Egyptian Journal of Aquatic Biology & Fisheries

Zoology Department, Faculty of Science,
Ain Shams University, Cairo, Egypt.
ISSN 1110 – 6131
Vol. 28(6): 211 – 227 (2024)
www.ejabf.journals.ekb.eg

The Role of Zooxanthellae in the Growth of the Giant Clam *Tridacna maxima* in Outdoor Aquaculture System, Red Sea, Egypt

Esraa E. AbouElmaaty[1], Asmaa H. Mohammed[2], Eslam Farg[3], Mahmoud H. Hanafy[4*]

[1]National Institute of Oceanography and Fisheries, (NIOF), Egypt
[2]Marine Sciences Department, National Authority for Remote Sensing and Space Sciences (NARSS), Cairo 11769, Egypt
[3]Agriculture Applications Department, National Authority for Remote Sensing and Space Sciences (NARSS), Cairo 11769, Egypt
[4]Marine Biology Department, Faculty of Science, Suez Canal University, Egypt

[*]Corresponding Author: asmahassan@narss.sci.eg

ARTICLE INFO

Article History:
Received: Oct. 30, 2024
Accepted: Nov. 7, 2024
Online: Nov. 9, 2024

Keywords:
Tridacna giant clams,
Growth,
Zooxanthellae,
Colors,
Red Sea

ABSTRACT

The Tridacninae subfamily of the giant clams is vital for the biological functioning of coral reefs in the Red Sea. Despite a rise in the commercial mariculture of the giant clams in developing countries, there is still limited understanding of the factors that influence the growth rate of Tridacna species. This study aimed to address this gap by investigating the factors affecting the growth rate of *Tridacna maxima* under cultured conditions, including seasonal fluctuations, temperature, mantle colors, zooxanthellae density, and light energy absorption. Our findings indicate that all these factors influence the growth patterns of this species. Monthly and seasonal growth rate fluctuations correlate directly with temperature variations. Specifically, extreme winter and summer temperatures are associated with reduced growth rates, while milder temperatures in spring and fall correspond to higher growth rates. Additionally, the mantle color suggests a potential three-way interaction between growth rate, symbiont color, and zooxanthellae density. Individuals with brown mantles exhibited higher growth rates and greater zooxanthellae density. The number of zooxanthellae varied significantly among individuals of different colors, with brown individuals having much higher concentrations compared to blue-brown and blue individuals. Understanding the complex relationships among environmental conditions, symbiotic interactions, and growth dynamics is crucial for developing effective conservation and management strategies to protect *T. maxima* populations.

INTRODUCTION

The giant clams, namely those belonging to the Tridacninae subfamily, play a crucial role in the ecological functioning of coral reefs throughout the Indo-Pacific countries and its extend in the Red Sea **(Richter *et al*., 2008; Neo *et al*., 2015, Rossbach *et al*., 2021)**. They are occurring naturally in subtropical and tropical marine water of the Indo-Pacific area. They serve as a food source for many predators and scavengers, provide refuge for commensal animals, and offer a substrate for epibionts to colonize. Additionally, they contribute to the structural integrity of reefs and act as reservoirs for *Symbiodinium*, dinoflagellate symbionts, commonly referred to as zooxanthellae **(Ramah *et al.*, 2017)**. Humans harvest them for food and ornamental uses as well **(Alcazar, 1986; Mies *et al.*, 2017)**. The giant clams are considered the largest living bivalves, with the largest species, *Tridacna gigas* **(Linnaeus, 1758)**, reaching a maximum recorded size of 137cm and weighing as much as 340kg **(Fartherree, 2006)**. However, the two most commonly found species of the giant clams recorded in Indo-Pacific waters are *T. maxima* and *T. squamosa* **(Andréfouët *et al.*, 2005; Fauvelot *et al.*, 2020)**. They reach sizes of 35cm to 40cm **(Calumpong, 1992)** and <40cm **(Gilbert *et al.*, 2006)**, respectively. Undoubtly, all reef organisms have a role to play, but giant clams perhaps deserve special consideration not only becaused they are unique among bivalves **(Muscatine, 1967; Fitt & Trench, 1981; Klumpp *et al.*, 1992)**; however, they are highly threatened throughout most of their geographic range **(Lucas, 1994)**. Although various strategies have been implemented to protect and sustain the giant clam populations globally, particularly in the Indo-Pacific region, the majority of giant clam species have been excessively harvested in recent decades for their meat and shells **(Mingoa-Licuanan & Gomez, 2002; Van Wynsberge *et al.*, 2015)**. All species of Tridacninae are susceptible to long-term exploitation, and are therefore classified as vulnerable; in addition, they are listed on both the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) and the International Union for Conservation of Nature (IUCN) **(Neo *et al.*, 2017)**.

The Egyptian coral reef areas fluctuate between 10,000 and 14,000t/ year, depending on years and estimates. The current fishing in the Red Sea greatly exceeds sustainability levels, which in coral reef areas are mostly below 5t/ km^2 of coral reefs/year worldwide **(Kotb *et al.*, 2008)**. Damage is further compounded by illegal practices such as seasonal fishing on spawning aggregations (80% of the catch) of the most valuable fish stocks, which accelerates stock depletion **(Salem, 1999)**. Tridacna is among the most extensively exploited invertebrates in the Egyptian Red Sea due to over and bad fishing practicing. There is no need for costly and laborious stock assessments to decide immediately that good management is urgently needed. Hence, introducing marine aquaculture using non-traditional and environmentally green techniques is the best solution for the existing complicated situation, and it could be an approach to reduce the potential of fishing on the natural stocks of the Red Sea minimizing the conflict rate between consumption and non-consumption uses of the Red Sea fish stocks.

Generally, the Indo-Pacific developing countries have witnessed a growth of commercial mariculture of giant clams in recent years, owing to various research and development funded projects. Several mariculture techniques have been developed and are recorded in aquaculture protocols i.e. **Heslinga *et al*. (1990)**, **Calumpong (1992)**,

Hart *et al*. (1998) and **Heslinga (2013)**. Despite the availability of protocols, there is still lack in characterizing the factors affecting the growth rate of *Tridacna* species. For instance, *T. maxima* has been recorded as very slow-growing in several studies, reaching a shell length of 100mm at around five years of age **(Chambers, 2007; Bin Othman *et al*., 2010)**. Therefore in this study, we attempted to fill this gap by characterizing factors affecting the growth rate of *T. maxima* under culture condition (i.e. seasonal variations, temperature, mantle colors, density of zooxanthellae, and light energy absorption).

MATERIALS AND METHODS

1-Hatchery condition

In the current study, *Tridacna maxima* juveniles were cultured at the HEPCA hatchery. The samples were placed in a growing area inside plastic boxes attached to small rocks that served as substrate. The seawater was generally characterized by temperatures between 18 and 28°C and a salinity of 38‰. The *T. maxima* samples were supplied with cultured zooxanthellae just three days post-fertilization upon reaching the D-veliger stage. No algal supply other than zooxanthellae was added, as the specimens relied mainly on photosynthesis and were unfed. All boxes were cleaned once a week, with attached algae removed from each specimen using a scrubbing brush while kept submerged in water.

2-Morphometric measurements

Shell length of about 50 randomly chosen individuals per tank was measured using a Vernier caliper to the nearest cm on a monthly basis from January 2022 to February 2023 to monitor the growth rate among the population.

3-Morphometric measurements of different colors

At the end of the experiment, 50 individuals per tank were selected according to the symbiont color categorized as follows; bicolor, green, blue, brown and purple (Fig. 1). The shell length of each individual was measured using a Vernier caliper to the nearest cm to estimate the growth rate relevant to the symbiont color.

Fig. 1. Different colors of symbionts reared in the hatchery

4-Counting zooxanthellae

15 individuals of each color were sacrificed for zooxanthellae counting. The average number of zooxanthellae per specimen was also determined. The process involved the removal part of the mantle approximately measuring 1cm, followed by mixing the tissues with 50ml of seawater. The amount of zooxanthellae in subsamples of this homogenate was quantified using a hemocytometer, and these data were utilized to calculate the mean number of zooxanthellae per individual.

5-Reflectance measurements from *In-situ*

Five different colors of *Tridacna* sp. were measured to obtain the reflectance and absorption. The measurements were obtained underwater using a portable "ASD Field Spec_4 instrument" linked to an underwater fiber optic cable 5m in length with sensor at the end (Fig. 2). The portable Spectro-radiometer is capable of recording a spectral range of 350–2500nm by a rapid data collection time of 0.2 seconds per spectrum. It has a spectral resolution of three nm in the visible wavelength range of 350-700nm and NIR and SWIR from 750 to 2500nm.

Fig. 2. The measurements of reflection *in-situ*.

The data measurements were subset from 350 to 750nm, as readings taken underwater showed limited reflectance beyond 750nm due to absorption. The readings were classified into different band ranges according to the WorldView scale: coastal range (350-450nm), blue (451-510nm), green (511-580nm), yellow (581-630nm), and red (631-750nm). The reflectance measurements were then converted to light absorption to determine the total amount of energy entering the Tridacna tissues, which is essential for the photosynthesis processes of the symbiotic zooxanthellae.

6-Statistical analysis

The growth rate was calculated as a percent monthly increase in the shell length using the following equation:

$$((Lc-Lp)/Lp)*100$$

Where, Lc=Shell lenght in the current month; Lp= Shell lenght in the previous month.

All graphs were performed using Excel. One way analysis of variance (ANOVA) using Minitab version 19 was performed to study the difference in lenght (mean ± S.E.) among months and varations in growth rates across seasons, symbionts color along with zooxanthallae occurance and light absorbance among different symbiont color. The correlation coefficients obtained from the various linear regression analyses were tested for significance. The statistical significance level was set at 0.05.

RESULTS

1. Growth rate

The growth patterns of *T. maxima* were significantly influenced by multiple factors, including seasonal variations ($P \leq 0.001$), temperature ($P \leq 0.001$), mantle colors ($P \leq 0.001$), density of zooxanthellae ($P \leq 0.001$), and light energy absorption ($P \leq 0.001$).

2. Periodical growth rates

At a monthly level, the mantle length of *T. maxima* exhibited consistent increments, ranging from an average of 3.2 ± 0.55cm in January 2022 to 7.1 ± 0.80cm in February 2023. Peak growth rates occurred in March and April 2022, reaching 11.02 and 11.57%, respectively. Conversely, the lowest estimated growth rates were recorded in June, July, August, and December 2022, along with January and February 2023, ranging from 2.28 to 5.28%. These variations showed significant differences between months and seasons ($P \leq 0.05$), with highly significant disparities observed among different seasons ($P = 0.000$) (Table 1 & Fig. 3).

Seasonal analysis revealed noticeable fluctuations, notably influenced by temperature. The lowest and highest average temperatures corresponded to significant declines and increases in growth rates, respectively. Winter and summer months demonstrated the lowest growth rates, whereas spring and autumn seasons showcased the highest rates, reaching 19.66 and 7.61%, respectively (Table 1 & Fig. 4).

Table 1. Monthly/seasonal length and growth rates of *T. maxima* displayed as mean± standard deviation along with the overall mean of temperature and the day length in the period from Jan. 2022 to Feb. 2023

Month/Season	Length	Growth rate %	Temperature	Day length
Jan.	3.2±0.55		19.8	10:38:58
Feb.	3.3±0.51	5.60±1.94	19.6	11:14:30
Winter	**3.3±0.50**		**19.7**	**10:56:44**
***P*-value**	**0.126**			
March	3.7±0.53	11.02±0.58	21.9	12:00:29
April	4.1±0.49	11.57±2.28	23.4	12:48:47
May	4.5±0.55	9.38±0.24	24.9	13:29:17
Spring	**4.1±0.50**	**10.66 ±1.13**	**23.3**	**12:46:11**
***P*-value**	**0.000**	**0.338**		
June	4.7±0.52	5.28±1.06	25.0	13:49:33
July	4.9±0.54	3.68±0.11	26.8	13:39:40
August	5.1±0.54	4.57±0.41	29.0	13:04:35

Summer	**4.9±0.50**	**4.51±0.53**	**28.3**	**13:31:16**
***p*-value**	**0.002**	**0.127**		
Sept.	5.5±0.52	6.88±0.88	29.1	12:18:35
Oct.	6.0±0.57	8.53±0.08	28.5	11:30:38
Nov.	6.4±0.59	7.41±0.42	25	10:49:03
Autumn	**6.0±0.6**	**7.61±0.46**	**25.6**	**11:32:45**
***p*-value**	**0.000**	**0.066**		
December	6.7±0.59	3.92±0.25	23.5	10:27:44
Jan. 23	6.9±0.63	3.80±0.24	21.0	10:38:45
Feb. 23	7.1±0.80	3.28±1.75	22.0	11:14:08
Winter 2023	**6.9±0.70**	**3.67±0.75**	**21.5**	**10:46:52**
***p*-value**	**0.003**	**0.000**		
***p*-value (months)**	**0.000**	**0.000**		
***p*-value (seasons)**	**0.000**	**0.000**		

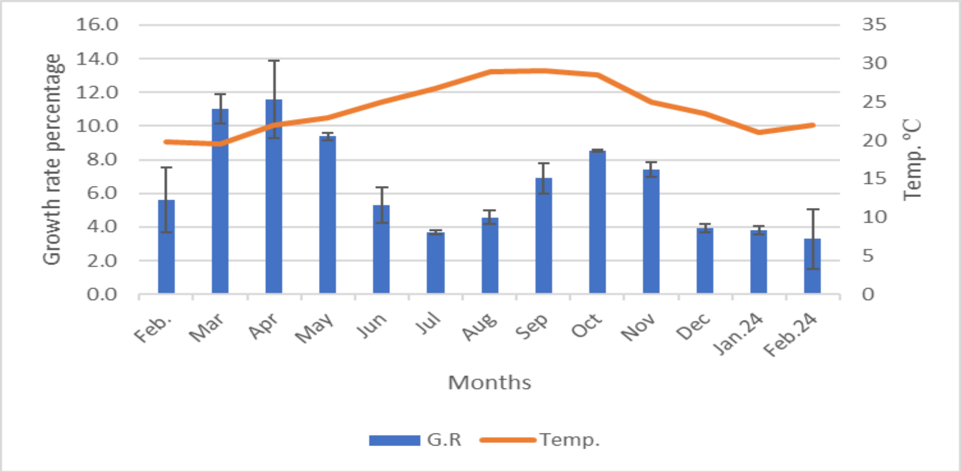

Fig. 3. Estimated monthly growth rates of *T. maxima* and average monthly recorded temperature

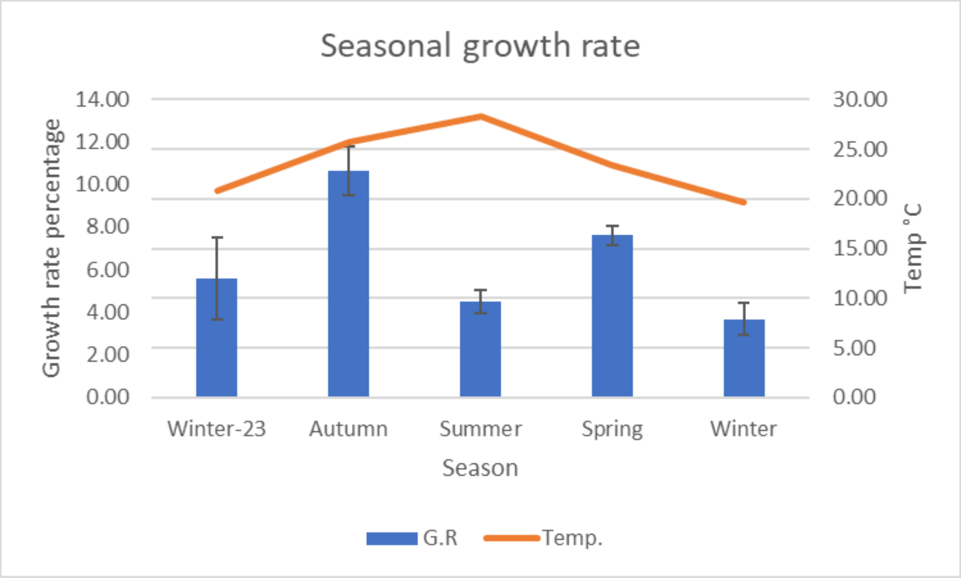

Fig. 4. Estimated seasonal growth rates as a percentage of shell length increment per seasons and seasonal overall means of temperature during the period between January 2022 and February 2023

3. Growth rate and zooxanthellae density among different mantle colors

Comparative analyses of growth rates based on symbiont color exhibited distinct patterns. Brown symbionts displayed the highest growth rates, expanding by approximately 112% of their original length, followed by blue (84%) and purple individuals (82%). Bicolor and green-symbiont individuals showed relatively lower growth rates, implying potential vulnerability to environmental stressors (Fig. 5). Furthermore, the density of zooxanthellae varied significantly among colors, with higher occurrences in brown and brown-blue symbionts compared to violet and green, aligning with their respective growth rates (Fig. 6).

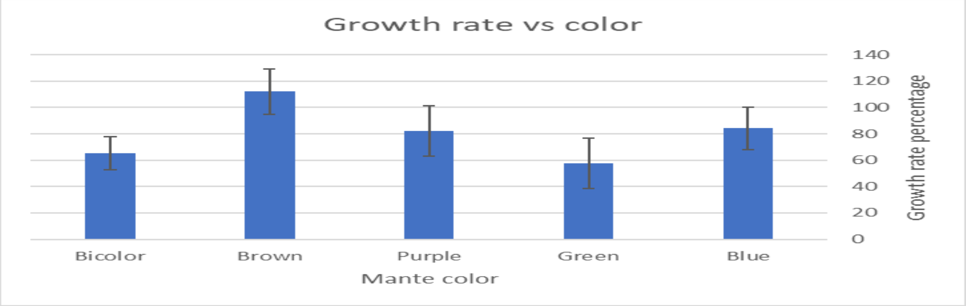

Fig. 5. Annual growth rates in *T. maxima* estimated for different mantle colors as a shell growth percentage to the initial shell length

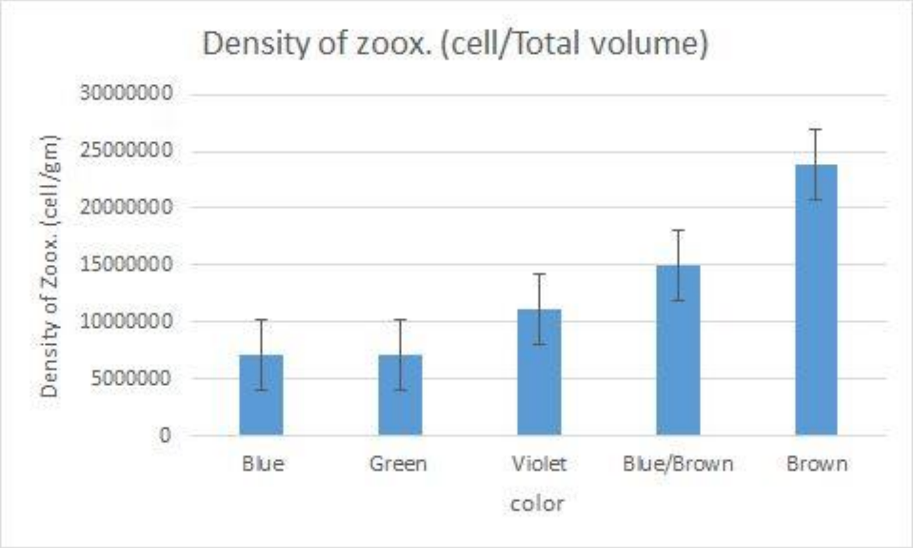

Fig. 6. Zooxanthellae density among different mantle colors

4. Light energy absorption

Distinct colors were categorized into different wavelength ranges to assess light absorption. Reflectance measurements displayed variance within specific wavelength ranges. For instance, as shown in Fig. (7), blue-colored samples exhibited high reflectance between 350 to 510nm (covering coastal and blue bands), followed by absorption in the subsequent ranges (511 to 650nm - covering green and yellow), with reflection occurring in the red range (700 to 750nm). In contrast, brown samples absorbed light, reflecting minimal amounts, especially beyond 700nm. Additionally, violet samples absorbed light along the wavelength, exhibiting substantial reflection beyond 700nm. Notably, brown-colored individuals recorded the highest light absorption levels, particularly in the near-infrared range, indicative of biological processes such as photosynthesis, releasing heat. Sequentially, blue-green, green, and violet-colored species exhibited decreasing levels of light absorption, with the blue-colored species demonstrating the lowest absorption.

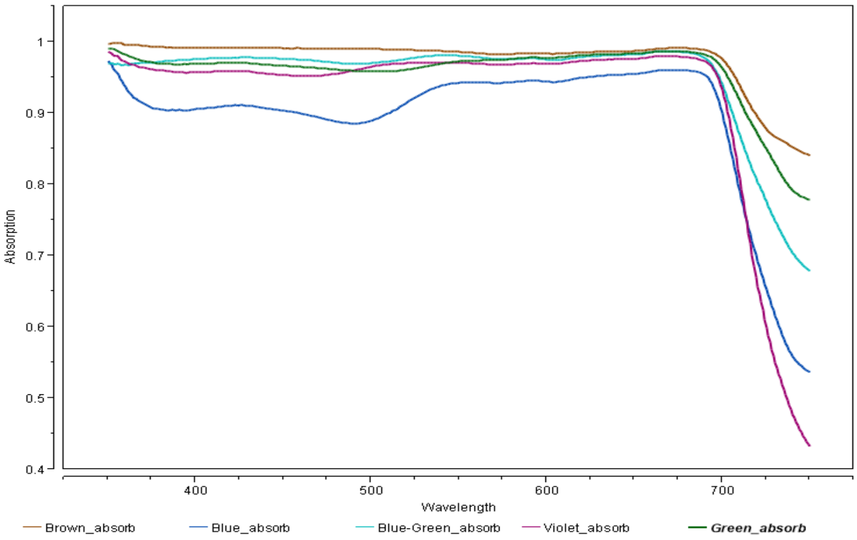

Fig. 7. The absorption of sun light (energy) for different colored individauls of tridacna

DISCUSSION

In general, the growth rates in *Tridaca maxima* is characterized with lower growth rate among other Tridacna species. The growth rates of Tridacna species, particularly *Tridacna maxima*, vary significantly based on environmental conditions. Under culture condition, *T. maxima* can exhibit growth rates ranging between less than 1.0cm in shell length per year **(Toonen *et al*, 2012)** to 1.5-2.1mm per month **(Mohammed *et al*, 2019; Lim *et al.* 2020)**. However, this rate can be influenced by factors like water quality, temperature, availability of light, and food sources.

These findings align with previous studies indicating that environmental factors profoundly impact the growth of marine organisms **(Lucas, *et al*., 1989; Gula & Adams, 2018; Hsieh, *et al*., 2023)**. The observed monthly fluctuations in growth rates, particularly the substantial variations between months and seasons, underscore the species' sensitivity to environmental changes. These fluctuations correlate with temperature variations, where extreme temperatures during winter and summer months coincide with lower growth rates. In contrast, milder temperatures during spring and autumn seasons correspond to higher growth rates. This aligns with the thermal sensitivity of Tridacna species reported in previous studies **(Poloczanska *et al*., 2013; Foo & Byrne, 2016; Van Wynsberge *et al*, 2017; Syazili *et al*., 2020)**.

Furthermore, mantle color emerged as a significant determinant of growth rates, where the brown individuals exhibited the highest growth rates, possibly indicating a favorable symbiotic relationship between these individuals and their zooxanthellae, as evidenced by higher zooxanthellae density. This observation concurs with studies highlighting the importance of symbiont density color in the growth and health of giant clams **(Fitt & Trench, 1981; Fitt *et al*., 1986; Gula & Adams, 2018, Li *et al*., 2024)**, as well as bleaching of zooxanthellae reduces the reproduction in Tridacna gigas **(Sayco *et al*., 2023 a&b)**.

The higher growth rates exhibited by individuals hosting brown-colored symbionts, alongside the elevated density of zooxanthellae within these specimens, underscored a potential symbiotic advantage. Brown symbionts exhibited not only superior growth rates but also a significantly higher occurrence of zooxanthellae compared to other color variants. This aligns with previous studies highlighting the pivotal role of zooxanthellae in facilitating the growth and metabolic processes of their host clams **(Belda-Baillie *et al*., 1998; Ambariyanto, 2007, Hernawan, 2010; Klueter, *et. al*., 2017)**.

Moreover, the density of zooxanthellae among different color variants exhibited distinct disparities. Brown symbionts harbored notably greater densities compared to blue-brown and blue individuals. This correlation between symbiont color, zooxanthellae density, and growth rates emphasizes the significance of symbiotic interactions in dictating growth dynamics within Tridacna species.

It is unclear whether the higher absorption of light energy recorded in brown symbionts is related to the increased density of zooxanthellae or the type of pigment. However, it is worth noting that some studies have reported an interaction between symbiotic zooxanthellae and mantle iridocytes **(Ghoshal *et al.*, 2016; Li *et al.*, 2022)**. An integrated optical system consists of spherical iridocytes that scatter light and microalgae that strongly absorb and scatter light **(Holt *et al*., 2014)**. This cooperation might also explain the enormous clam mantle tissue coloration. These coloration spans from vibrant blue, showing a high concentration of iridocytes and a low number of symbiotic zooxanthallea, to dark brown which corresponds a low concentration of iridocytes with a high number of zooxanthellae **(Rossbach *et al*., 2020)**. Hence, the higher absorbance of light energy recorded in brown symbiont might be attributed to the fewer iridocytes that scatter light and higher abundance of microalgae zooxanthallea that strongly absorb and scatter light. Actually, more investigation is recommended to clarify the raised point.

The relationship between light energy absorption and growth rates also elucidates the critical role of light in the growth processes of *T. maxima*. Different mantle colors exhibited varying levels of light absorption, with brown-colored individuals displaying the highest absorption, likely facilitating optimal photosynthetic activity. This aligns with studies demonstrating the influence of light availability on the growth and physiology of symbiotic organisms within corals and clams **(Iglesias-Prieto *et al*., 2004, Lajeunesse *et al*., 2018; Rossbach *et al*., 2019; Liu *et al*., 2020)**.

Understanding these intricate relationships between environmental factors, symbiotic interactions, and growth dynamics is pivotal for effective conservation and management strategies aimed at protecting *T. maxima* populations. These findings underscore the importance of maintaining suitable environmental conditions and symbiotic relationships to ensure the sustained growth and resilience of these iconic marine species in the face of environmental fluctuations.

CONCLUSION

The growth rates of *Tridacna maxima* fluctuate significantly based on environmental conditions. Monthly growth rates also show considerable variation due to sensitivity to seasonal temperature changes. Additionally, mantle color, which partially depends on zooxanthellae density, affects growth rates; as zooxanthellae density increases, growth rates also rise, as evidenced by enhanced light absorption. These findings underscore the importance of maintaining suitable environmental conditions and symbiotic relationships to support the sustained growth and resilience of these vital marine species.

REFERENCES

Alcazar, S. N. (1986). Observations on predators of giant clams (Bivalvia: Family Tridacnidae). Silliman Journal, 33(1–4), 54– 57.

Ambariyanto, A. (2007). The growth of giant clams juvenile is influenced by nutrient addition. Biota, 12(2): 127-130

Andréfouët, S.; Gilbert, A.; Yan, L.; Remoissenet, G.; Payri, C. and Chancerelle, Y. (2005). The remarkable population size of the endangered clam *Tridacna maxima* assessed in Fangatau Atoll (Eastern Tuamotu, French Polynesia) using in situ and remote sensing data. ICES Journal of Marine Science, 62(6), 1037– 1048. **https://doi.org/10.1016/j.icesjms.2005.04.006**

Belda-Baillie, CA; Leggat, W. and Yellowlees, D. (1998). Growth and metabolic responses of the giant clam-zooxanthellae symbiosis in a reef-fertilisation experiment. Marine Ecology-progress Series - MAR ECOL-PROGR SER. 170. 131-141. 10.3354/meps170131.

Brown, J. H. and Muskanofola, M. R. (1985). An investigation of stocks of giant clams (family Tridacnidae) in Java and of their utilization and potential. *Aquaculture Research*, 16(1): 25– 39. https://doi.org/10.1111/j.1365-2109.1985.tb00294.x

Calumpong, H. P. (1992). The Giant Clam: an Ocean Culture Manual. Australian Center for International Agricultural Research Canberra.

Chambers, C. N. L. (2007). Pasua (Tridacna maxima) size and abundance inTongareva Lagoon, Cook Islands. SPC Trochus Inform. Bull. 13, 7–12.

Liu, C.; Li, X.; Wu, C.; Wang, A. and Gu Z. (2020). Effects of three light intensities on the survival, growth performance and biochemical composition of two size giant clams Tridacna crocea in the Southern China Sea, Aquaculture, Volume 528, 735548, ISSN 0044-8486, https://doi.org/10.1016/j.aquaculture.2020.735548.

De Goeij, J. M.; Van Oevelen, D.; Vermeij, M. J. A.; Osinga, R.; Middelburg, J. J.; de Goeij, A. F. P. M. and Admiraal, W. (2013). Surviving in a marine desert: The sponge loop retains resources within coral reefs. *Science*, 342(6154), 108– 110.

De Grave, S. (1999). Pontoniinae (Crustacea: Decapoda: Palaemonidea) associated with bivalve molluscs from Hansa Bay, Papua New Guinea. *Bulletin van het Koninklijk Belgisch Instituut voor Natuurwetenschappen. Biologie = Bulletin de l'institut Royal des Sciences Naturelles de Belgique Biologie*, 69, 125– 141.

Ellis, S. (1999). Lagoon Farming of Giant Clams (Bivalvia: Tridacnidae). Center for Tropical and Subtropical Aquaculture Publication Number 139.

Ellis, S. (2000). Nursery and grow-out techniques for giant clams (Bivalvia: Tridacnidae). Center for Tropical and Subtropical Aquaculture Publication CTSA, 143, 99.

Fauvelot C, Zuccon D, Borsa P, *et al.* (2020). Phylogeographical patterns and a cryptic species provide new insights into Western Indian Ocean giant clams phylogenetic relationships and colonization history. *J Biogeogr*. 47: 1086–1105. https://doi.org/10.1111/jbi.13797

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

Fitt, W. K., Fisher, C. R. and Trench R. K. (1986). Contribution of the symbiotic dinoflagellate *Symbiodinium microadriaticum* to the nutrition, growth and survival of larval and juvenile tridacnid clams. *Aquaculture* 55: 5–22.

Foo, S.A. and Byrne, M. (2016). Acclimatization and Adaptive Capacity of Marine Species in a Changing Ocean. Adv Mar Biol:74:69-116.

Ghoshal A.; Eck E.; Gordon M. and Morse D. E. (2016). Wavelength-specific forward scattering of light by Bragg-reflective iridocytes in giant clams. J. R. Soc. Interface.132016028520160285.

Gula, L,R and Adams, D. K. (2018). Effects of Symbiodinium Colonization on Growth and Cell Proliferation in the Giant Clam *Hippopus hippopus*. Biol Bull, 234 (2):130-138.

Hernawan, U.E. (2010) Study on giant clams (Cardiidae) population in Kei Kecil Waters, Southeast Maluku. Widyariset, 13(3): 101-108 (In Indonesian

Holt A. L.; Vahidinia S.; Gagnon Y. L.; Morse D. E. and Sweeney A. M. (2014). Photosymbiotic giant clams are transformers of solar fluxJ. R. Soc. Interface.11: 2014067820140678.

Hsieh, H.-Y.; Tew, K.-S. and Meng, P.-J. (2023). The Impact of Changes in the Marine Environment on Marine Organisms. J. Mar. Sci. Eng., 11,809.

Huber, M. (2010). Compendium of Bivalves. A full-color guide to 3,300 of the World's Marine Bivalves. A status on Bivalvia after 250 years of research. - Hackenheim: ConchBooks, 901 pp, 1 CD.

Iglesias-Prieto, R. Beltran, V.H.; Lajeunesse, T.C; Reyes-Bonilla H. and Thome, P.E (2004). Comparative performances of symbiotic dinoflagellates in culture: insights into the relative contribution of algal factors to coral thermal tolerance. Journal of Experimental Marine Biology and Ecology, 271(2), 175-188.

IUCN. (2016). *Red List of Threatened Species.* Available online at: wwwiucnredlistorg Version 2016-3.

Jantzen, C., Wild, C., El-Zibdah, M., Roa-Quiaoit, H. A., Haacke, C., and Richter, C. (2008). Photosynthetic performance of giant clams, *Tridacna maxima* and *T. squamosa*, Red Sea. *Mar. Biol.* 155, 211–221. doi: 10.1007/s00227-008-1019-7.

Kilada, R., Zakaria, S., and Farghalli, M. E. (1998). Distribution and abundance ofthe giant clam Tridacna maxima (Bivalvia: Tridacnidae) in the northern RedSea. Bull. Natl. Instit. Oceanogr. Fish. 24, 221–240.

Klueter, A.; Trapani, J.; Archer,F.,I; McIlroy, S. E. and Coffroth, M. A. (2017). Growth rates of cultured marine dinoflagellates in the genus *Symbiodinium* and the effects of temperature and light. Published online 2017 Nov 29. doi: 10.1371/journal.pone.0187707

Klumpp, D.W. Bayne, B.L. Hawkins A.J.S., (1992). Nutrition of the giant clam *Tridacna gigas* (L.). I. Contribution of filter feeding and photosynthates to respiration and growth. J. Exp. Mar. Biol. Ecol., 155 pp. 105-122

Klumpp, D. W., and Griffiths, C. L. (1994). Contributions of phototrophic and heterotrophic nutrition to the metabolic and growth requirements of four species of giant clam (Tridacnidae). *Marine Ecology Progress Series*, 115, 103– 115. https://doi.org/10.3354/meps115103.

Kotb, M. M. A.; Hanafy, M. H.; Rirache, H.; Matsumara, S.; Al-Sofyani, A. A.;Ahmed, A. G.; Bawazir, G. and Al-Horani, F. (2008). Status of coral reefs in theRed Sea and Gulf of Aden Region. In: Status of Coral Reefs of the World: 2008,Wilkinson, C.E. (ed.), Townsville (Australia): Global Coral Reef MonitoringNetwork and Reef and Rainforest Research Centre. pp. 67-78.

LaJeunesse, T. C.; Parkinson, J. E.; Gabrielson, P. W.; Jeong, H. J.; Reimer, J. D.; Voolstra, C. R.; et al. (2018). Systematic revision of symbiodiniaceae highlights the antiquity and diversity of coral endosymbionts. Curr. Biol. 28: 2570–2580. doi: 10.1016/j.cub.2018.07.008.

Li, Y.; Zhou, Y.; Wei, J.; Shi, G.; Liao Q.; Guo, S.; Zhou, Z.; Li, J.; Qin, Y.; Ma, H.; Yu, Z. and Zhang, Y. (2022). Study on the Individual Coloring Mechanism of Iridescent Cells in the Mantle of the Boring Giant Clam, Tridacna crocea. Frontiers in Marine Science. 9. 883678. 10.3389/fmars.2022.883678.

Li, M., Yang, W., Hong, X., Wang, A., Yang, Y., Yu, F. and Liu, C., (2024). Effects of the daily light-dark cycle on rhythms of behavior and physiology in boring giant clam Tridacna crocea. *Marine Biology*, *171*(8), 149.

Li, J.; Zhou, Y.; Qin, Y.; Wei, J.; Shigong, P.; Ma, H.; Li, Y.; Yuan, X.; Zhao, L.; Yan, H.; Zhang, Y. and Yu Z. (2022). Assessment of the juvenile vulnerability of symbiont-bearing giant clams to ocean acidification, Science of The Total Environment, Volume 812, 152265, ISSN 0048-9697, https://doi.org/10.1016/j.scitotenv.2021.152265.

Lim, K. K.; Rossbach, S.; Geraldi, N. R.; Schmidt-Roach, S.; Serrao, E. A. and Duarte, C. M. (2020). The small giant clam, Tridacna maxima exhibits minimal population genetic structure in the Red Sea and genetic differentiation from the Gulf of Aden. Front. Mar. Sci. 7:889. doi: 10.3389/fmars.2020.570361.

Lucas, J. S.; Nash, W. J.; Crawford, C.M. and Braley, R.D. (1989). Environmental influences on growth and survival during the ocean-nursery rearing of giant clams, *Tridacna gigas* (L.). Aquaculture, 80, Issues 1–2: 45-61.

Mekawy, M. S.; and Madkour, H. A. (2012). Studies on the Indo-Pacific tridacnidae (Tridacna maxima) from the Northern Red Sea, Egypt. Intern. J. Geosci. 3,1089–1095.

Mies, M. (2019). Evolution, diversity, distribution and the endangered future of the giant clam–Symbiodiniaceae association. *Coral Reefs*, 38(6), 1067– 1084. https://doi.org/10.1007/s00338-019-01857-x.

Mies, M.; Dor, P.; Güth, A. Z., and Sumida, P. Y. G. (2017). Production in giant clam aquaculture: Trends and challenges. *Reviews in Fisheries Science and Aquaculture*, 25(4): 286– 296. https://doi.org/10.1080/23308249.2017.1285864.

Mohammed, T.A.A; Mohamed, M. H.; Zamzamy, R. M. and Mahmoud, M.A.M. (2019). Growth rates of the giant clam Tridacna maxima (Röding, 1798) reared in cages in the Egyptian Red Sea. The Egyptian Journal of Aquatic Research, Volume 45, Issue 1, 67-73.

Muscatine, L. (1967). Glycerol Excretion by Symbiotic Algae from Corals and Tridacna and Its Control by the Host. Science 156,516-519. DOI:10.1126/science.156.3774.516

Neo, M. L., Eckman, W., Vicentuan, K., Teo, S.- L.-M. and Todd, P. A. (2015). The ecological significance of giant clams in coral reef ecosystems. *Biological Conservation*, 181: 111– 123. https://doi.org/10.1016/j.biocon.2014.11.004.

Pappas, M. K., He, S., Hardenstine, R. S., Kanee, H. and Berumen, M. L. (2017). Genetic diversity of giant clams (*Tridacna* spp.) and their associated Symbiodinium in the central Red Sea. Mar. Biodiv. 47, 1–14. doi: 10.1007/978-3-319-23534-9_1.

Poloczanska, E.S.; Brown, C. J.;Sydeman, W. J.; Kiessling, W.;Schoeman, D. S.; Moore, P. J.; Brander, K.; Bruno, J. F.:Buckley, L. B.; Burrows, M. T.; Duarte,C. M.; Halpern, B. S.; Holding, J.; Kappel, C. V; O'Connor, M. I; Pandolfi, J. M;Parmesan, C; Schwing, F; Thompson, S. A; & Richardson, A. J.; (2013). Global imprint of climate change on marine life. Nature Climate Change, 3(10), 919-925.

Rachel L. Gula and Diane K. Adams. (2018). Effects of Symbiodinium Colonization on Growth and Cell Proliferation in the Giant Clam Hippopus hippopus. Biol. Bull. 234: 130–138.

Ramah S., Taleb-Hossenkhan N. and Bhagooli R. (2017). Differential substrate affinity between two giant clam species, Tridacna maxima and Tridacna squamosa, around Mauritius. Western Indian Ocean Journal of Marine Science (Special Issue) 1: 13-20

Richter, C.; Roa-Quiaoit H.A.; Jantzen C.; A l-Zibdah M. and M. Kochzius M., (2008). Collapse of a new living species of giant clam in the Red Sea. - Current Biology, 18 (17): 1349-1354.

Roa-Quiaoit H. A.F. (2005). The ecology and culture of giant clams (Tridacnidae) in the Jordanian sector of the Gulf of Aqaba, Red Sea. - Thesis, University Bremen, Germany, 100 pp.

Rossbach, S.; Saderne, V.; Anton, A. and Duarte, C. M. (2019). Light-dependent calcification in Red Sea giant clam *Tridacna maxima*. Biogeosciences 16, 2635–2650.

Rossbach S.; Subedi R.; Ng T. K.; Ooi B. S. and Duarte C. M. (2020). Iridocytes Mediate Photonic Cooperation Between Giant Clams (Tridacninae) and Their Photosynthetic Symbionts. Frontiers in Marine Science volume **https://doi.0.3389/fmars.2020.00465**

Rossbach, S.; Hume, B. C. C.; Cárdenas, A.; Perna, G.; Voolstra, C. R. and Duarte, C. M. (2021). Flexibility in Red Sea Tridacna maxima-Symbiodiniaceae associations supports environmental niche adaptation. *Ecology and Evolution*, 11(7), 3393–3406. https://doi.org/10.1002/ece3.7299

Salem, M. (1999). Management of fishing in the Ras Mohammed National Park with special reference to the fishery for *Lethrinus nebulosus* (Forsskal, 1775). PhD thesis, University of York.

Sayco, S. L. G.; Cabaitan, P. C. and Kurihara, H. (2023 a). Bleaching reduces reproduction in the giant clam *Tridacna gigas*. Marine Ecology Progress Series. 706: 47-56.

Sayco, S. L. G; Pomares, A. A.; Cabaitan, P. C. and Kurihara, C. H. (2023 b). Reproductive consequences of thermal stress-induced bleaching in the giant clam *Tridacna crocea*. Marine Environmental Research 193:106280.

Smith, S.D.A., (2011). Growth and population dynamics of the giant clam Tridacna maxima (Röding) at its southern limit of distribution in coastal, subtropical eastern Australia. Molluscan Res. 31 (1), 37–41.

Syazili, A.; Syafiuddin; Niartiningsih, A. and Jompa, J. (2020). Effect of ocean acidification and temperature on growth, survival, and shell performance of fluted giant clams (*Tridacna squamosa*). IOP Conf. Ser.: Earth Environ. Sci. 473 012141.

Toonen, R. J; Nakayama, T.; Ogawa, T. and 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, 2012, 92(4), 731 –740.

Toonen, R.J.; Nakayama, T.; Ogawa, T;, Rossiter, A. and Delbeek, J.C., (2012). Growth of cultured giant clams (Tridacna spp.) in low pH, high-nutrient seawater speciesspecific effects of substrate and supplemental feeding under acidification. J. Mar. Biol. Assoc. United Kingdom 92, 731–740.

Ullmann, J. (2013). Population status of giant clams (Mollusca: Tridacnidae) in the northern Red Sea, Egypt. Zool. Middle East 59, 253–260. doi: 10.1080/09397140.2013.842307.

Van Wynsberge, S.; Andrefouet, S.; Gaertner-Mazouni, N.; Wabnitz, C.; Gilbert, A.; Remoissenet, G.; et al., (2016). Drivers of density for the exploited giant clam Tridacna maxima: a meta-analysis. Fish Fish. 17, 567–584.

Van Wynsberge S.; Andréfouët S.; Gaertner-Mazouni N.; Wabnitz CCC.; Menoud M, Le. And Moullac G, et al. (2017). Growth, Survival and Reproduction of the Giant Clam *Tridacna maxima* (Röding 1798, Bivalvia) in Two Contrasting Lagoons in French Polynesia. PLoS ONE 12(1): e0170565. https://doi.org/10.1371/journal.pone.0170565.

Vicentuan-Cabaitan, K.; Neo, M. L.; Eckman, W.; Teo, S.-M. and Todd, P. A. (2014). Giant clam shells host a multitude of epibionts. *Bulletin of Marine Science*, 90(2), 795– 796. **https://doi.org/10.5343/bms.2014.1010.**

Wangpraseurt, D. et al. (2020). Light microenvironment and photo-acclimation of the giant clam Tridacna maxima in a simulated shallow reef flat. Frontiers in Marine Science, 7, 336.