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PRIMARY RESEARCH PAPER

Physiological and morphological responses of 'Irukandji' polyps to thermal and osmotic conditions: consequences for niche profiling

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Abstract The Irukandji jellyfish (*Carukia barnesi)* is a medically important species. While the medusa stage of this species is well known, due to its highly venomous sting, the benthic polyp has core roles in regulating both the timing and abundance of medusa making it a research priority. However, due to their small size, *Carukia barnesi* polyps have never been found in situ and, basic ecological knowledge surrounding this life stage is limited. In this study we adopt a lab-based approach, utilizing physiological tolerance as a functional tool, to gain new insights into the *in situ* location for *Carukia barnesi* polyps. The physiological tolerance of *Carukia barnesi* polyps was characterized by measuring the oxygen consumption rates of polyps exposed to different salinity/temperature combinations. A total of nine salinities and seven temperatures were investigated, ranging from 11 °C/16‰ to 34 °C/42.5‰, encompassing the spectrum of environments experienced on the Great Barrier Reef. Polyps were also monitored for morphological changes such as asexual reproduction, polyp deterioration, and mortality. Salinity did not have a significant effect on oxygen consumption rates, with *Carukia barnesi* polyps displaying a significant tolerance to a wide range of salinities. The effect of temperature, however, was statistically significant with oxygen °consumption rates increasing alongside water temperature. There was no statistical evidence to support an interactive effect between salinity and temperature. Based on these results, we conclude that the polyp stage of this species is likely located in an environment with stable temperatures and fluctuating salinities and, consequently, future endeavors aimed at locating this life stage should expand targeted survey areas outside stable oceanic environments, typical of medusa, and encompass dynamic environments such as estuaries and submarine freshwater upwellings.

Keywords Irukandji · Metabolic rate · In situ location · Niche modeling · Oxygen consumption · Logistically difficult species

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Introduction

Understanding species distributions is critical for a wide range of ecological applications, ranging from invasive species control to the forecast of species adaptability to climate change (Thomsen & Willerslev, 2015). Typically, this involves correlating species abundance with a set of biotic and abiotic factors (such as temperature, terrain, and habitat availability) (Kearney & Porter, 2009; Kearney et al., 2010). However, for organisms that are logistically difficult or dangerous to detect in the field, this traditional approach to biological understanding is near impossible, limiting our ability to effectively manage the species (Rowley et al., 2020). The 'Irukandji' jellyfish *Carukia barnesi* Southcott, 1976 is particularly difficult to track in the field due to its very small (~35 mm), transparent, cube-shaped bell, and highly venomous sting (Carrette et al., 2012). Being the namesake of the 'Irukandji syndrome', contact with this near-invisible marine invertebrate can lead to extreme pain and death (Southcott, 1967; Pereira et al., 2010; Carrette et al., 2012).

Carukia barnesi medusae are present in the tropical waters of north-eastern Australia and exhibit marked seasonality in synchrony with the monsoonal month's (Barnes & Kinsey, 1986; Carrette et al., 2012; Courtney et al., 2015, 2016a, b). During this 'stinger season', the loss of revenue for the local tourism industry is significant and the direct costs associated with treating sting victims in Northern Queensland is approximated to be between one and three million dollars per year (Carrette et al., 2012). However, despite this species' significant economic consequences uncertainty still surrounds its ecology (Courtney et al., 2016a, c). Vital ecological information, for example a well-supported consensus on the causal drivers of seasonal medusa presence and abundance alongside geographic distribution limits, remain unknown (Carrette et al., 2012; Courtney et al., 2016b).

Carukia barnesi has a metagenetic life cycle, alternating between a sexually reproducing, free swimming, medusa and an asexually reproducing, sessile polyp (Werner et al., 1971; Cutress & Studebaker, 1973; Arneson & Cutress, 1976; Hartwick, 1991). While it is the sexually mature medusa stage that possesses a direct threat to humans, and consequently has been the focus of existing literature, research surrounding the role of the polyp is growing. It is now understood that this life stage is a major driver of both, seasonal periodicity; through synchronous timing of medusa production, and medusa abundance; through polyp settlement and asexual reproduction (Courtney et al., 2016a, c). However, despite this fundamental link, the current state of knowledge on the distribution, and basic ecology of the polyp stage is very limited (Courtney et al., 2016a; Boco et al., 2019). This is predominantly due to factors such as their small size (~1 to 2 mm), patchy distribution, seasonality, and cryptic nature, making foundational ecological investigations extremely difficult (Courtney et al., 2016a, c). Consequently, the polyps of *C. barnesi* have never been found in situ, and laboratory-based cultures form the foundation of all research on this species (Courtney et al., 2016a).

A recent study examined the effects of two fundamental environmental parameters, salinity and temperature, on population expansion in *C. barnesi* polyps via asexual budding (Courtney et al., 2016a). Utilizing reproductive output, and focusing on long-term trends, the authors gained vital ecological clues into aspects of the hypothetical in situ location for this species. However, while reproduction is one way of measuring species fitness and environmental suitability, questions remain as to the mechanistic ecophysiological drivers of these trends and the overall functional biology of the polyp.

Metabolic data are commonly used for marine organisms as a mechanistic link, and ecological profiling tool, aimed toward the measure of environmental suitability and overall organism fitness (Verberk et al., 2016). Using tools such as metabolic 'scope', and physiological performance profiles, information can be obtained about physiological tolerance and preference of the target organism (Kearney & Porter, 2009). Concerning jellyfish polyps, very few studies have examined this functional relationship and, of those that have, the literature is dominated by i) research on the more common scyphozoan species and ii) studies that focus on the metabolic consequences of temperature alone (Mangum et al., 1972; Gambill & Peck, 2014; Höhn et al., 2017).

Here, we aim to build on current literature by investigating the physiological and morphological response of *C. barnesi* polyps to varying salinity and temperature regimes. The ultimate goal is to better describe the fundamental physiological niche

of *C. barnesi* polyps to better manage this medically important logistically difficult species. This was achieved through a lab-based approach and evaluating the effects of salinity and temperature on polyp physiology (determined as oxygen consumption) and morphology. We selected the particular thermal and osmotic ranges to represent potential niche habitats for this species throughout the Great Barrier Reef.

Methods and materials

Polyp origin and maintenance

Experimental *C. barnesi* polyps were obtained from laboratory-based cultures. These polyp cultures were established from wild medusae, caught approximately 24 months before experiments, from Double Island Queensland Australia (Courtney et al., 2016b). For the months before experimental trials, all cultures were maintained in bio-orbs at a constant temperature of 27 °C, salinity of 34‰, and in complete darkness with constant aeration. Polyps were fed freshly hatched *Artemia salina* (Linnaeus,1758) nauplii every two days but were starved for 24 h preceding experimental initiation to avoid the effect of digestion on rates of oxygen consumption.

Condition observations and pre-treatment acclimation

Prior to experiments, *C. barnesi* polyps were hand-selected, gently detached from bio-orbs, and observed, for physical condition. Only healthy polyps with fully extended tentacles were targeted. This ensured that life stages were consistent across all treatments (all experimental polyps were in their formed mature stage) and that polyps were of a consistent size. Any polyps showing physical signs of asexual reproduction (budding) before experiments were removed. Following selection, polyps were washed in autoclaved seawater and underwent an acclimation process to meet experimental conditions.

Acclimation involved polyps being held in an intermediate apparatus (external to respirometry chambers) consisting of aerated 1L glass beakers held in a temperature-controlled water bath. Here, the temperature and salinity parameters were altered (either increased or reduced—depending on treatment) at a rate of 2 °C/h and 3‰/h. In prioritizing the rate of change over the duration of change we were able to alter temperature and salinity from housing conditions to experimental conditions gradually avoiding animal shock. The temperature was altered using a heater/chiller unit and salinity was altered using a mix of aquarium-grade salt and milli-Q water administered on a continuous drip system. Acclimation periods were staggered to ensure target salinity and temperature were met in synchrony. Once at the correct parameters, each polyp sat for one hour before being loaded into the respiration chambers.

Polyp oxygen consumption measurements

The oxygen consumption rates of individual *C. barnesi* polyps were measured using a fibreoptic presence sensor dish reader system equipped with 24 individual 0.5 ml chambers. Chamber size was selected to accommodate for organism size while also enabling polyp respiration to be registered without stirring. Prior to the addition of polyps, all respiration chambers were situated to experimental conditions by submersion in water baths and pre-filled with water at the correct salinity. This ensured that chambers were at the correct temperatures, upon experiment initiation, and that oxygen sensor spots were suitably hydrated at the correct water parameters. Saltwater was exchanged before the addition of polyps (and experiment initiation) to safeguard water quality and ensure 100% air saturation. To reduce bacterial contamination all seawater used in experiments was autoclaved and filtered (0.22 µm).

Carukia barnesi oxygen consumption was measured in response to a combination matrix consisting of seven temperatures (14, 18, 21, 25, 28, 31, 34 °C ± 0.5) and nine salinities (16, 19, 22.5, 26, 29, 34, 36, 39‰, and 42.5 ± 0.5). Temperature and salinity parameters were selected as they encompass the spectrum of temperature/salinity regimes experienced on the Great Barrier Reef while also including conditions typically experienced in bordering coastal and estuarine environments.

Individual polyps were loaded into chambers using a pipette and chambers were checked for microbubbles and then subsequently sealed. A three-step system was used to seal chambers consisting of parafilm, a silicon mat, and a weighted block. All chambers were re-submerged within a temperature-controlled (±0.5 °C) water bath and the first measurement

occurred 30 min following loading. This 30-min delay enabled chamber plates to re-reach experimental temperature following animal loading and for polyps to settle. Over the course of several hours, the oxygen concentration of the chamber was recorded once every minute. Oxygen within the chamber never dropped below < 70% saturation. All chambers were cleaned and dried between trials.

A total of 62 experimental trials were conducted each with 20 experimental chambers holding an individual polyp, and four control chambers containing autoclaved seawater and a small amount of transfer water. One salinity/temperature combination was omitted from experimental trials due to equipment failure (26‰/14 °C).

Recording morphological effects

Upon completion of each trial, every polyp was observed and scored for a health condition, and signs of asexual reproduction, using a dissection microscope. Polyps were noted as either exhibiting (i) no morphological change (ii) deterioration—classified as a significant reduction in size, retraction of tentacles, or polyp encystment, or (iii) death—classified as complete structural breakdown. Morphological features were assigned based on images of polyps. Asexual reproduction was defined as any polyp exhibiting evidence of this budding, and signs ranged from conspicuous indicators of budding, such as bulging on polyp stalk, to complete bud formation and detachment. All morphological classifications.

Mass estimates

Due to the small size (~ 1 to 2 mm), and number, of experimental *C. barnesi* polyps all individual polyp oxygen consumption rates, were mass adjusted by an average polyp mass of 28.9 µg. This was to allow for the obtained results to be compared with existing research alongside research on other species in the future. The average polyp mass was derived from a selection of 30 individual *C. barnesi* polyps (obtained from the same experimental cultures). Each polyp was washed in reverse osmosis water, to eliminate polyp salt content, and subsequently lyophilized for 24 h. Upon completion, each lyophilized polyp was weighed three times using a six-point microbalance and a mean value was calculated. The information on all individual weights can be found in Supplementary Table 1.

Statistical analysis

The oxygen consumption rate was calculated from the slope of the linear decrease in O_2 concentration versus time (as per Gambill and Peck 2014). Only slopes with a correlation coefficient (R^2) of 0.7 or above were deemed to be representative of raw physiological recordings and were retained in the analysis. To account for background respiration the mean slope of the four control chambers was subtracted from each experimental chamber. Individual oxygen consumption rates were adjusted to account for an average polyp mass and the mean rate of oxygen consumption (nmol O_2 h μg^{-1}) for each salinity/temperature combination was generated with the associated error (for a full table of sample size see Supplementary Table 2).

The effect of temperature and salinity on *C. barnesi* polyp oxygen consumption rates were analyzed using a generalized linear model (GLM), assuming a gamma error with an inverse link function. This statistical approach was selected as the primary objective of this study was to observe general physiological trends and tolerance. All figures were produced, and statistics conducted, using R software (R Core Team, 2012).

Results

Over the duration of this research, a total of 63 individual experiments were run over nine salinities and seven temperatures. Temperatures and salinities ranged from 11 to 34 °C and 16 to 42‰ respectively, and encompassed a total of 1240 individual *C. barnesi* polyps. All experiments ran for an average of 24 h with morphological changes observed upon experimental completion and polyp oxygen consumption rates calculated for the first 10 h.

Effects of salinity and temperature on polyp health condition and asexual reproduction.

Upon the completion of experimental trials, polyp physical conditions varied (Fig. 1). Overall, rates of polyp mortality throughout salinity/temperature treatments were low. Two experimental trials resulted

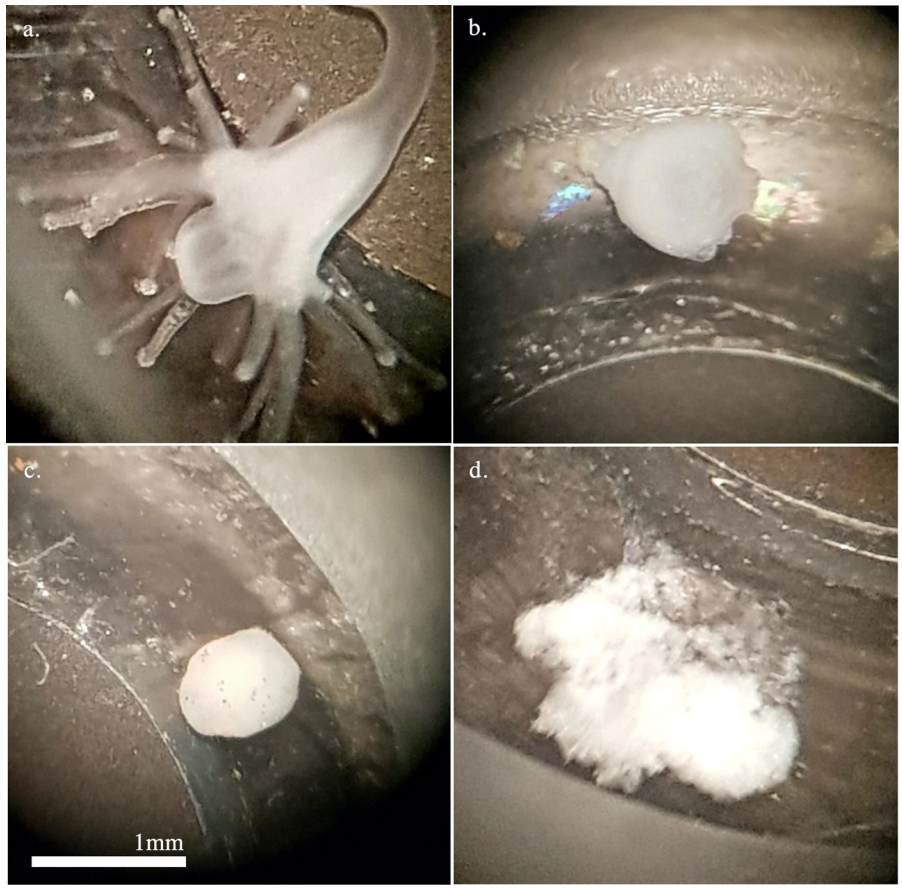

Fig. 1 Polyp morphological conditions. The final condition of polyps exposed to different salinity and temperature regimes **a** 'normal' (25ºC/22 ‰), **b** contracted tentacles' (18ºC/16 ‰), **c** 'encysted' (34ºC/19 ‰) and **d** 'dead' (14ºC/16 ‰)

in 100% polyp mortality; however, both treatments were at limit conditions (16‰/14 °C, 19‰/14 °C). Of the remaining 60 treatments, only one individual salinity/temperature combination displayed a polyp mortality rate above 50% and the mean mortality rate across all trials was 2.25%. Likewise, the proportion of *C. barnesi* polyps that exhibited signs of physical deterioration, upon trial completion, was small. Excluding those polyps that died, there was an 8.6% deterioration rate recorded across all thermal/osmotic treatments. Similar to trends in polyp mortality, nearly all deteriorated polyps were identified in experimental trials at salinity/temperature extremes. A small number of polyps also exhibited signs of asexual reproduction (budding) throughout the duration of experimental trials. However, in total, this encompassed only 5% of all *C. barnesi* polyps and only four salinity/temperature combinations had polyp budding rates above 30%. For a comprehensive depiction of polyp mortality, deterioration, and asexual reproduction rates across treatments see Supplementary Figs. 1 & 2.

Due to low sample size (see Supplementary Table 2 and Supplementary data), the effects of health condition/budding on polyp oxygen consumption rates were not statistically assessed. However, to ensure consistency in polyp condition, and to safeguard the robustness of our statistical approach, all polyps which exhibited any visible signs of asexual reproduction throughout the duration of experiments were removed from oxygen consumption analysis. In addition, the oxygen consumption rate of polyps that died was assumed to be zero.

Effects of temperature and salinity on polyp oxygen consumption

Over the seven temperatures and nine salinities, all oxygen consumption rates were between 0.001 and 0.48 nmol O_2 h μg^{-1} representing significant change over the experimental range. The slope of oxygen

consumption for each chamber was consistently linear. Only 2% of all trials had a regression coefficient less than 0.7 meaning modeled oxygen consumption slopes were highly representative of recorded data.

Temperature had a significant effect on the oxygen consumption rates of *C. barnesi* polyps ($t_{1,1119,} = -5.715$, $P < 0.01$). This relationship was positive, with an increase in temperature resulting in an increase in oxygen consumption (Fig. 2a, Supplementary Fig. 3). The shape of this metabolic response was typically non-linear as an increase in slope gradient was observed by rising experimental temperatures. Additionally, a 'flattening off' of polyp oxygen consumption rates was observed at the upper experimental temperatures (24–31 °C). There was also evidence of inflection in polyp oxygen consumption rates around 31 °C and, using a polynomial squared term, this inflection in polyp oxygen consumption was identified as significant ($t_{1,120} = 0.328$, $P = 0.01$) indicating a downward shift in polyp oxygen consumption trends at thermal extremes (identified here at approximately 34 °C). It is hypothesized

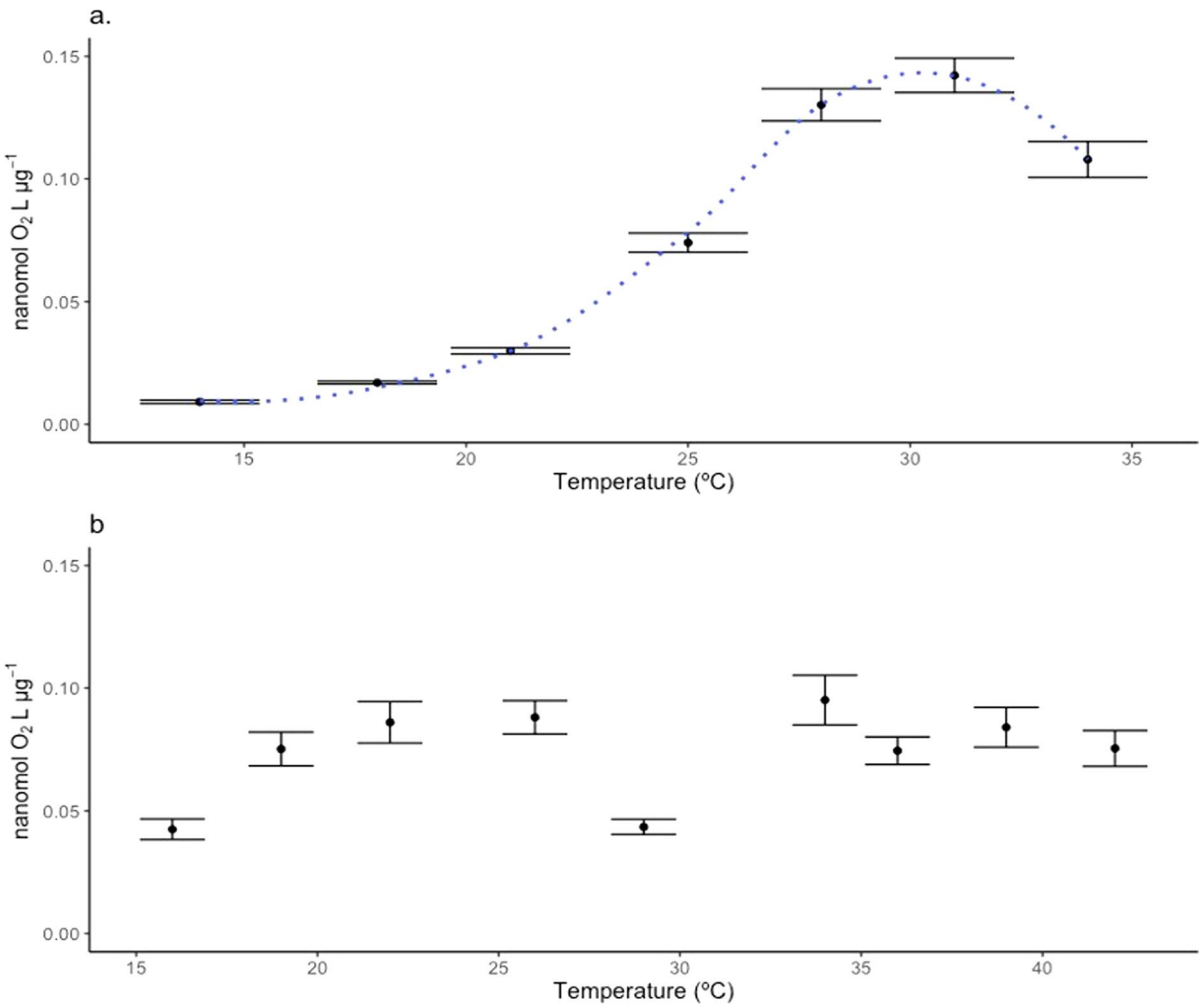

Fig. 2 Carukia barnesi polyp oxygen consumption rate vs pooled temperature and salinity. Oxygen consumption rates of individual polyps over a range of temperatures and salinities. **a** Oxygen consumption rate vs temperature, **b** oxygen consumption rate vs salinity. The dotted line represents the smoothed means and has been added to represent the shape of the polyp physiological profile in response to temperature. Data has been pooled and points represent group means ± SE. For a detailed index of sample size see Table 1 in the supplementary material. All budding and dead polyps have been removed from the analysis

these features potentially allude to the thermal 'optimal' and/or physiological limits for this organism (Fig. 2a).

In contrast, salinity did not have a significant effect on the oxygen consumption rates of *C. barnesi* polyps ($t_{1,1119,} = 0.079$, $P = 0.937$), and oxygen consumption rates were consistent across the range of osmotic treatments (Fig. 2b, Supplementary Fig. 3). Likewise, there was also no statistical evidence to support an interaction effect between temperature and salinity ($t_{1,119,} = -0.325$, $P = 0.745$).

Discussion and conclusion

The logistically difficult nature of Irukandji polyps, and the consequential lack of ecological understanding, have driven a requirement for 'rethinking' approaches to niche exploration for this medically important species. Over the duration of this study, a total of 1240 individual *C. barnesi* polyps were exposed to a matrix of nine salinities and seven temperatures with the desire to classify their thermal and osmotic eco-physiological profiles. While oxygen consumption rates did fluctuate, Irukandji polyps were more tolerant to fluctuations in salinity than temperature. As a result, polyp thermal tolerance windows were narrower than their osmotic counterparts and temperature drove all trends in oxygen consumption. No evidence was found to suggest an interactive effect of salinity and temperature on polyp oxygen consumption rates but we do provide anecdotal evidence showing polyps' ability to behaviourally adapt in conditions deemed sub-optimal.

Temperature was observed as the primary driver of oxygen consumption rates for *C. barnesi* polyps with an increase in temperature increasing organism oxygen consumption rate. The dominance of temperature as an eco-physiological factor, and the sensitivity of marine organisms to thermal fluctuations, has been identified for multiple other species of marine invertebrates, including jellyfish polyps, with studies on scyphozoan species such as *Cassiopea xamachana* Bigelow, 1892, *Aurelia aurita* (Linnaeus, 1758), and *Chrysaora quinquecirrha* (Desor, 1848), finding similar results (Mangum et al., 1972; Fitt & Costley, 1998). We believe, however, this study to be the first of its kind to comprehensively investigate the effect of this core environmental factor on Cubozoan polyps. The response of *C. barnesi* polyps to temperature in this study was fast, with a clear change in oxygen consumption observed after a thermal modification rate of two degrees per hour and a relatively short settling period. The rapid nature of this metabolic response demonstrates a clear capacity, of this organism, to withstand abrupt changes in their thermal environment and is characteristic of poikilothermic marine organisms who occupy dynamic environments (Ikeda et al., 2017). Polyp oxygen consumption rates were low between 14ºC and 18ºC, with little overall variation, but increase markedly between 18ºC and 28ºC until a slight 'flattening out' was observed in the response curve between 28ºC and 34ºC. While identifying the exact thermal and osmotic limits for *C. barnesi* polyps is not within the scope of this study, reductions in oxygen consumption rates and a slowing of metabolic increases are key characteristics traditionally used when investigating the scope of metabolic performance windows (Rees et al., 2014). Thus, while these polyps can withstand a wide range of environmental temperatures, we believe there is evidence of a thermal performance window between approximately 28 °C and 34 °C. The observed curving in metabolic trend between the two most extreme temperatures may also be a potential indicator of thermal maximal but to be certain the trend needs to be observed beyond this thermal limit. Furthermore, these metabolic trends are short-term as they were obtained over less than 24 h. Thus, due to a lack of knowledge surrounding this species, the true ecological relevance of these trends cannot be realized and certainly, given a longer assessment period, have the potential to change.

In contrast, the oxygen consumption rates of *C. barnesi* polyps were consistent over a very wide range of salinities spanning 19 to 42‰. This suggests *C. barnesi* polyps are likely euryhaline and, within the scope of this research, demonstrate the capacity, and physiological tolerance, to occur in very dynamic environments where changes in salinity are significant. These results not only support the findings of existing literature on scyphozoan and hydrozoan polyps (Condon et al., 2001; Ikeda et al., 2017; Schäfer et al., 2021) but also reinforce the outcomes of Courtney et al (2016a, b) who found rates of asexual reproduction in *C. barnesi* polyps to be robust to perturbations in salinity. However, through the establishment of a physiological profile, we challenge the idea that

these polyps have a 'preference' for lower salinity environments as we found little evidence of an overall metabolic trend. In actuality, of all the salinities tested, the average oxygen consumption rate for polyps at the lowest salinity (16‰) was slightly reduced compared to the other treatments. Thus, if we view oxygen consumption rate as an indicator of the capacity for the target organisms to carry out necessary life processes (Verberk et al., 2016), then for this species, an environmental salinity this low would not be desirable. This disparity, between metabolic profile and reproductive output, maybe a consequence of the experimental time frame and the capacity of polyps to adapt when adverse conditions remain consistent, and/or the nature of response data and the resolution at which it was collected (continuous physiological data vs. categorical start-finish comparisons). Perhaps though, what these findings highlight is just how little is understood about the biology of this organism as we are yet to fully comprehend the adaptive significance of asexual reproduction for this species. Thus, the establishment of a functional link between polyp metabolic rate and asexual budding certainly warrants further exploration.

Marine environments are multivariate, dynamic, systems, and thus organisms that inhabit them are subjected to simultaneous variability in multiple environmental factors. The factorial design of this study not only enabled the assessment of the metabolic consequences of salinity and temperature in isolation but also allowed for investigating the interactive effect of these key environmental components together. However, no significant interaction effect between temperature and salinity was identified in this study. Thus, while for some osmo-conforming marine species there is some evidence to suggest that in high temperatures the negative effects of extreme salinity can be negated through thermally driven osmoregulation (Torres et al., 2021) there is not sufficient evidence to support this in *C. barnesi* polyps.

Physiological limits for jellyfish polyps have also been linked to changes in polyp health condition and mortality with some studies showing a significant reduction in polyp physical condition when exposed to environmental conditions deemed 'sub-optimal' and outside expected eco-physiological ranges (Mangum et al., 1972; Ikeda et al., 2017). While this was not a primary aim of this study, the health condition of polyps was observed upon both trial initiation and completion. Individuals exposed to experimental extremes had the highest rates of mortality and in three cases rates of polyp mortality were 100%. In addition, polyps trialed at the thermal and osmotic limits of this study were anecdotally observed to have significantly reduced tentacle length and smaller body size, when compared to other treatments, and on occasion, polyps underwent full encystment. However, in order to fully understand the observations made here further research is needed.

As it stands, *C. barnesi* polyps remain to be identified *in* situ and, as a result, the geographic ecology and distribution limits for this species remain unknown. However, by utilizing the eco-physiological profiles gained from this study and considering these trends alongside both, what is known about the ecology and distribution of the medusa and, the known in situ locations of two closely related cubozoan polyp species, we can start to piece together potential niche characteristics, and gain insight into hypothetical distributions, for this logistically difficult species. The medusa life stage for *C. barnesi* is considered an oceanic species, with sting and capture records highly correlated with coastal islands and offshore reefs (Carrette et al., 2012; Courtney et al., 2015, 2016a). While the southern distribution for this species, and life stage, is yet to be confirmed, stings have been recorded as far south as Fraser Island on Queensland's eastern coast (Carrette et al., 2012; Courtney et al., 2016a). Ocean temperatures at Fraser Island average around 20 ºC, with fluctuations as low as 18ºC in the winter months and 27 ºC come summer (Ban et al., 2012). While these temperatures fit within the observed survivable scope for *C. barnesi* polyps', in the winter months they are considered at the thermal limit and well below temperatures which we would deem favorable for this species (approximately 28—34ºC). In addition, typical eco-physiological ranges of oceanic conformers tend to be very narrow. This is a result of the stable nature of large water bodies and the fact thermal and osmotic perturbations in these environments are rare Fields(Verberk et al., 2016). This, however, was not what we observed. Instead, while *C. barnesi* polyps did have a clear thermal profile, they displayed generalist tendencies and exhibited significant tolerance to a very wide range of salinities. What these eco-physiological trends suggest is that, when seeking

the in situ location for this organism, survey efforts should be targeted toward environments with widely fluctuating salinity ranges but relatively stable temperatures. Environments such as estuaries, oceanic margins, and, potentially even, areas of submarine freshwater upwellings such as wonky holes. Furthermore, of the two species of Cubozoan polyps that have been located in situ both have been identified in similar environments with *Chironex fleckeri* Southcott, 1956 identified attached to the underside of a rock in a river mouth in Queensland (Hartwick, 1991) and *Carybdea marsupialis* (Linnaeus, 1758) identified in a mangrove habitat adhered to a shell (Cutress & Studebaker, 1973).

In conclusion, the link between geographic distribution and physiological profiles is well established with research on many target organisms including marine cnidarians (Mangum et al., 1972; Gambill & Peck, 2014; Höhn et al., 2017). Throughout this study, we used physiological profiling to investigate the hypothetical niche characteristics for polyps of the medically important Irukandji jellyfish. We have shown that the capacity for Irukandji polyps to survive in situ is predominantly driven by temperature and that the ability of polyps to withstand osmotic perturbations is wide. Consequently, we suggest there is a high probability this species occurs in environments such as estuaries or submarine freshwater upwellings. In the future, investigations should strive to take the information gained from this study and, in conjunction with other existing literature, develop a niche model for both life stages of this species. This would provide a framework to further ecological exploration, opening the scope for much-needed investigations such as those aimed at understanding the potential ecological overlap for the differing life stages of this species. This information would also assist in situ survey efforts for *C. barnesi* polyps and, through utilizing new survey techniques that do not rely on direct species identification such as Environmental DNA, we believe physiological profiles and theoretical niche models can target field efforts to specific geographic locations of interest. What results is an enhanced probability of detection success and, hopefully, furthering the ecological understanding of this medically important species.

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Data availability The datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

Declarations

Conflict of interest There are no conflicts of interest to disclose. The authors are not aware of any competing interests and funding for this project was provided by the ER Walker bequest bursary.

References

Arneson, A. & C. Cutress, 1976. Life History of Carybeda alata Reynaud. Coelenterate Ecology and Behaviour, Springer, New York:

Ban, N., R. Pressey & S. Weeks, 2012. Conservation objectives and sea-surface temperature anomalies in the Great Barrier Reef. Conservation Biology 26: 799–809.

Barnes, T., & B. Kinsey, 1986. Barnes on box jellyfish. James Cook University of North Queensland.

Boco, S., K. Pitt & S. Melvin, 2019. Extreme, but not moderate climate scenarios, impart sublethal effects on polyps of the Irukandji jellyfish, *Carukia barnesi*. Science of the Total Environment 685: 471–479.

Carrette, T., A. Underwood & J. Seymour, 2012. Irukandji syndrome: a widely misunderstood and poorly researched tropical marine envenoming. Diving and Hyperbaric Medicine 42: 214–223.

Condon, R. H., M. B. Decker & J. E. Purcell, 2001. Effects of low dissolved oxygen on survival and asexual reproduction of scyphozoan polyps (Chrysaora quinquecirrha). Hydrobiologia 451: 89–95.

Courtney, R., S. Browning, T. Northfield & J. Seymour, 2016a. Thermal and osmotic tolerance of "Irukandji" Polyps: Cubozoa; Carukia barnesi. PLoS ONE 11: 10–16.

Courtney, R., S. Browning & J. Seymour, 2016b. Early life history of the "irukandji" jellyfish *Carukia barnesi*. PLoS

ONE 11: 1–13. https://doi.org/10.1371/journal.pone.0151197.
Courtney, R., N. Sachlikidis, R. Jones & J. Seymour, 2015. Prey capture ecology of the cubozoan *Carukia barnesi*. PLoS ONE. https://doi.org/10.1371/journal.pone.0124256.
Cutress, C., & J. Studebaker, 1973. Development of the Cubomedusae, *Carybdea marsupilas*. Proceedings of the Association of Island Marine Labrotories of the Caribbean 9.
Fitt, W. & K. Costley, 1998. The role of temperature in survival of the polyp stage of the tropical rhizostome jellyfish *Cassiopea xamachana*. Journal of Experimental Marine Biology and Ecology 222: 79–91.
Gambill, M. & M. Peck, 2014. Respiration rates of the polyps of four jellyfish species: potential thermal triggers and limits. Journal of Experimental Marine Biology and Ecology 459: 17–22. https://doi.org/10.1016/j.jembe.2014.05.005.
Hartwick, R., 1991. Distributional ecology and behaviour of the early life stages of the box-jellyfish *Chironex fleckeri*. Hydrobiologia 216–217: 181–188.
Höhn, D., C. Lucas & S. Thatje, 2017. Respiratory response to temperature of three populations of *Aurelia aurita* polyps in northern Europe. PLoS ONE 12: 1–14.
Ikeda, H., C. Mizota & S. Uye, 2017. Bioenergetic characterization in *Aurelia aurita* (Cnidaria: Scyphozoa) polyps and application to natural polyp populations. Marine Ecology Progress Series (Halstenbek) Inter-Research 568: 87–100.
Kearney, M. & W. Porter, 2009. Mechanistic niche modelling: combining physiological and spatial data to predict species' ranges. Ecology Letters 12: 334–350.
Kearney, M., S. J. Simpson, D. Raubenheimer & B. Helmuth, 2010. Modelling the ecological niche from functional traits. Philosophical Transactions of the Royal Society London B 365(1557): 3469–3483.
Mangum, C., M. Oakes & J. Shick, 1972. Rate-temperature responses in scyphozoan medusae and polyps. Marine Biology 15: 298–303.
Pereira, P., J. Barry, M. Corkeron, P. Keir, M. Little & J. Seymour, 2010. Intracerebral hemorrhage and death after envenoming by the jellyfish *Carukia barnesi*. Clinical Toxicology 48: 390–392.
R Core Team, 2012. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/
Rees, H., B. Maddison, D. Middleditch, J. Patmore & K. Gough, 2014. The detection of aquatic animal species using environmental DNA – a review of eDNA as a survey tool in ecology. Journal of Applied Ecology 51: 1450–1459.
Rowley, O., R. Courtney, S. Browning & J. Seymour, 2020. Bay watch: Using unmanned aerial vehicles (UAV's) to survey the box jellyfish *Chironex fleckeri*. PLoS ONE 15: 1–17. https://doi.org/10.1371/journal.pone.0241410.
Schäfer, S., S. K. M. Gueroun, C. Andrade & J. Canning-Clode, 2021. Combined effects of temperature and salinity on polyps and ephyrae of aurelia solida (Cnidaria: Scyphozoa). Diversity 13: 573.
Southcott, R., 1967. Studies on Australian Cubomedusae, including a new genus and species apparently harmful to man. Australian Journal of Zoology 15: 651–671.
Thomsen, P. & E. Willerslev, 2015. Environmental DNA – an emerging tool in conservation for monitoring past and present biodiversity. Biological Conservation 183: 4–18. https://doi.org/10.1016/j.biocon.2014.11.019.
Torres, G., G. Charmantier, D. Wilcockson, S. Harzsch & L. Giménez, 2021. Physiological basis of interactive responses to temperature and salinity in coastal marine invertebrate: implications for responses to warming. Ecology and Evolution. https://doi.org/10.1002/ece3.7552.
Verberk, W., F. Bartolini, D. Marshall, H. Pörtner, J. Terblanche, C. White & F. Giomi, 2016. Can respiratory physiology predict thermal niches? Annals of the New York Academy of Sciences 1365: 73–88.
Werner, B., C. Cutress, & J. Studebaker, 1971. Life cycle of Trepedalia cystophora Conant (cubomedusae). Nature 582–583.