squamosa* and other giant clam species are a priority for further research and an important consideration in both the management of wild populations and hatchery rearing to help enhance the survival of giant clams in a changing ocean.

Acknowledgements

The authors thank Prof. Philip L. Munday for the use of laboratory equipment and aquarium space, Dr. Jennifer M. Donelson for helpful comments on analyses, the staff of the Marine and Aquaculture Research Facility Unit at James Cook University for technical assistance and two anonymous reviewers for their comments on the manuscript.

References

Blackford, J.C. & Gilbert, F.J. (2007) pH variability and CO_2 induced acidification in the North Sea. *Journal of Marine Systems* 64, 229–241.

Caldeira, K. & Wickett, M.E. (2003) Anthropogenic carbon and ocean pH. *Nature* 425, 365.

Doney, S.C., Fabry, V.J., Feely, R.A. & Kleypas, J.A. (2009) Ocean acidification: the other CO_2 problem. *Annual Review of Marine Science* 1, 169–192.

Ganachaud, A.S., Gupta, A.S., Orr, J.C., Wijffels, S.E., Ridgway, K.R., Hemer, M.A., Maes, C., Steinberg, C.R., Tribollet, A.D., Qiu, B. & Kruger, J.C. (2011) Observed and expected changes to the tropical Pacific Ocean. In: Bell, J.D., Johnson, J.E. & Hobday, A.J. (Eds.), *Vulnerability of Tropical Pacific Fisheries and Aquaculture to Climate Change*. Secretariat of the Pacific Community, Noumea, New Caledonia, pp. 101–188.

Gazeau, F., Quiblier, C., Jansen, J.M., Gattuso, J.P., Middelburg, J.J. & Heip, C.H.R. (2007) Impact of elevated CO_2 on shellfish calcification. *Geophysical Research Letters* 34: L07603, doi:07610.01029/02006GL028554.

Havenhand, J.N., Buttler, F.R., Thorndyke, M.C. & Williamson, J.E. (2008) Near-future levels of ocean acidification reduce fertilization success in a sea urchin. *Current Biology* 18: R651.

Kleypas, J.A., Feely, R.A., Fabry, C., Langdon, C., Sabine, C. & Robbins, L.L. (2006) Impacts of ocean acidification on coral reefs and other marine calcifiers: a guide for future research. A report of a workshop held 18–20 April 2005, St. Petersburg, FL, sponsored by NSF, NOAA, and the U.S. Geological Survey, 88 pp. Unpublished report.

Langdon, C., Broecker, W.S., Hammond, D.E., Glenn, E., Fitzsimmons, K., Nelson, S.G., Peng, T.H., Hajdas, I. & Bonani, G. (2003) Effect of elevated CO_2 on the community metabolism of an experimental coral reef. *Global Biogeochemical Cycles* 17, 1011, doi:1010.1029/2002GB001941.

Lucas, J.S. (1988). Giant clams: description, distribution and life history. In: Copland, J. & Lucas, J.S. (Eds.), *Giant clams in Asia and the Pacific*. ACIAR, Canberra, pp. 21–32.

Meehl, G.A., Stocker, T.F., Collins, W.D., Friedlingstein, P., Gaye, A.T., Gregory, J.M., Kitoh, A., Knutti, R., Murphy, J.M., Noda, A., Raper, S.C.B., Watterson, I.G., Weaver, A.J. & Zhao, Z.-C. (2007) Global Climate Projections. In: Solomon, S., Qin, D., Manning, M., Chen, Z., Marquis, M., Averyt, K.B., Tignor, M. & Miller, H.L. (Eds.), *Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge and New York, NY, pp. 747–845.

Meinshausen, M., Smith, S.J., Calvin, K., Daniel, J.S., Kainuma, M.L.T., Lamarque, J.-F., Matsumoto, K., Montzka, S.A., Raper, S.C.B., Riahi, K., Thomson A., Velders G.J.M. & van Vuuren, D.P.P. (2011) The RCP greenhouse gas concentrations and their extensions from 1765 to 2300. *Climatic Change* 109, 213–241. DOI 10.1007/s10584-011-0156-z.

Michaelidis, B., Ouzounis, C., Paleras, A. & Pörtner, H.O. (2005) Effects of long-term moderate hypercapnia on acid-base balance and growth rate in marine mussels *Mytilus galloprovincialis*. *Marine Ecology Progress Series* 293, 109–118.

Miller, G.M., Watson, S.-A., Donelson, J.M., McCormick, M.I. & Munday, P.L. (2012) Parental environment mediates impacts of increased carbon dioxide on a coral reef fish. *Nature Climate Change*. Online prepublication, 1–4.

Parker, L.M., Ross, P.L. & O'Connor, W.A (2009) The effect of ocean acidification and temperature on the fertilization and embryonic development of the Sydney rock oyster *Saccostrea glomerata* (Gould 1850). *Global Change Biology* 15, 2123–2136.

Pickering, T.D., Ponia, B., Hair, C.A., Southgate, P.C., Poloczanska, E.S., Patrona, L.D., Teitelbaum, A., Mohan, C.V., Phillips, M.J., Bell, J.D. & Silva, S.D. (2011) Vulnerability of aquaculture in the tropical Pacific to climate change. In: Bell, J.D., Johnson, J.E. & Hobday, A.J. (eds) *Vulnerability of Tropical Pacific Fisheries and Aquaculture to Climate Change*. Secretariat of the Pacific Community, Noumea, New Caledonia, pp. 647–732.

Poloczanska, E.S., Babcock, R.C, Butler, A., Hobday, A.J., Hoegh-Guldberg, O., Kunz, T. J., Matear, R., Milton, D.A, Okey, T.A. & Richardson, A.J. (2007) Climate change and Australian marine life. *Oceanography and Marine Biology: an Annual Review* 45, 407–478.

Rosewater, J. (1965) The Family Tridacnidae in the Indo-Pacific. *Indo-Pacific Mollusca* 1, 347–408.

Shirayama, Y. & Thornton, H. (2005) Effect of increased atmospheric CO_2 on shallow water marine benthos. *Journal of Geophysical Research* 110: C09S08, doi:10.1029/2004JC002618.

Talmage, S.C & Gobler, C.J. (2010) Effects of past, present, and future ocean carbon dioxide concentrations on the growth and survival of larval shellfish. *Proceedings of the National Academy of Sciences* 107, 17246–17251.

Talmage, S.C & Gobler, C.J. (2011) Effects of elevated temperature and carbon dioxide on the growth and survival of larvae and juveniles of three species of northwest Atlantic bivalves. *PLoS ONE*, 6, e26941.

Toonen, R.J., Nakayama, T., Ogawa, T., Rossiter, A. & Delbeek, J.C. (2012) Growth of cultured giant clams (*Tridacna* spp.) in low pH, high-nutrient seawater: species-specific effects of substrate and supplemental feeding under acidification. *Journal of the Marine Biological Association of the United Kingdom* 92, 731–740.

Watson, S.-A., Southgate, P.C., Tyler, P.A. & Peck, L.S. (2009) Early larval development of the Sydney rock oyster *Saccostrea glomerata* under near-future predictions of CO_2-driven ocean acidification. *Journal of Shellfish Research* 28, 431–437.

Watson, S.-A., Peck, L.S., Tyler, P.A., Southgate, P.C., Tan, K.S., Day, R.W. & Morley, S.A. (2012) Marine invertebrate skeleton size varies with latitude, temperature, and carbonate saturation: implications for global change and ocean acidification. *Global Change Biology* 18, 3026–3038, doi: 10.1111/j.1365-2486.2012.02755.x

Wells, S. 1996. *Tridacna* spp. In: IUCN 2012. IUCN Red List of Threatened Species. Version 2012.1. Available online at http://www.iucnredlist.org [Accessed on 05 July 2012.]

Zeebe, R.E., Zachos, J.C., Caldeira, K. & Tyrrell, T. (2008) Oceans - Carbon emissions and acidification. *Science* 321, 51–52.