ISSN 2321-340X



© Department of Aquatic Biology & Fisheries, University of Kerala

Ethological Studies on the Jellyfish, *Crambionella orsini* (Vanhöffen, 1888) (Scyphozoa: Catostylidae) in Captivity

Soumya, K.R., Riyas, A., Mithun, S. and Biju Kumar, A.*

Department of Aquatic Biology and Fisheries, University of Kerala, Thiruvananthapuram-695581, Kerala, India *Email: bijupuzhayoram@gmail.com

Abstract

83

Jellyfishes, especially those cnidarians in the class Scyphozoa, Cubozoa and Hydrozoa, are integral components of marine biodiversity, which are also used extensively for research in ethology to bioengineering. They are also extensively used as exhibits in public aquaria. Here, we record the behavioural responses of jellyfish *Crambionella orsini* Vanhöffen, 1888 (Family: Catostylidae) in captivity under conditions of acclimatization, feed types and light regimes. Acclimatization of jellyfish happened within two days following a dominant resting period and aggregation responses. Analysis of various stages of bell propulsions showed that swimming movements in scyphozoans are mediated by subsequent bell contractions and relaxations resulting in the formation of successive vortices that generates accelerative responses. Medusal preferences to live feeds (*Artemia* nauplii and copepods) were indicated with better consumption and swimming activities. Exposure of medusae to variable light intensities showed light-dependent swimming responses highlighting the photoreceptor induced orientation and distribution patterns. Weaker pulsation rates and swimming movements under captivity and reduction in size in captivity demands, detailed studies on the aquarium adaptability of the species.

Keywords: Jellyfish, Behaviour, Artemia, Acclimatization, Pulsation rate, Feed preference, Light response, Aquarium adaptability

1. Introduction

Behaviour forms the ability of living organisms to respond to changes in the environment, including all the integrated processes where an animal senses both the environmental and internal states (Manning, 1988). Knowledge on the behaviour provides information about animal's requirements, preferences, likes and dislikes, internal states (Mench, 1998), and their interaction at inter and intraspecific grades, which ultimately enlightens success, survival and evolutionary processes of the animal. Behaviour is generally considered the animal's first adaptation to environmental change (Mench and Manson, 1997). Progress of research in animal behaviour has made an important contribution to conservation (Sutherland, 1998). Behaviour can be considered an indicator of an organism's condition and the condition of the environment (Kotler et al., 2007).

Jellyfish are important because of their ability to form seasonal blooms (Purcell *et al.*, 2007; Condon *et al.*, 2012). Recent reports on jellyfish blooms have increased from different parts of the world (Purcell *et al.*, 2007; Condon *et al.*, 2012; Boero *et al.*, 2016; Cruiz-Rivera and Abu El-Regal, 2016; Quinones *et al.*, 2018; Dong, 2019; Riyas *et al.*, 2021). Of late, jellyfish receives considerable attention globally in due recognition of their role in marine ecosystems under anthropogenic interventions (Daryanabard and Dawson, 2008; Richardson *et al.*, 2009; Brotz *et al.*, 2012; Kingsford *et al.*, 2018). They perform vital trophic roles in the marine ecosystems, and their behavioural patterns remain highly under-studied (Doyle *et al.*, 2008).

Jellyfish lack brain, which indicates that a well-organized behaviour is minimal (Gehring, 2001). The nervous system of Cnidaria is relatively simple, and it diffuses with some degree of neuronal condensation that functions as an integrative nervous system (Scatterlie, 2002; Anderson, 2004; Mackie, 2004; Watanabe, 2009). The central nervous system, a combination of nerve nets and bundles, is responsible for the different types of behaviour activities that help medusae escape from predators and promote foraging and successful reproduction (Albert, 2010). Cnidarians such as sea anemones, hydrozoans and scyphozoans possess mechanoreceptors and chemoreceptors that remain associated with cnidocytes which can regulate nematocyst sensitivity (Purcell and Anderson, 1995; Thurm et al., 2004; Oliver et al., 2008) and are sensitive to the chemical scent of an organism, thus helping in prey recognition (Watson and Hessinger, 1994). Scyphozoans possess distinct rhopalia with photoreceptive function, and together with statoliths, they sense gravity (Hyman, 1940), and it serves as the control stimulus for migration and positioning mechanisms to adjust themselves within the water column (Hays et al., 2008).

In addition to that, many adaptive behavioural responses have been shown by scyphozoans that include directional swimming (Hamner *et al.*, 1994), approach to feed (Arai 1991), escape from predators (Hansson and Kultima, 1996; Hansson, 1997), and diving patterns concerning turbulence (Albert, 2007). Behaviours such as vertical swimming patterns in response to touch by a neutral object, avoidance of rock walls, low salinity avoidance and

sunlight stimulated directional swimming in Aurelia labiata was noticed from Roscoe Bay, Canada (Albert, 2008). Other adaptive behaviour patterns have been reported from Aurelia sp. by the possession of receptors sensitive to light, touch, gravity, chemicals, sound pressure waves, direction, vibration, and hydrostatic pressure (Albert, 2011). Mimicry (Purcell, 1980), migration and navigation (Hamner and Hauri, 1981), and courtship behaviour (Werner et al., 1971) are the major behaviour responses of jellyfish. Research by Nath et al. (2017) reveals a sleep-like stage in the upside-down jellyfish (Cassiopea elegans) during the night, which has been shown to be regulated by homeostatic and circadian rhythms. Ethological studies of jellyfish are minimal, while most experiments were conducted only with the moon jellyfish Aurelia (Archdale et al., 2002; Albert, 2008; 2011; 2014, Pereira et al., 2014; Yoon et al., 2017). This study records the response of the scyphozoan jellyfish Crambionella orsini (Vanhoffen, 1888) under conditions of acclimatization, feed types and light regimes.

2. Materials and Methods

Live specimens of *Crambionella orsini* were collected from the shallow waters of Perumathura (8°37'N; 76°47' E), Thiruvananthapuram coast, Kerala in November 2017 (Fig 1). Individual medusae were collected from the surface layers of water with minimum disturbance from a small motor boat using scoop net (mesh size 1 mm) and transferred to an aerated tank with water from the collecting site. The specimens were transported to the wet lab and the morphometric measurements such as OAL (Oral Arm Length) BD (Bell Diameter) and TL (Total Length) were taken by the followed methods of Morandini and Marques (2010). Weight of the individual medusae was measured using an electronic weighing balance.

Two experimental aquarium tanks (122 x 47 x 70 cm) provided with biological filtration system were used for acclimatization, feeding and light experiments (Fig 2 ad). Lighting and the feeding conditions in the experiment followed the methods of Klein et al. (2016). Jellyfish were exposed to 14:10 hr light-dark cycle to mimic diurnal and nocturnal patterns in the laboratory conditions. The salinity was maintained to 33 ppt throughout the experiment as the condition similar to the natural waters. After acclimatization, feeding of the medusa was done with newly hatched Artemia nauplii once daily in the afternoon. Video recordings of the medusae movement were made under yellow fluorescent light. Night recordings were carried out using a low-intensity red bulb. Gentle aeration and continuous water circulation were maintained in the tank to maintain oxygen saturation and to remove the bottom settled debris. Water temperature was maintained similar to that of jellyfish collected locations. Fluctuations in the salinity due to evaporation was corrected with the addition of freshwater (Klein et al., 2016). Parameters such as bell contractions, pulsation rate, feeding, vertical and horizontal movement, period of rest or no bell propulsion and speed of movement were measured during acclimatization.



Fig. 1. Map of Kerala coast showing jellyfish collection sites

2.1. Feeding behaviour studies

The feeds used in the experiment consisted of live Artemia nauplii and live copepods (Temora turbinata, Parvocalanus crassirostris and Pseudodiaptomous serricaudatus) and frozen Artemia. A feeding experiment was conducted for eight days. About four medusae each were distributed in 2 separate experiment tanks. Feeding at desired concentration was done every afternoon, which was evaluated by the remaining feed concentration present in the tank after one hour of broadcasting the feed. During the experiment, the water circulation system was turned off during the experiment to prevent the escape of feed and the clogging of the filter by excess feed. The approach of animals to different feed types feed preference of jellyfish, size variation, and health and activity of the animal in terms of pulsation and movement are the factors recorded during the experiment.

2.2. Behaviour in response to light

The experiment was implemented in a dark room to ensure that natural light has no influence on the behaviour. Five medusae each were transferred to the two experimental tanks, one of which was covered by a thick, black plastic sheet on all the sides, including the tank's surface except the front display portion for visualizing the response of jellyfish to light, while the other tank was left uncovered. A regulator adjusted the light intensity of a 100-Watt incandescent bulb, and the response of jellyfish at five different intensities (100 lux, 250 lux, 500 lux, 1000 lux and 1500 lux) light for the one-hour interval for each intensity was recorded during the experiment.

To compare the behaviour of jellyfish in the natural environment and captive conditions, the jellyfish species *Crambionella orsini* was also observed in the natural environment. The natural movements of *Crambionella orsini* were recorded from the shallow waters of the Vizhinjam coast using a GoPro camera (Fig. 2 e).

3. Results

3.1. Acclimatization

Right from the collection, transportation and transfer to acclimatization tank, medusae produced copious amounts of mucous. Mucous production continued for several hours, clouding the aquarium water, even though the amount of mucous got considerably reduced with time. Mucous harboured an enormous amount of cnidoblasts.



Fig. 2. Jellyfish collection and experimental set-up: (a) Collection of *C. orsini* from the shallow waters of Perumathura; (b) experimental tanks; (c) biological filtration system; (d) *C. orsini* transferred to the tank just after brought from the collection site; (e) Underwater video of *C. orsini* bloom for studying movements in natural environment

Medusae were less active during the initial hours with a lesser pulsation rate and constant settlement to the bottom of the tank. It was observed that medusae got stabilized to the aquarium conditions within 12 hours time which were evident from the better pulsation rate and movement of the animal throughout the tank. Thus, animals got fully adapted to the aquarium conditions in two days' time, and no mucous production was further noticed during the entire acclimatization period.

A period of rest or no bell propulsion was pronounced during the dark period than in the light period during the initial days of acclimatization. This was also prominent during the late light and early dark periods. But the resting period got reduced on further days of acclimatization, which later got confined to dark hours only. A kind of aggregation behaviour was noticed in the medusae primarily during the initial days of acclimatization, where they confined to corners of the tank with prominent bell propulsions. This response was recorded near the region of the water inlet, which had the influence of water current.

3.2. Swimming behaviour

The swimming of *Crambionella orsini* is similar to other scyphozoans by the contraction of its bell, which forms a vortex behind the animal and propels it forward. It is followed by the relaxation of the bell, which results in increased drag towards the next pulse. The jellyfish's acceleration happens during the bell's contraction, and as the bell relaxes next time, a second vortex forms above it. The vortex rolls underneath the bell, moving in the same direction the jelly is travelling and continuing to push it forward.

The pulsation rate per minute was more during the daytime (103) than during the night (82) (Table 1). The pulsation rate of *Crambionella orsini* observed in the natural environment during daytime (121) was higher than that in captivity.

Both swimming in terms of vertical and horizontal directions were recorded. The swimming speed of the acclimatized animals recorded in captivity showed that on a daily cycle (Fig. 4), the horizontal movements of the animals were higher during the light period (6.00 am - 8.00 pm) and lower during the dark period (8.00 pm-6.00 am). Similarly, the medusae exhibited vertical upward movements more frequently with higher speed during the light period (6.00 am-8.00 pm) than during the dark period (8.00 pm-6.00 am) (Fig.5). Also, vertical movements were comparatively higher during the afternoon hours of the light period.

Also, vertical downward movements were faster during the light period (6.00 am-8.00 pm) than in the dark period (8.00 pm-6.00 am) (Fig. 6). The highest peak in vertical movements were noticed during the afternoon hours of a day in the 24-hour light-dark cycle.



Fig. 3. Successive movement of the bell of the *Crambionella* orsini during propulsion

3.3. Resting behaviour

Crambionella orsini spent more time swimming during the light period, while resting was more pronounced during the dark period (Fig. 7). On average, the animal spent 2411 and 1189 seconds per hour in swimming and resting during the light period, respectively, while it was 1459 and 2141 seconds per hour during the dark period.

3.4. Feeding behaviour

Feeding response of medusae to live feeds *Artemia* nauplii and copepods (*Temora turbinata*, *Pseudodiaptomous serricaudatus* and *Parvocalanus crassirostris*) was better than frozen feed. The animals were found to be actively swimming throughout the tank on the approach of feed (Fig. 8) with minimum rest. Feeding is enabled by the regular contractions and relaxations of the oral arms and the muscle movements that direct the food materials towards the mouth and all their way into the gastric apparatus where they are digested. These kinds of responses by medusae were similar for all feed types. A reduction in the quantity of feed in the tank indicated the feeding activity of medusae.

Documentation of the pulsation rate of medusae for frozen *Artemia*, copepod and *Artemia* nauplii showed higher numbers of bell pulsations (117 No.s/min) for frozen *Artemia*, *Artemia* nauplii (109 No.s/min) and copepods (102 No.s/min) respectively (Fig. 9). On administration

Table 1. Mean pulsation rate of *Crambionella orsini* in captivity and in wild

Environment		Mean Pulsation rate per minute recorded in the same							
		time period on various days of Acclimatization							Average
	Days	1	2	3	4	5	6	7	
Captivity	Light period	97	104	102	112	107	103	99	108
	Dark period	86	78	86	81	85	82	79	82
Wild	Day hours	120	118	120	115	126	121	124	121



Fig. 4. Horizontal swimming speed of *Crambionella orsini* (mm per second) at various hours of the day



Fig. 5. Vertical upward swimming speed of *Crambionella orsini* (mm per second) at various hours of the day



Fig. 6. Vertical downward swimming speed of *Crambionella orsini* (mm per second) at various hours of the day

of frozen *Artemia*, the medusae produced some amount of mucous, which entrapped the feed and carried along with the animal. Mucous production ceased shortly with a reduction in the feed concentration in the tank. The medusae produced no mucous for the live feed. Thus, mucous production, together with excessive bell pulsations, was assumed to be the result of stress encountered by the animal in response to non-preferred feed type. A noticeable reduction in the animal's size was observed in *Crambionella orsini* in an aquarium for one month. The animals' average bell diameter decreased from 17.59 cm to 12.16 cm and weight from 1446.25 gram to



Fig. 7. Average time (seconds per hour) spent on swimming and rest during the day and night hours by *Crambionella orsini* in the aquarium



Fig. 8. Time spent on swimming and rest by *Crambionella orsini* in the aquarium in response to live and frozen feed



Fig. 9. Pulsation rate of Crambionella orsini per minute under various feeding conditions

760 gram, respectively. This kind of shrinking observed was either due to the differential food preference of *Crambionella orsini*, as the water quality parameters were optimum during the experimental feeding.

3.5. Behaviour in relation to light

The behaviour and response of jellyfish under five different light intensities were dissimilar (Fig. 10). This was apparent from the bell contractions, movement, and the speed of movement exhibited by jellyfish subjected to various light intensities. The activity of medusae increased with an increase in light intensity from 100 to 500 lux. Medusae were found distributed at the surface of the tank on exposure to 100 lux and 250 lux. In 500 lux intensity, medusae were found to be distributed throughout the tank. At higher light intensities (1000 and 1500 lux), the time spent by the animals on the surface showed a sudden decline, instead got distributed towards the bottom of the tank.

Another characteristic feature noticed was that medusae produced mucous when they were exposed to high light intensities (1000 and 1500 lux) during the initial two days of the experiment. This later got reduced and finally ceased so that no mucous production was noticed even when animals were exposed to 1000 lux and 1500 lux.



Fig. 10. Variation in the speed of movement of *Crambionella orsini* (mm per second) in relation to various intensities of light and darkness in the aquarium



Fig. 11. Pulsation rate of *Crambionella orsini* per minute in various light intensities and in darkness

An analysis of the pulsation rate (Fig. 11) of jellyfish showed an increase with an increase in the intensities of light. In contrast to this, the animals in the shaded tank showed a lesser pulsation rate and activity.

The field observations using the underwater video recordings show that the medusa distributions greatly rely on the intensity of sunlight. The occurrence of medusa on the surface waters significantly reduced with an increase in light intensities. Thus, the abundance of medusae on the surface waters were observed more during morning and evening hours when the intensity of incoming light is much less. With higher intensities of light, the medusae moved down vertically.

4. Discussion

4.1. Acclimatization

Pre-experimental acclimatization enabled medusae to accommodate artificial conditions maintained in captivity. Mucous production and resultant clouding of water was a salient feature observed during the initial hours of acclimatization. This could be a natural process of defense by the jellyfish as cnidoblasts were recorded from the mucous secreted. The mucus produced by marine invertebrates, including jellyfish, represents a complex mixture of proteins and polysaccharides and play pivotal roles in the movement, mechanical support, feeding and defense against environmental stresses, predators, parasites, and pathogens (Stabili *et al.*, 2015).

Aggregating behaviour and resting behaviour of the medusae was another notable feature found in *C. orsini* during acclimatization. Aggregation behaviour has been earlier reported from the previous studies conducted with *Aurelia* sp (Hamner *et al.*, 1994; Toyokawa *et al.*, 1997; Purcell *et al.*, 2000; Magome *et al.*, 2007). It was reported that aggregation could be considered as a social behaviour among jellyfish species. Aggregation occurs in those regions of lagoons and semi-closed bays where the influence of external factors like tides, winds and currents were less (Lo and Chen, 2008). Also, aggregations

occurred in regions of abundant prey concentrations (Purcell et al., 2000; Albert, 2007). Kaartvedt et al. (2015) documented apparent social behaviour among jellyfish Periphylla periphylla, which forms small ephemeral groups both at surface and depths. This was made with visual and ROV documentation, which reported aggregations and occasional pair formations by the entanglement of tentacles and are considered to be active group formations. Dense aggregations also occur in other species of scyphozoan jellyfish such as Stomolophus meleagris, Pelagia noctiluca, Mastigias sp. and Linuche unguiculata (Hamner and Hauri, 1981; Shanks and Graham, 1987; Malej, 1989). Resting or a state with reduced pulsation and least responsiveness, especially during dark hours was a common behavioural feature observed in C. orsini in captivity. An advanced form of rest or sleep regarded as reversible behavioural quiescence has been noticed in Cassiopea elegans. This was evaluated by the least active state of the medusae, which spends most of the time sitting upside down at the bottom of the tank or ocean floor during night. Nath et al. (2017) described this particular behaviour as a stage of coma or consciousness accompanied by reduced ability to respond to stimuli compared to active state with reduced pulsation rate. Thus, it was also revealed that during night time both the homeostatic and circadian system regulates quiescence stage, and the animal needs sleep to function (Nath et al., 2017).

The pulsation rate of *C. orsini* in aquarium conditions was comparatively lesser with respect to wild conditions, and also, the resting time spent by *C. orsini* in the aquarium was greater. It was also found that the speed of movement exhibited during locomotion was less. This might be because that *C. orsini* is a typical marine species that migrate to longer distances along water currents and hence show greater speed in natural water bodies and are not fully adapted for a life in confinement. Further research including hydroacoustic studies (Yoon *et al.*, 2002) in the marine environment is required to document the occurrence, distribution and analysis of behavioural patterns.

4.2. Swimming

The pattern of swimming generated by the scyphozoan jellyfish Crambionella orsini used in our studies included horizontal swimming, vertical upward swimming, vertical downward swimming, diagonal as well as irregular patterns. In all modes, swimming was affected by the active propulsion of the bell. The sequence of bell contractions and relaxations made the movement and locomotion of animal in the water column. The speed of bell contractions was one of the factors under consideration in our study. Swimming performance can be defined as the ability of medusae to translate its body through the surrounding fluid (Colin and Costello, 2002). The speed of swimming generated by *C. orsini* was relatively higher with faster bell contractions and relaxations, which led to the propulsion of the animal in the water.

Excellent research by Costello *et al.* (2015) demonstrated that the jellyfish is one of the most energy-efficient swimmers in the oceans. For propulsion, jellyfish contract

the circular muscles that line their bell's undersurface, which contracts their mesoglea bell. The shape of the bell, the size of the velum (relative to the bell diameter) and contraction characteristics also determine how medusae could interact with the surrounding fluid (Colin and Costello, 2002). The pattern of diel vertical migration was described as one of the prominent behaviour exhibited by jellyfish in the wild. Such kind of movement enables them to migrate to deep waters during daytime and to the surface during night time. This is also beneficial to escape from their predators (Hamner, 1995; Arai, 1997; Graham *et al.*, 2001). Some of the studies indicate that the vertical movement of jellyfish is linked to searching the water column for prey like fish (Hays *et al.*, 2012)

4.3. Feeding

Feeding experiments are a common component of behavioural studies in jellyfish. The active response of medusae to live feed and mucous production on the approach of frozen feed were significant observations of the current study. Most research incorporated chemoreception and feeding in jellyfish and used natural prey as main components, and response to prey extracts and natural units (amino acids and peptides) were recorded with observations on feeding behaviour exhibited by the animal (Archdale and Anraku, 2005). Moreover, the jellyfish can digest only the contents of the brine shrimp and the remaining shells were discarded and will be deposited at the bottom of the tank, often contaminating the water. Widmer (2008) states that the cyst may eventually turn black and make a hole through the bell and rot; before feeding jellyfish, it is better to enrich Artemia in SELCO (Self Emulsifying Lipid Concentrate) medium for 18 hours.

The feed preference of C. orsini in aquarium ranged from Artemia nauplii > Copepod > Frozen Artemia. Gut content analysis of wild-collected Chrysaora caliparea by Kanagaraj et al. (2010) expressed dominance of copepod followed by molluscs and fish eggs and larvae. Feeding experiments with the acclimatized species in the same study also explained various stages and duration for copepod digestion. Prey selection behaviour demonstrated by Zeman et al. (2016) on Chrysaora fuscescens showed positive selectivity for non-motile prey such as fish eggs while showing negative selection for motile forms like copepod. However, prey selection indices showed a dominance of copepod in gut content analysis. Determination of feed selectivity on Aurelia aurita showed a preferential selection of copepods and fish eggs when offered a mixture of fish eggs, larvae and wild plankton (Pereira et al., 2014). The feeding behaviour of S. tubulosa, a hydrozoan jellyfish, studied by Hansson and Kiorboe (2006), showed that the capture of copepod elicits a pronounced behavioural response involving the immediate contraction of the capture tentacle and the mouth ingests only one prey at a time, but tentacles not engaged in food transfer may capture another prey while the mouth is busy. Another study on the feeding behaviour of Auralia aurita reveals that prey selection of jellyfish is based on the taste preferences, and the taste is recognised by oral arms (Archdale et al., 2002).

4.4. Influence of light

Light has a profound influence on the orientation, distribution and swimming movements of the jellyfish medusae. This can be validated by the light-induced orientation patterns of *C. orsini* when subjected to different light intensities. The adaptive responses of the medusa to various light intensities thus highlight the presence of highly complex photoreceptor organs that shape distributional mechanisms while choosing the most favourable light intensity for its normal processes. Production of mucous by medusae on exposure to higher light intensities resulted from the stress experienced by the animal under unfavourable light conditions.

Acoustic observations on the influence of absolute light intensity on the dial vertical migration of deep-water jellyfish Periphylla periphylla revealed the avoidance of light by medusae above a certain threshold and preferred for very low light intensities (Dupont et al., 2009). This observation can be related to our experiment, where medusae avoided the surface when subjected to higher light intensities and preferred low light intensities. Other studies also reported that in Chrysaora quinquecirrha aggregations are noticeably higher at low light intensities. It showed negative photoactive movement because of the absence of light-sensing ocelli in marginal sense organs (Schuyler and Sullivan, 1997). This highlights that C. orsini also possesses the photoreceptive ability, which shapes their orientation patterns, since locomotion and aggregation were more during morning and early evening when the light intensity is minimal in the natural environment.

Experiments on jellyfish with light are relatively less due to underdeveloped photoreceptors. However, most of the light experiments were conducted in combination with other parameters such as salinity. And also, light does not profoundly influence every jellyfish process but only affects the orientation and distribution of medusae in response to different light intensities.

5. Conclusion

Knowledge of the feeding patterns of jellyfish is indispensable to ascertain their potential influence on trophic structure and relationship within their ecosystem. Understanding the photoreceptor responses of medusae is essential to determine their orientation and distribution patterns within the water column concerning the light intensity. Our results show that Crambionella orsini acclimatized to aquarium condition within two days, even though activity was comparatively less than in the wild. The feed preference of the medusae ranged from Artemia nauplii>Copepod>Frozen Artemia, although quantification and gut content analysis was not performed. Medusae also exhibited a higher pulsation rate during feeding, which relates feeding and swimming activities to each other. The patterns of behaviour expressed by medusae were different at different light intensities. At higher intensities, the medusae left surface waters and resided to tank bottoms. Mucus production by medusae during acclimatization, unpreferred feed type and higher intensities of light with subsequent size reduction was indicative of the extraneous environment prevalent within the aquarium.

Acknowledgements

Authors thank the financial support of Kerala State Council for Science, Technology and Environment (KSCSTE), Government of Kerala, India (Order No. 766/ 2015/KSCSTE) for the research project on jellyfish and venom proteomics studies. We gratefully acknowledge the Department of Aquatic Biology and Fisheries, the University of Kerala, to provide necessary research facilities.

6. References

- Albert, D.J. 2007. Aurelia labiata medusae (Scyphozoa) in Roscoe Bay avoid tidal dispersion by vertical migration. Journal of Sea Research, 57: 281–287.
- Albert, D.J. 2008. Adaptive behaviours of the Jellyfish Aurelia labiata in Roscoe Bay on the West coast of Canada. Journal of Sea Research, 59: 198-201.
- Albert, J.D. 2011. What's on the mind of a jellyfish? A review of behavioural observations on *Aurelia* sp. jellyfish. *Neuroscience* and *Biobehavioural Reviews*, 35: 474-482.
- Albert, J. 2014. Field observations of four *Aurelia labiata* jellyfish behaviours: swimming down in response to low salinity preempted swimming up in response to touch, but animal and plant materials were captured equally. *Hydrobiologia*, 736: 61–72.
- Anderson, P.A.V. 2004. Cnidarian neurobiology. What does the future holds?. *Hydrobiologia*, 530/531: 107-116.
- Arai, M.N., 1991. Attraction of Aurelia and Aequorea to prey. Hydrobiologia, 216/217: 363–366.

Arai, N.A. 1997. A Functional Biology of Scyphozoa. Chapman & Hall, London, 316 pp.

Archdale, M.V., Yamanouchi, T. and Anraku, K. 2002. Feeding behavior of Aurelia aurita towards Artemia and artificial pellets. Japanese Journal of Taste and Smell Research, 9: 747–750.

- Archdale, M.V. and Anraku, K. 2005. Feeding Behaviour in Scyphozoa, Crustacea and Cephalopoda. *Chemical Senses (Suppl)* 30: 303-304.
- Brotz, L., Chung, W.W.L. and Kleisner, K. 2012. Increasing jellyfish population: trend in Large Marine Ecosystems. *Hydrobiologia*, 69: 3-20.
- Colin, S.P. and Costello, J.H. 2002. Morphology, swimming performance and propulsive mode of six co-occurring hydromedusae. The *Journal of Experimental Biology*, 205: 427-437.
- Condon, R.H., Graham, W.M., Duarte, C.M., Pitt, K.A., Lucas, C.H., Haddock, S.H.D., Sutherland, K.R., Robinson, K.L., Dawson, M.N., Decker, M.B., Mills, M.E., Purcell, J.E., Purcell, J.E., Mianzan, H.W., Uye, S.-I, Gelcich, S. and Madin, L.P. 2012. Questioning the Rise of Gelatinous Zooplankton in the World's Oceans. *Bioscience*, 62(2): 160–169.
- Cruz-Rivera, E. and Abu El-Regal, M. 2016. A bloom of an edible scyphozoan jellyfish in the Red Sea. Marine Biodiversity, 46: 515–519.
- Daryanabard, R. and Dawson, M.N. 2008. Jellyûsh blooms: Crambionella orsini (Scyphozoa: Rhizostomeae) in the Gulf of Oman, Iran, 2002–2003. Journal of Marine Biological Association of United Kingdom, 88: 477–483.

- Dong, Z. 2019. Blooms of the moon jellyfish *Aurelia*: Causes, consequences and controls. In: World Seas: An Environmental Evaluation Sheppard C (ed), 2nd edition. Academic Press, pp 163-171.
- Doyle, T.K., Houghton, J., McDevitt, R., Davenport, J. and Hays, G.C. 2008. The energy density of jellyfish: Estimates from bomb-calorimetry and proximate-composition. *Journal of Experimental Marine Biology and Ecology*, 343: 239-252.
- Dupont, N., Klevjer, T. A., Kaartvedt, S. and Aksnes, D. L. 2009. Diel vertical migration of the deep-water jellyfish *Periphylla periphylla* simulated as individual responses to absolute light intensity. *Limnology and Oceanography*, 54: 1765-1775.
- Gehring, W. J. 2001. The genetic control of the eye development and its implications for the evolution of various eye-types. *Zoology (Jena)* 104: 171-183.
- Graham, W.M., Pages, F. and Hamner, W.M. 2001. A Physical context for gelatinous zooplankton aggregations : a review. *Hydrobiologia* 451: 199-212.
- Hamner, W. M. and Hauri, I. R. 1981. Long distance horizontal migration of zooplankton (Scyphomedusae : Mastigias). *Limnology* and Oceanography. 31: 411-423.
- Hamner, W. H., Hamner, P. P. and Strand, S.W. 1994. Sun-compass migration by *Aurelia aurita* (Scyphozoa) population retention and reproduction in Saanich Inlet, British Columbia. *Marine Biology*, 119: 347-356.
- Hamner, W.M. 1995. Sensory ecology of Scyphomedusae. Marine and Freshwater Behaviour and Physiology, 26: 101-118.
- Hansson, L.J., Kultima, K., 1996. Behavioural response of the scyphozoan jellyfish Aurelia aurita (L.) upon contact with the predatory jellyfish Cyanea capillata (L.). In: Zooplankton: Sensory Ecology and Physiology Lenz, P.H., Hartline, D.K., Purcell, J.E., Macmillan, D.L. (Eds.). Gordon & Breach, UK, pp. 493–499.
- Hansson, L.J. 1997. Capture and digestion of scyphozoan jellyfish Aurelia aurita by Cyanea capillata and prey response to predator contact. Journal of Plankton. Research 19: 195–208.
- Hansson, L. H. and Kiørboe, T. 2006. Prey specific encounter rates and handling efficiencies as causes of prey selectivity in ambush feeding hydromedusae. *Journal of Plankton Research*, 28: (10):1-6.
- Hays, G.C., Doyle, T.K., Houghton, J.R., Lilley, M.K.S., Metcafle, J.D., Righton, D. 2008. Diving behaviour of jellyfish equipped with electronic tags. *Journal of Plankton Research*, 30: 325–331.
- Hays, G.C., Bastian, T., Doyle, T.K., Fossette, S., Gleiss, A.C., Gravenor, M.B., Hobson, V. J., Humphries, N.E., Lilley, M.K.S., Pade, N.G., Sims, D.W. 2012. High activity and Lévy searches: jellyfish can search the water column like fish *Proc. R. Soc. B.* 279: 465–473: http://doi.org/10.1098/rspb.2011.0978.
- Hyman LH. 1940. Metazoa of the tissue grade of construction the radiate phyla Phylum Cnidaria. In: Hyman LH, editor. The Invertebrates: Protozoa through Ctenophora. New York: McGraw-Hill, pp. 365–661.
- Kanagaraj, G., Ezhilarasan, P., Sampathkumar, P., Morandini, A. C., Shivakumar., V. P. 2010. Field and Laboratory Observations on Predation and Prey Selectivity of the Scyphomedusa *Chrysaora cf. caliparea* in Southeast Indian Waters. *Journal of Ocean University of China*, 10 (1): 47-54.
- Kaartvedt, S., Uglang, K. I., Klevjer, T. A., Røstad, A., Titelman, J., and Solberg, I. 2015. Social behaviour in mesopelagic jellyfish. Scientific Reports, 5:11310 | DOI: 10.1038/srep11310
- Kingsford MJ, Beckenb S, Bordehorec C, Fuentesd VL, Pitt KA, Yangihara AA. 2018. Empowering Stakeholders to Manage Stinging Jellyfish: A Perspective. *Coast Management*, 46: 1–18.
- Klein, S. G., Pitt, K. A. and Carroll, A. R. 2016. Reduced salinity increases the susceptibility of zooxanthellate jellyfish to herbicide toxicity during a simulated rainfall event. *Environmental Pollution*, 209: 79-86.
- Kotler, B. P., Morris, D. W., Brown, J. S., 2007. Behavioral indicators and conservation: wielding "the biologist's tricorder". *Israel Journal of Ecology and Evolution*, 53: 237–244.
- Lo, W, T., Chen, I., L. 2008. Population succession and feeding of scyphomedusae, *Aurelia aurita*, in a eutrophic tropical lagoon in Taiwan. *Estuarine Coastal and Shelf Science*, 76: 227–238
- Mackie, G. O. 2004. Central neural circuitry in the Jellyfish Aglantha. Neurosignals, 13: 5-19.
- Magome, S., Yamashita, T., Kohama, T., Kenada, A., Hayami, Takashashi, S. and Takeoka, H. 2007. Jellyfish patch formation investigated by aerial photography and drifter experiment. *Journal of Oceanography*, 63: 761-773
- Malej, A. 1989. Behaviour and trophic ecology of the Jellyfish Pelagia noctiluca (Forsskal, 1775). Journal of Experimental and Marine Biology and Ecology, 126: 259-270.
- Manning, A., Dawkins, M. S. 1988. An Introduction to Animal Behaviour. Cambridge University Press. Cambridge, U. K.
- Mench, J.A. 1998. Why it is important to understand animal behavior. *Institute for Laboratory Animal Research Journal*, 39: 20-26.
- Mench, J.A. and Mason, G.J. 1997. Behavior. In: Animal Welfare, Appleby MC, Hughes BO, editors. Wallingford CT: CAB International, pp, 127-142.
- Morandini, C.A. and Marques, C. A. 2010. Revision of the genus *Chrysaora* Peron & Lesueur, 1810 (Cnidaria :Scyphozoa). *Zootaxa* 2464 : 1-97.
- Nath, D.R. Bedbrook, N. C., Abraham, J.M., Basinger, T., Bois, S.J., Prober, A.D., Sternberg, W.P., Gradinaru, V. and Goentror, L. 2017. The jellyfish *Cassiopea* exhibits a sleep-like state. *Current Biology* 27(19): 2984-2990.
- Oliver, D., Brinkmann, M., Sieger, T., Thurm, U., 2008. Hydrozoan nematocytes send and receive synaptic signals induced by mechano-chemical stimuli. *Journal of Experimental Biology*, 211: 2876-2888.
- Pereira, R., Teodosio, M. A. and Garrido, S. 2014. An experimental study of Aurelia aurita feeding behaviour: Inference of the potential predation impact on a temperate estuarine nursery area. Estuarine, Coastal and Shelf Science, 146: 102-110.
- Purcell, J.E. 1980. Influence of Siphonophore behavior upon their natural diets: evidence for aggressive mimicry. *Science*, 209: 1045-1047.
- Purcell, J.E and Anderson, P.A.V., 1995. Electrical responses to water-soluble components of fish mucus recorded from the cnidocytes of a fish predator, *Physalia physalis. Marine and Freshwater behavioural and Psycology*, 26: 149-162
- Purcell, T. E., Brown, E. D., Stokesburg, K. D. E., Haldorson, L. H. and Shirley, T. C. 2000. Aggregations of the Jellyfish Aurelia labiata: abundance, distribution, association with age – 0 Walleye Pollock and behaviours promoting aggregation in Prince William Sound, Alaska, USA. Marine Ecology Progress Series, 195: 145-158.

- Purcell J.E., Uye S. and Low W.T. 2007. Anthropogenic causes of jellyfish blooms and their direct consequences for humans: a review. *Marine Ecology Progress Series*, 350:153–174.
- Quinones J., Chiaverano L.M. and Ayon P. 2018. Spatial patterns of large jellyfish *Chrysaora plocamia* blooms in the Northern Humboldt Upwelling System in relation to biological drivers and climate. *ICES Journal of Marine Science*, 75:1405-1415.
- Riyas, A., Dahanukar, N., Krishnan, K.A. and Kumar A.B., 2021. Scyphozoan jellyfish blooms and their relationship with environmental factors along the South-eastern Arabian Sea. *Marine Biology Research*, 17:2, 185-199 DOI: 10.1080/ 17451000.2021.1916034.
- Richardson A.J., Bakun A., Hays G.C. and Gibbons M.J. (2009) The jellyfish joyride: causes, consequences and management responses to a more gelatinous future. *Trends in Ecology and Evolution*, 24: 312-322.
- Scatterlie, R. A. 2002. Neural control of swimming in Jellyfish: a comparative story. Canadian Journal of Zoology 80: 1654-1669.
- Schuyler, Q. and Sullivan, B. K. 1997. Light responses and diel migration of the scyphomedusa *Chrysaora quinquecirrha* in mesocosms. *Journal of Plankton Research*. 19(10): 1417-1428.
- Shanks, A.L. and Graham, W.M. 1987. Oriented swimming in the jellyfish *Stomolophus meleagris* L. Agassiz (Scyphozoan: Rhizostomida). *Journal of Experimental Marine Biology and Ecology*, 108:159-169.
- Stabili, L., Schirosi, R., Parisi, M.G., Piraino, S. and Cammarata, M. 2015. The mucus of Actinia equina (Anthozoa, Cnidaria): An unexplored resource for potential applicative purposes. Marine Drugs, 13: 5276-5296.
- Sutherland, W.J. 1998. The importance of behavioural studies in conservation biology. Animal Behaviour, 56: 801-809.
- Thurm, U., Brinkmann, M., Golz, R., Holtmann, M., Oliver, D., Sieger, T. 2004. Mechanoreception and synaptic transmission of hydrozoan nematocytes. *Hydrobiologia*, 530/531: 97-105
- Toyokawa, M., Inagaki, T. and Terazaki, M. 1987. Distribution of *Aurelia aurita* (Linaeus, 1758) in Tokyo Bay : Observations with echosounder and plankton net. In: Proceedings of the 6 th International Conference on Coel. Biol., 1995. National Naturhistorisch Museum, Leiden, Netherlands: 483-490.
- Watanabe, H., Fujisawa, T. and Holstein, W. T. 2009. Cnidarians and the evolutionary origin of the nervous system. *Developmental Growth and Differentiation Journal*, 51: 167-183.
- Watson, G.M. and Hessinger, D.A. 1994. Antagonistic frequency tuning of hair bundles by different chemoreceptors regulates nematocyst discharge. *Journal of Experimental Biology*, 187: 57
- Werner, B., Cutress, C. E. and Studebaker, J. P. 1971. Life Cycle of *Tripedalia cystophora* Conant (Cubomedusae). *Nature*, 232 : 582-583.
- Widmer. C.L. 2008. How to Keep Jellyfish in Aquariums. An introductory guide for maintaining healthy jellies. *Wheat mark*, USA, 192 pp.
- Yoon, E. A., Hwang, D. J., Chae, J., Yoon, W. D., and Lee, K. 2017. Behavior and Frequency Analysis of Aurelia aurita by Using in situ Target Strength at a Port in Southwestern Korea. Ocean Science Journal, 53(1):53-62.
- Zeman, S. M., Brodeur, R. D., Daly, E. A., and Sutherland, K. R. 2016. Prey selection patterns of *Chrysaora fuscescens* in the northern California current. *Journal of Plankton Research* 38(6): 1433-1443.

