Abstract

Adult *Carukia barnesi* medusae feed predominantly on larval fish; however, their mode of prey capture seems more complex than previously described. Our findings revealed that during light conditions, this species extends its tentacles and ‘twitches’ them frequently. This highlights the lure-like nematocyst clusters in the water column, which actively attract larval fish that are consequently stung and consumed. This fishing behavior was not observed during dark conditions, presumably to reduce energy expenditure when they are not luring visually oriented prey. We found that larger medusae have longer tentacles; however, the spacing between the nematocyst clusters is not dependent on size, suggesting that the spacing of the nematocyst clusters is important for prey capture. Additionally, larger specimens twitch their tentacles more frequently than small specimens, which correlate with their recent ontogenetic prey shift from plankton to larval fish. These results indicate that adult medusae of *C. barnesi* are not opportunistically grazing in the water column, but instead utilize sophisticated prey capture techniques to specifically target larval fish.

Introduction

Cnidarians utilize a diverse array of food acquisition/prey capture strategies ranging from reliance on symbiotic zooxanthellae and filter feeding, to active prey capture with nematocyst laden tentacles [1–4]. Those that use nematocysts may implement simple prey capture strategies which rely on size and tentacle structure to opportunistically graze within the water column [5], while others use propulsion and induced swimming kinematics to increase potential prey and food particle contact with trailing tentacles [6]. Others, such as Cubozoans, are highly mobile and possess complicated visual structures, which have been hypothesized to play a role in prey capture [7–10].

Perhaps the most extreme prey capture strategy recorded so far is seen in Siphonophores, which use modified tentacles as ‘lures’ in a form of aggressive mimicry [11]. They actively
attract and lure specific prey types, either through resembling schooling conspecifics, or by mimicking the prey items of the targeted species [3,11–13]. Many Siphonophore lures not only mimic the appearance of other species but also their movements. Specifically, these lures are motile and are often moved using a ‘jigging’ or ‘twitching’ motion, which resembles the movements of specific prey types [3,11].

In many Cnidarians, the diurnal light-dark cycle often mediates a condition-specific behavioral response. For example, numerous Anthozoan and Siphonophore species extend their feeding tentacles only during the day while others only at night [14–16]. Similarly, many species of Hydromedusae and Scyphomedusae use light to facilitate vertical migrations in the water column in order to locate food, while others laterally migrate with the sun to increase solar exposure for symbiotic zooxanthellae [17,18]. Cubozoans also undergo a diurnal behavioral shift [19,20], and vision seems to be one of the factors involved in this diurnal differentiation in behavior [21,22].

Interestingly, a variety of visual systems are utilised by Cnidarians. These range from simple eye spots and pigment cup ocelli to advanced pigment cups with lenses [23–28], with the most advanced visual sensory structures belonging to the medusa stage of the Cubozoans [24,29]. However, there has been contention as to the usefulness of these complex eyes, due to the apparent lack of either neural branches to process the information [30], or a nervous system able to interpret visual images [31].

Cubomedusae do however exhibit many light mediated behaviors [32–34]. These include targeting light shafts for feeding [7], obstacle avoidance [35], actively swimming away from dark objects [36], or decreased activity at night [20]. However, the extent that vision is used in prey capture by Cubozoans is unknown. One highly venomous Cubozoan that possesses sophisticated visual organs is Carukia barnesi Southcott, 1967 [24,33,37,38]. The general ecology and biology of C. barnesi is not well understood. The medusa stage of this species is seasonally present coastally along north-eastern Australia typically from November to May each year. This species is considered oceanic and is found around coral reefs and islands, and under certain conditions, on beaches [39–42]. Juvenile C. barnesi feed predominantly on crustaceans and during maturation undergo an ontogenetic venom change, correlated with a prey shift, from planktonic invertebrates to larval fish [38].

Carukia barnesi have four sets of six ‘eyes’, which is typical among Cubozoans, consisting of a pair of simple light sensitive pigment cups, a pair of light sensitive pigment slits, and a pair of complex eyes that each has a cornea, a lens, and a retina [24,29,36,37]. However, the acuity and use of these eyes is unknown. The complete lifecycle and feeding ecology of this species is poorly understood and has not been described to date. This study describes part of the feeding ecology of the Cubozoan C. barnesi and aims to understand the mechanisms employed by this species to capture its prey.

Method
Species Description
Carukia barnesi is a small (approximately 20 mm bell-width), oceanic, planktonic Carybdeid that inflicts a potentially fatal sting that causes Irukandji Syndrome [39–43]. This species has four tentacles in total and each extends from a pedalia attached to each corner of the bell. These tentacles are up to 750 mm long and have an alternating pattern of large and small nematocyst clusters often referred to as nematocyst-bearing rings or crescents [38,44,45]. These are referred to in this paper as large and small ‘nematocyst clusters’. The bell sizes of the specimens used in these experiments ranged from 8 to 21 mm niche bell (Nb) height (a longitudinal measure from the center of the rhopalia to the apex of the bell).
Specimen Collection

No specific permissions were required for the collection locations/activities as the species involved is not endangered or protected and the collection site did not require permits. Medusae of *C. barnesi* were collected near Double Island, North Queensland, Australia (16°43.5′S, 145°41.0′E) during November 2013, between 1900 and 2200 h. To attract medusae, high-powered LED lights were submerged on each side of a small (five meter) research vessel. Medusae were captured as they approached the light and were transferred into individual 500ml plastic containers. The sea surface temperature varied from 27.5°C to 30°C with an average salinity of 35‰. The water depth at the capture sites varied between three to six meters. Post capture, specimens were transported to the laboratory and placed in a constant temperature controlled cabinet set at 28°C for a minimum of six hours prior to the commencement of experimental trials.

Experimental Tank

Specimens were housed in a purpose-built plankton kreisel (a circular tank [1170 mm X 400 mm wide with an effective volume of ~ 375 liters] in which seawater rotates vertically). Seawater was maintained at 35‰ and 28°C, to mimic oceanic conditions at the specimen capture site. A photoperiod of 13 h light:11 h dark was maintained, with the light period occurring from 0600 to 1900 h to simulate the local November photoperiod. The illumination cycle was achieved by fixing lights on each side of the kreisel that provided an average light intensity of 21μmol photons/s/m², and dark, achieved by turning the lights off with an electronic timer. An infra-red sensitive digital video camera was positioned approximately one meter from the face of the kreisel. Five infra-red spotlights, which remained on continuously, were positioned around the kreisel to allow for filming in darkness.

Size Dependent Tentacle Morphology

In order to determine the relationship between medusae bell size and tentacle length, two *C. barnesi* were placed into the kreisel around midday and allowed to acclimate for approximately six hours prior to each experimental trial. The specimens were then filmed for 24 hours (i.e., a full 13:11 light:dark cycle) beginning with the dark cycle. This was repeated three times, with newly captured specimens, resulting in 24 hour video sequences for six *C. barnesi* medusae. Recorded video sequences were subsequently analyzed in 30 to 60 minute increments, where each tentacle was measured from the pedalia to its terminal end. As identifying individual tentacles on each specimen between time sequences was impossible, all tentacles at any one time were measured and the mean tentacle length of each specimen was calculated. In order to elucidate whether larger specimens, with larger bells, had longer tentacles, regression analysis was used to determine the relationship between bell size (niche bell height mm) and the maximum recorded mean tentacle length of each specimen over 24 hours. Similarly, in order to quantify the relationship between bell size and the distance between the large nematocyst clusters, the distance between six consecutive large nematocyst clusters on an individual extended tentacle were measured to the nearest millimeter for each specimen. The mean large nematocyst cluster distance for each specimen was then calculated and regressed against animal size (niche bell height mm), to determine the relationship between bell size and the distance between the large nematocyst clusters.
The Influence of Light on Tentacle Extension

The effect of the light on tentacle extension (i.e., zero percent extension = shortest and 100% extension = longest tentacle length of each specimen) was determined at 0, 30, 60, 120, 240 and 360 minutes of exposure to both light and dark treatments. These values were arcsine square root transformed (to normalize proportional data) prior to analysis, which consisted of a two-way repeated measures ANOVA to determine if: a) light or dark; or b) the amount of time exposed to light or dark; or c) an interaction between the two, affected the percent tentacle extension. All statistical analyses were conducted using the statistics package IBM SPSS.

The Effect of Bell Size, Light and Tentacle Extension on ‘Twitch Rate’

During the previous experiments, the extended tentacles would frequently contract in a jerking or ‘twitching’ motion, and then relax. To quantify the occurrence of these twitches, one minute sections of the video footage were analyzed in nine approximately 30-minute intervals for each specimen (i.e., 6 specimens measured 9 times each). The number of these contractions, or ‘twitches’, during each one minute sample was recorded. A ‘twitch’ was counted any time a tentacle rapidly contracted in a distinct pulse during each one minute measure, resulting in a value for ‘twitch rate per minute’ (see S1 Video). This was conducted for each specimen, and only footage from the light treatment was analyzed as twitching was not recorded in dark conditions (refer to Experimental Tank section). Linear regression was performed in order to determine if the rate of these twitches was affected by the state of a specimens tentacles (i.e., percent extended). Following this, to elucidate whether this relationship was driven by a specimen size effect (bell size), percent tentacle extension was pooled into 10 percent groups (i.e., 0–10%, 11–20%, etc.) and an ANCOVA conducted to determine if tentacle extension influenced the twitch rate, with bell size set as the covariate.

Prey Capture

On three occasions, two C. barnesi medusae were housed in the kreisel with approximately ten larval/juvenile fish (Acanthochromis sp.; approximately 10–15 mm in length). The larval/juvenile fish were reared, housed and used as outlined in the ethics approval “Approval for Animal Based Research or Teaching—A2061” (granted to Dr Jamie Seymour by the James Cook University Animal Ethics Committee). Breeding pairs of Acantochromis sp. were held in a 3,000 liter tank and the larval/juvenile fish feed naturally on crustaceans, such as copepods and amphipods, which occur within the 50,000 liter recirculating aquarium system. All fish used were free feeding at the beginning of this study and were only held with the C. barnesi for approximately 10 minutes per feeding event. Fish that were stung were consumed by the C. barnesi and any fish that were not consumed were returned to the larval/juvenile fish tank. During these feeding events the fish were seen to rapidly move towards the twitching tentacles and were subsequently envenomed and caught. This process was captured on video on numerous occasions and still images were extracted to investigate the prey capture method implemented by C. barnesi.

Results

Size Dependent Tentacle Morphology

There was a statistically significant positive relationship between bell size (niche bell height mm) and tentacle length, where larger specimens had longer tentacles than smaller specimens ($R^2 = 0.796, F_{1,4} = 16.642, p = 0.017$) (see Fig 1). Conversely, the distance between the large
nematocyst clusters was not correlated with bell size ($R^2 = 0.003, F_{1, 4} = 0.13, p = 0.916$), with a mean distance of 30 mm ($\pm 6$ mm 95%CI) on extended tentacles.

The Influence of Light on Tentacle Extension

*Carukia barnesi* tentacles were significantly longer during the light treatment than in the dark treatment ($F_{1, 5} = 7.112, p = 0.045$), while time had no significant effect ($F_{5, 25} = 0.216, p = 0.952$). However, there was a significant interaction effect between the light/dark treatments and time ($F_{5, 25} = 10.100, p < 0.001$). Tentacles contracted as the dark treatment progressed reaching a contracted state of less than 20% after approximately two hours. After the lights were turned on, tentacles began to extend reaching maximum mean extension of approximately 80% after approximately six hours exposure to the light treatment (see Fig 2).

The Influence of Bell Size, Light and Tentacle Extension on ‘Twitch Rate’

There was a significant positive relationship between tentacle extension and twitch rate, with elongated tentacles twitching more frequently (twitches per minute) than retracted tentacles ($R^2 = 0.492, F_{1, 53} = 50.397, p < 0.001$) (see Fig 3), while bell size also affected the twitch rate
(F<sub>4, 54</sub> = 2.718, p = 0.040), where larger animals ‘twitch’ their tentacles more frequently than small specimens (see Fig 4). The average twitch rate during the light was 6.3 twitches per minute however no twitching was recorded during the dark.

Prey Capture

Larval fish (*Acanthochromis* sp.) were often attracted to the nematocyst clusters on the extended fishing tentacles of *C. barnesi* especially when they were being ‘twitched’. Fish would pursue these clusters and become ‘stung’ around the mouth region or head, resulting in death (see Fig 5 and S2 Video).

Discussion

Adult *C. barnesi* are known to feed almost exclusively on larval fish [38]; however, their mode of prey capture seems more complex than previously described. Our findings suggest that *C. barnesi* are active predators that capture visually orientated prey, in this case larval fish, by using a lure-like system to simulate the size and movements of the fish’s prey (e.g., small plankton). This method of prey capture has previously been described in some Siphonophores.
Prey Capture Ecology of the Cubozoan *Carukia barnesi*

[3,11], and considered unique compared to other Cnidarians. Many larval fish are visual hunters and because of this feed predominately during light conditions [46], and this correlated well with the luring behavior seen in *C. barnesi* that occurs only during daylight hours. Luring at night would be less efficient resulting in reduced prey capture and contracting their tentacles at night would decrease swimming induced drag, thus reducing energy expenditure. This suggested feeding cycle is consistent with the diurnal feeding cycle observed in another Cubozoan (i.e., *Chironex fleckeri*, Southcott, 1956), which is known to become inactive at night to conserve energy [20].

The nematocyst clusters along the extended tentacles are also motile, where *C. barnesi* ‘jig’ or ‘twitch’ these tentacles frequently. Fish, including larval fish, are known to be attracted to prey by movement, and may preferentially attack prey items of specific sizes [47]. In order to increase catch rates, twitching, or movement of the nematocyst clusters, would appear to serve this purpose, where movement of the nematocyst clusters would highlight these lures in the water column. Once larval fish are attracted to these nematocyst clusters they are consequentially ‘stung’ and consumed. Furthermore, larger *C. barnesi* were found to twitch their tentacles more frequently than smaller specimens, which may be related to their recent ontogenetic transition from planktonic to vertebrate prey [38]. Smaller medusae (under 8 mm) have a
preference for plankton, and these prey items are almost certainly captured in a similar manner as used by other Cnidarian medusae, that is, by haphazardly encountering prey in the water column. As such, twitching of tentacles, which presumably increases energy consumption, would be inefficient for the capture of small plankton, which may explain the lower twitch rate observed in the smaller specimens (8–10 mm).

Not surprisingly, larger medusae were found to have longer tentacles, which would presumably increase their chance of prey capture and correlates with the change in prey preference from plankton to larval fish. However, it was surprising that the distance between the nematocyst clusters, or lures, was similar regardless of the length of their tentacles. This suggests that the distance between the nematocyst clusters are important for the visual stimulation of prey and/or to optimize prey capture (i.e., the lures are set at an optimum distance for prey capture). The function of the alternation between large and small nematocyst clusters along the tentacles is unknown; however, they may be used to target different sizes of larval fish by presenting a choice of lure/food particle sizes. Further research is required to determine the specific function of the large and small nematocyst clusters.

Cubomedusae have been shown to be more sophisticated in many areas of their ecology than most other Cnidarians. For example, they have elevated swimming speeds [48,49], greater

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**Fig 4.** The mean number of tentacle twitches recorded for *Carukia barnesi*, over one minute intervals (twitch rate per minute) plotted against medusae bell size in millimeters. Error bars represent 95% confidence intervals (n = 6).

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vision capabilities [24,33,50], more sophisticated behaviors (e.g., sleeping) [19,20] and highly toxic venoms [40,43,51]. In conclusion, this research has demonstrated that *C. barnesi* utilize sophisticated prey capture techniques to actively lure prey. Future investigation into other species of Cubomedusae is now required to determine if they too employ sophisticated prey capture mechanisms.

**Supporting Information**

**S1 Video.** Quantification of a ‘twitch’ of the tentacles of *Carukia barnesi*. Note the two distinct twitch events during this 11 second video sequence. The first twitch event occurs after approximately one second of elapsed time. The second twitch event occurs eight seconds later. (MP4)

**S2 Video.** Envenomation of a larval fish (*Acanthochromis* sp.) that was captured by a twitching tentacle of an adult *Carukia barnesi*. The bell size of this specimen is approximately 15 mm in height and the fish is approximately 10 mm in length. Note the envenomation site is on the head region of the fish. (MP4)
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Author Contributions

Conceived and designed the experiments: RC NS JS. Performed the experiments: RC JS. Analyzed the data: RC RJ JS. Contributed reagents/materials/analysis tools: RC JS. Wrote the paper: RC NS RJ JS.

References

1. Arai MN. A functional biology of Scyphozoa. London: Chapman & Hall; 1997.
2. Grossowicz M, Benayahu Y. Differential morphological features of two Dendronephthya soft coral special suggests differences in feeding niches. Marine Biodiversity. 2012; 42: 65–72. doi: 10.1007/s12526-011-0093-0
3. Mapstone GM. Global diversity and review of Siphonophorae (Cnideria: Hydrozoa). PLoS One. 2014; 9(2). doi: 10.1371/journal.pone.0087737
4. Venn AA, Loram JE, Douglas AE. Photosynthetic symbioses in animals. Journal of Experimental Botany, Special Issue. 2008; 59; 1069–1080.
5. Brewer RH. The annual pattern of feeding, growth, and sexual reproduction in Cyanea (Cnideria: Scyphozoa) in the Niantic River Estuary, Connecticut. Biological Bulletin. 1989; 176(3): 272–281. Available: http://www.jstor.or/stable/1541985.
6. D’Ambra I, Costello JH, Bentivegna F. Flow and prey capture by the scyphomedusa Phyllorhiza punctata von Lendenfeld, 1884. Hydrobiologia. 2001; 451: 223–227.
7. Buskey EJ. Behavioral adaptations of the cubozoan medusa Tripedalia cystophora for on feeding copepod. Marine Biology. 2003; 142: 225–232. doi: 10.1007/s00227-002-0938-y
8. Matsumoto G. Observations on the anatomy and behaviour of the cubozoan Carybdea rastonii Haacke. Marine and Freshwater Behaviour and Physiology. 1996; 26: 139–148.
9. Pearse J, Pearse V. Vision in cubomedusan jellyfishes. Science. 1978; 199: 458. PMID: 22934
10. Stewart SE. Field behaviour of Tripedalia cystophora (Class Cubozoa). Marine and Freshwater Behaviour and Physiology. 1996; 27(2–3): 175–188.
11. Purcell JE. Influence of Siphonophore behavior upon the natural diets: Evidence for aggressive mimicry. Science, New Series. 1980; 209(4460):1045–1047. PMID: 17747233
12. Haddock S, Dunn C, Pugh P, Schnitzler C. Bioluminescent and red-fluorescent lures in a deep-sea Siphonophore. Science. 2005; 309: 263. PMID: 16002609
13. Pugh P, Haddock S. Three new species of Resomid Siphonophore (Siphonophora: Physonectae). Journal of the Marine Biological Association of the United Kingdom. 2010; 90(6): 1119–1143. doi: 10.1017/S0025315409990543
14. Purcell JE. V dietary composition and deil feeling patters of epipelagic Siphonophores. Marine Biology. 1981; 65: 83–90.
15. Sebens K P, DeRiemer K. Diel cycles of expansion and contractions in coral reef Anthozoans. Marine Biology. 1977: 43: 247–256.
16. Sorek M, Diaz-Almeyda E, Medina M, Levy O. Circadian clocks in symbiotic corals: The duet between Symbiodinium algae and their coral host. Marine Genomics. 214; 14: 47–57. doi: 10.1016/j.mgene.2014.01.003 PMID: 24508015
17. Graham WM, Pages F, Hamner WM. A physical context for gelatinous zooplankton aggregations: A review. Hydrobiologia. 2001; 451: 199–212.
18. Hamner WM, Hauri IR. Longdistance horizontal migrations of zooplankton (Scyphomedusea: Mastilgias). Limnology Oceanography. 1981; 26: 414–423.
19. Gordon MR, Seymour JE. Quantifying movement of the tropical Australian cubozoan Chironex fleckeri using telemetry. Hydrobiologia. 2009; 616: 87–97. doi: 10.1007/s10750-008-9594-720
20. Seymour JE, Carrette TJ, Southerland PA. Do box jellyfish sleep at night? The Medical Journal of Australia. 2004; 181(11): 707.
21. Garm A, Bielecki J, Petrie R, Nisson DE. Opposite patterns of diurnal activity in the box jellyfish Tripedalia cystophora and Sapula sivickisis. Biological Bulletin. 2012; 222: 35–45. PMID: 22426630
22. Land MF. The evolution of lenses. Ophthalmic & Physiological Optics. 2012; 32: 449–460.
23. Blumer MJ, Von Salvini-Plawen L, Kikinger R, Büchinger T. Ocelli in a Cnidarian polyp: The ultrastructure of the pigment spots in Stylocoronella riedli (Scyphozoa, Stauromedusae). Zoomorphology. 1995; 115: 221–227.
24. Nilsson D-E, Gislén L, Coates MM, Skogh C, Garm A. Advanced optics in a jellyfish eye. Letters to Nature. 2005; 435: 201–205.
25. Norstom K., Wallen R, Seymour J, Nilsson D. A simple visual system without neurons in jellyfish larvae. Proceedings of the Royal Society of Biological Sciences. 2003; 270: 2349–2354. PMID: 14667350
26. Singla CL. Ocelli of hydromedusae. Cell and Tissue Research. 1976; 170: 325–339. PMID: 8210
27. Yamashita T, Yoshida M. Electron microscopy on the photoreceptors of an anthomedusan and a scyphomedusa. Pub Seto Marine Biology Laboratory. 1973; 20: 757–778.
28. Yamashita T, Yoshida M. Fine structure of complex ocelli of a cubomedusan, Tamoya bursaria Haeckel. Cell and Tissue Research. 1976; 170: 325–339. PMID: 17395227
29. Martin VJ. Photoreceptors of cnidarians. Canadian Journal of Zoology. 2002; 80: 1703–1722.
30. Gerhart J, Kirschner M. Cells, embryos, and evolution. Malden, MA: Blackwell Science; 1997.
31. Nilsson D-E, Pelger S. A pessimistic estimate of the time required for the eye to evolve. Proceedings of the Biological Sciences. 1994; 256(1346): 53–58.
32. Barnes J. Studies on three venomous cubomedusae. In: Rees W, editor. The Cnidaria and their evolution. New York: Academic Press; 1966. pp. 307–332.
33. Coates MM. Visual ecology and functional morphology of the Cuboza. Integrative and Comparative Biology. 2003; 43: 542–548. doi: 10.1093/icb/43.4.542 PMID: 21680462
34. Hartwick R. Observations on the anatomy, behaviour, reproduction and life cycle of the cubozoan Carybdea sivickisi. Hydrobiologia. 1999; 216/217: 181–188. PMID: 313492
35. Garm A, O’Connor L, Parkelfelt L, Nilsson D-E. Visually guided obstacle avoidance in the box jellyfish Tripedalia cystophora and Chiropesella bronze. The Journal of Experimental Biology. 2007; 210: 3616–3623. doi: 10.1242/jeb.004044 PMID: 17921163
36. Hamner WM, Jones MS, Hamner PP. Swimming, feeding, circulation and vision in the Australian box jellyfish, Chironex fleckeri (Cnidaria:Cubozoa). Marine and Freshwater Research. 1995; 46: 985–990.
37. Piatigorsky J, Horwitz J, Kuwabara T, Cutress CE. The cellular eye lens and crystallins of cubomedusan jellyfish. Journal of Comparative Physiology. 1989; 164: 577–587. PMID: 2565398
38. Underwood A, Seymour JE. Venom ontogeny, diet and morphology in Carukia barnesi, a species of Australian box jellyfish that causes Irukandji syndrome. Toxicon. 2007; 49: 1073–1082. doi: 10.1016/j.toxicon.2007.01.014 PMID: 17395227
39. Barnes J. Cause and effect in Irukandji stings. The Medical Journal of Australia. 1964; 1: 897–905. PMID: 14172390
40. Carrette TJ, Underwood AH, Seymour JE. Irukandji Syndrome: A widely misunderstood and poorly researched tropical marine envenoming. Diving and Hyperbaric Medicine. 2012; 42(4): 214–223. PMID: 23258458
41. Kingsford MJ, Seymour JE, O’Callaghan, MD. Abundance patterns of cubozoans on and near the Great Barrier Reef. Hydrobiologia. 2012; 69: 257–268. doi: 10.1007/s10750-012-1041-0
42. Kinsey BE. More Barnes on box jellyfish. Unpublished folio manuscripts held in the archives of James Cook University, North Queensland; 1988.
43. Pereira P, Barry J, Corkeron M, Keir P, Little M, Seymour JE. Intracerebral hemorrhage and death after envenoming by the jellyfish Carukia barnesi. Clinical Technology. 2012; 48: 390–392. doi: 10.3109/15563651003662675
44. Bentlage B, Lewis C. An illustrated key and synopsis of the families and genera of Carybdea box jellyfishes (Cnidaria: Cuboza: Carybdeida), with emphasis on the “Irukandji family” (Carukiidae). Journal of Natural History. 2012; 46(41–42): 2595–2620. doi: 10.1080/00222933.2012.717645
45. Southcott RV. Revision of some Carybdeidae (Scyphozoa: Cubomedusae), including a description of the jellyfish responsible for the “Irukandji syndrome”. Australian Journal of Zoology. 1967; 15: 651–671.
46. Puvanendran V, Brown JA. Foraging, growth and survival of Atlantic cod larvae reared in different light intensities and photoperiods. Aquaculture. 2002; 214: 131–151.
47. Hunter JR. The feeding behavior and ecology of marine fish larvae. In: Bardack JE, Magnuson JJ, May RC, Reinhart JM editors. Fish behavior and its use in the capture and culture of fishes. ICLARM
48. Colin SP, Costello JH, Katija K, Seymour JE, Kiefer K. Propulsion in Cubomedusea: Mechanisms and utility. PLoS ONE. 2013; 8(2). doi:10.1371/journal.pone.0056393

49. Shorten M, Davenport J, Seymour JE, Cross M, Carrette T, Woodward G, et al. Kinematic analysis of swimming in Australian box jellyfish—Chiropsalmus sp. and Chironex fleckeri (Cubozoa, Cnidaria, Chir-rodopidae). Journal of Zoology. 2005; 267: 371–380.

50. Garm A, Coates MM, Gad R, Seymour JE, Nilsson DE. The lens eyes of the box jellyfish Tripedalia cystophora and Chiropsalmus sp. Are slow and color-blind. Journal of comparative Physiology A-Neuroethology Sensory Neural and Behavioral Physiology. 2007; 193(5): 547–557.

51. Charousis S, Smout M, Wilson D, Loukas A, Mulvenna J, Seymour JE. Rapid short term and gradual permanent cardiotoxic effects of vertebrate toxins from Chironex fleckeri (Australian box jellyfish) venom. Toxicon. 2014; 80: 17–26. doi:10.1016/j.toxicon.2014.01.007 PMID: 24462661