Extreme changes in salinity drive population dynamics of *Catostylus mosaicus* medusae in a modified estuary

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Abstract

Modifications to estuaries through the construction of barrages alters the natural dynamics of inhabitant species by controlling freshwater inputs into those systems. To understand the effects of these changes on scyphozoan jellyfish such as *Catostylus mosaicus*, we analysed a 20-year observational dataset from the Fitzroy River, Queensland, and studied the effect of salinity changes on adult medusae in the laboratory. Two experimental simulations examined the effect of sudden and prolonged salinity decreases (30, 20, 10 ‰; such as experienced when the barrage is opened), and short term decreases in salinity (20, 15, 10 ‰; such as occurs during a moderate rainfall event) on medusae health and survival. Major decreases in salinity occurred approximately 16 times over the 20-year period in the Upper estuary and medusae disappeared from the Upper estuary following every major flow event. Salinity was the most influential variable contributing to variation in the number of Upper estuary sites reporting jellyfish. Medusae were unable to survive extended periods at extreme low salinities, such that they would experience when a barrage opens fully but survived and recovered from short-term freshwater inputs such that they would experience during a rainfall event. This demonstrates for the first time that modification of freshwater flow by a barrage regulates the population dynamics of the estuarine jellyfish *Catostylus mosaicus*. Future artificial modifications of freshwater flows following the construction of barrages are likely to modify estuarine medusa population dynamics. Such investigations highlight the need for robust, long term datasets, as well as to firmly embed experimental approaches in realistic ecological contexts.

Keywords

Estuaries; Barrages; Jellyfish; Medusa; Salinity; Population dynamics

Declarations

Funding

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Conflicts of interest/competing interests

The authors have declared that no competing interests exist.

Data Availability Statement

The water quality and jellyfish dataset analysed in this study is available upon request from water.data@qld.gov.au. Experimental data are available from the corresponding author on reasonable request.

Compliance with Ethical Standards

The blue blubber jellyfish *Catostylus mosaicus* is not a protected species in the area of study. All international, national, and/or institutional guidelines for the care and use of animals were followed where applicable.

1 Introduction

Estuaries are highly dynamic environments that are often subject to rapid changes in environmental conditions associated with varying freshwater flows (Gillanders and Kingsford, 2002; Morais, 2008). Modifications to natural flow, through the construction of dams and barrages used to store freshwater and mitigate flooding, alter the natural dynamics within estuaries, with potentially severe consequences for estuarine species (Xian et al., 2005; Montagna et al., 2012; Amorim et al., 2018). Whilst estuarine species can generally tolerate reasonable salinity fluctuations (Lee et al., 2017; Heim-Ballew and Olsen, 2019), extreme reduced salinity is often detrimental to animals (Holst and Jarms, 2010; Amorim et al., 2018). Determining how species respond to modifications in their environment will enable stakeholders to better manage estuaries and waterways (Gillanders and Kingsford, 2002; Bunn et al., 2010; Amorim et al., 2018).

Jellyfish are important components of many coastal and estuarine systems and frequently form spectacular blooms that affect ecosystem structure and marine food webs (Goldstein and Steiner, 2017; Schnedler-Meyer et al., 2018). Scyphozoan jellyfish life cycles are comprised of a pelagic sexual medusa and a benthic asexual polyp (Lucas et al., 2012). Their ability to take rapid advantage of favourable conditions, coupled with the medusa lifespan of a few months (Pitt, 2000), leads to transient population booms, termed ‘jellyfish blooms’ (Schiariti et al., 2014). Interactions between polyp colonies and their environment lead to variations in the timing and appearance of these blooms, with some evidence that anthropogenic disturbances may modify natural dynamics (Purcell, 2012; Pitt et al., 2018). In coastal areas, blooms often interfere with human enterprise and recreation (Purcell et al., 2007; Kingsford et al., 2018), but jellyfish also provide valuable resources to pharmaceutical and scientific industries (Leone et al., 2015; Brotz et al., 2017). Determining how changes to environmental flows affect estuarine jellyfish populations will help stakeholders understand their population dynamics and provide insights into managing potentially problematic species (Jones and Moss, 2011).

Although many species of gelatinous zooplankton inhabit estuaries that are subject to varying salinity (Brewer, 1989; Wang et al., 2016; Baumsteiger et al., 2018), only two studies have examined how varying freshwater flows affect jellyfish medusae (Xian et al., 2005; Amorim et al., 2018). Most research examining scyphozoan jellyfish populations in estuaries has focused on settlement of planula larvae and polyp reproduction, and on how salinity changes affects medusa production (Conley and Uye, 2015; Takao and Uye, 2018). Both the planula and polyp stages have limited capacity to move away from areas of reduced salinity (Webster and Lucas, 2012). Thus, low salinity may hinder bloom formation because it inhibits larval settlement and increases rates of polyp morphological deformities, which impairs their ability to feed (Cargo and King, 1990; Conley and Uye, 2015; Widmer et al., 2016). As osmoconformers, medusae have limited ability to respond to changes in salinity, and if subjected to rapid changes the animal will shrink or swell (Albert, 2014). Some species of pelagic medusae actively avoid low salinity in surface waters by swimming below the halocline (Albert, 2014). Consequently medusae are generally observed in higher salinity areas of estuaries, although further details on how they respond to changes in salinity are still lacking (Albert, 2014; Amorim et al., 2018; Heim-Ballew and Olsen, 2019).

Catostylus mosaicus, commonly referred to as the Blue Blubber jellyfish, is a rhizostome medusa native to the Australian east coast and the Central Indonesian Pacific (Pitt and Kingsford, 2003b; Purcell et al., 2013). The medusae are large, frequently growing to bell sizes of 250-300mm (Pitt, 2000) and have been harvested in small quantities in Australia and Asia (Omori, 1981; Kingsford et al., 2000). Despite a growing commercial interest in this species and the medusae being abundant in many eastern Australian coastal lagoons and estuaries (Dawson, 2005; Dawson et al., 2015), little is known about the drivers behind the spatial and temporal patterns of *C. mosaicus* medusae. Sightings outside of estuaries and coastal embayments are rare (Kingsford et al., 2000) and although anecdotal observations indicate that medusae may endure short-term reductions in salinity, such that may occur following rainfall, they are unlikely to survive reduced salinity for multiple weeks to months (Pitt and Kingsford, 2000). Severe modifications of freshwater flows, therefore, could result in significant changes to estuarine medusa population dynamics (Amorim et al., 2018).

We aimed to understand how the modification of an estuary (in this case a barrage used for flood mitigation) affects the population dynamics of *C. mosaicus* medusae through two different approaches. Firstly, we used a 20-year data set to identify how the occurrence of medusae related to environmental parameters. Secondly, we used two laboratory experiments to investigate the effect of salinity changes on medusae health and survival, by mimicking: (i) severe and prolonged reductions in salinity such as occurs when the barrage is opened; and (ii) a transient rainfall event, resulting in temporary reductions in salinity, such that would occur during the dry season. The following hypotheses were tested: (i) long term decreases in salinity impair survival, pulsation, and respiration rates of *C. mosaicus* medusae; and (ii) short term decreases temporarily impair pulsation and respiration but medusae recover when salinity returns to normal levels.

2 Materials and Methods

2.1 Study Site

The Fitzroy River (S 23°48.643’, E 150°65.309’) is a sub-tropical estuary in Queensland, Australia (Dobbie et al., 2003). The Fitzroy Barrage, 53km upstream from the river mouth, separates fresh water upstream from the tidal salt water downstream and is used to mitigate flooding. Two hydrological states are observed below the barrage: low and high (>1000 ML day^{-1}) flow (Dobbie et al., 2003). In a high flow state salinity can be reduced to zero 30 km below the barrage, while turbidity increases dramatically (Dobbie et al., 2003). Marine conditions return over a period of 4-6 months following cessation of the freshwater flow, consistent with the exchange time for the estuary water of 100 days. The estuary depth varies from 3 to 7 metres at mid tide with the tides varying from 0.3 to 4 metres near the barrage and at the mouth, respectively. When the barrage is closed, flows are generally small (median 7 m^{3}s^{-1}) and tidal currents cause fine sediments (<100 µm) to be pumped upstream (Margvelashvili et al., 2003).

2.2 Effects of freshwater discharge on the occurrence of medusae

Each month from April 1999 to February 2019, 11 environmental variables were monitored along the Fitzroy Estuary at 15 sites below the Barrage by the Queensland Department of Environment and Science (Table 1). No observations were taken in 2001, and only one observation was recorded in 2002, resulting in a total of 538 observations across the 15 sites. Sampling sites were grouped into three regions; Upper estuary (5 sites), the first of which is located at the barrage, with the others extending 9 km downstream; Mid estuary (4 sites), extending from 15 to 32 km from the barrage; and Lower estuary (6 sites) 41 km to 59 km from the barrage, at the mouth of the estuary (Appendix 1). The number of sites at which *C. mosaicus* was observed each month was recorded within each of the three regions.

Table 1. Variables collected by the EHMP.

Variable	**Type**	**Unit**	**Sites measured at**
Chlorophyll-a	Biological	µg/L	Upper, Mid, Lower
Pheopigments	Biological	µg/L	Mid, Lower
Total Nitrogen (TN)	Physio-chemical	mg/L	Upper, Mid, Lower
Nitrogen Ammonia (NH3)	Physio-chemical	mg/L	Mid, Lower
Oxygen	Physio-chemical	mg/L	Upper, Mid, Lower
pH	Physio-chemical	Unit	Upper, Mid, Lower
Total Phosphorous	Physio-chemical	mg/L	Upper, Mid, Lower
Salinity	Physio-chemical	‰	Upper, Mid, Lower
Specific Conductance at 25°C	Physical	mS/cm at 25°C	Mid, Lower
Turbidity	Physio-chemical	Nephelometric Turbidity Units (NTU)	Upper, Mid, Lower
Secchi Disk Depth	Physical	meter	Upper, Mid, Lower
Catostylus mosaicus medusae	Biological	Presence/absence	Upper, Mid, Lower

Data Analysis

The relationship between the occurrence of *C. mosaicus* and other environmental variables was tested within each region using partial least squares regression models (PLSR). PLSR combines features from principal component analysis (PCA) and multiple regression. It reduces a large set of predictor variables to a smaller set of uncorrelated latent variables (equivalent to principal components in PCA) and is well suited for dealing with multicollinearity in datasets, allowing for correlated explanatory variables to be included in the analysis (Rosipal and Krämer, 2005; Carrascal et al., 2009).

All variables were standardised before PLSR models were fitted using the orthogonal scores algorithm (NIPALS algorithm). Cross validation of the model using leave-one-out segments determined the appropriate number of latent variables, as well as a cross-validation error Root Mean Square Error (RMSE) plot. Variable Importance in Projection (VIP) coefficients were extracted from the relevant latent variables to determine which of the initial variables significantly influenced the occurrence of medusae within the model. VIP scores were calculated as the weighted sum of the squared correlations between the latent variables and the original variable. The weights were calculated separately for each latent variable and were weighted proportionally to the reduction in the sums of squares for each latent variable. Despite PLSR's ability to take multicollinearity between variables into account, the VIP score cut-off value was selected as 1.5 for very important variables, and 1 for relevant variables. These levels were selected due to very high multicollinearity between numerous variables as well as the lack of consensus within the modelling community as to which cut-off value to use (Chong and Jun, 2005; Chi-Hyuck et al., 2009). Finally, regression coefficients were extracted for each model, to inform on how important variables influenced the presence of medusae in each region. Analyses were done in R v3.6.3.

2.3 Experimental simulations: Barrage opening vs Short-term rainfall event

Medusae were collected on 8th January 2020 from Deception Bay, Queensland (S 27°10.800', E 153°03.292'). Surface water temperature was 29.7°C and salinity was 35 ‰. Thirty-two medusae of varying sizes were collected and transferred in buckets to the Griffith Sea Jellies Research Laboratory.

Medusae were maintained in a 12:12 hr light:dark regime and were each fed twice daily with 150 mL one-day old *Artemia* nauplii mixed at a concentration of 1600/mL with 0.1g Polyplab Reef-roids, a dried crushed zooplankton mix. Ten to fifteen percent of water was replaced daily with water of the same temperature and salinity. Seawater was sourced from a depth of ~1 m from the Gold Coast Broadwater on a flooding tide and filtered through a 10 µm felt filter and passed over a protein skimmer. Reduced salinity water was created by adding fresh tap water (treated with sodium thiosulfate to neutralise chlorine) to seawater until the desired salinity was achieved.

Barrage opening simulation

Individual medusae of similar sizes (wet weight; 511 g ± 108 SE) were placed into sixteen 100L kreisels at ambient salinity (34.5±1 ‰). The experiment consisted of four salinity treatments; a control maintained at 34.5 ‰ and three experimental salinities of 30, 20, and 10 ‰. Four medusae were randomly allocated to each treatment. Kreisels were randomly interspersed across a 24±1°C temperature controlled room. Salinity was decreased over 6 hours until the target salinity for each treatment was achieved. Medusae were maintained at experimental salinities for 12 days, or until they recorded no pulsating across three consecutive days and began to disintegrate.

Short-term rainfall simulation

Sixteen medusae of similar sizes (241g ± 81g) were placed in individual 87L kreisels (+65L sump) at ambient salinity (33±1 ‰). Due to increased rainfall at the time of the experiment, average ambient salinity was 1.5±1 ‰ lower than for the previous experiment. To simulate a rainfall event the salinity of each kreisel was lowered over six hours to one of three different salinities (20, 15, and 10 ‰) or maintained as a control at ambient salinity. Salinity remained at experimental levels for 48 hours, before it was increased over 4 days (Klein et al., 2016) to ambient salinity. All medusae remained at 33±1 ‰ for the remaining 12 days of the experiment.

Experimental variables

In both experiments, survival and pulsation rates were recorded daily prior to feeding. Pulsation rates were measured as the number of complete pulsations per minute, averaged across three 1-minute intervals recorded 15 seconds apart. Respiration rates were measured prior to feeding on Day 0, 2, 7 and 12 for experiment 1, and Day 0, 3, 8, 13, and 18 for experiment 2. Respiration was measured using airtight 23L Perspex chambers, each fitted with an oxygen sensor spot (OXSP5; Pyroscience). Sensor spots were calibrated using a 2-point (100% and 0% oxygen saturation) calibration. O_2 concentrations were measured via a compatible FireSting O2 (FSO2-4) oxygen and temperature meter fitted with an oxygen fiberoptic sensor (3mm tip diameter). Two medusae were incubated individually for 2-hours alongside a blank filled with seawater of the same salinity. Oxygen concentrations (mg L^{-1}) were measured every 30 minutes. Oxygen consumption (µg O_2 hr^{-1} g^{-1}) was calculated using the slope of the five measurements. For logistical reasons, the 16 medusae were measured over 2 days, and each medusa was randomly assigned Group A or Group B at the start of the experiment to determine on which day they were measured. Within each group the order in which they were measured was random.

Analysis of experimental data

Assumptions of normality and homoscedasticity were tested using residuals and Q-Q plots. Survival of medusae differed among treatments creating unbalanced data sets. Subsets of data including only treatments where all 4 medusae were alive were analysed to prevent an unbalanced analysis. Where significant differences occurred, post hoc Tukey HSD tests identified which means differed.

Barrage opening - Separate ANOVAs were used to compare pulsation rates among all treatments on Day 0, 2 and 3. A repeated measures ANOVA compared pulsation rates between the control and 30 ‰ treatment across all 12 days of the experiment. Separate ANOVAs were done to compare respiration rates among all treatments on Day 0 and 2; and between the control and 30 ‰ treatments on Day 7 and 12.

Short-term rainfall event - Pulsation rates were analysed using separate ANOVAs on Day 0, 2, and 8. A repeated measures ANOVA compared the control and 20 ‰ pulsation rates across 18 days. Respiration rates were analysed using ANOVA. Comparisons were made among all four treatments on Day 0 and 3; among the control, 20, and 15 ‰ treatments on Day 8; and between the control and 20 ‰ treatments on Day 13 and 18.

3 Results

3.1 Effects of freshwater discharge on occurrence of medusae

Major decreases in salinity occurred approximately 16 times over the 20-year period in the Upper estuary and medusae disappeared from the Upper estuary following every major flow event (Fig. 1). After cross validating the PLSR model, two latent variables (LVs) captured 40.54% of the variation in the predictors (LV1: 31.18%; LV2: 9.36%), and 47.16% of the variation in the outcome variable (LV1: 40.63%; LV2: 6.53%). Additional latent variables provided minimal improvement (14 LVs = 48.24% of variation in the outcome variable). ‘Salinity’ and ‘Specific Conductance at 25°C’ were the most influential variables contributing to variation in the number of Upper Estuary sites reporting jellyfish, both with VIP scores >1.5 (Table 2). Other relevant variables in order of importance included ‘Secchi Disk Depth’, ‘O_2’ and ‘Month’. Any variables that scored below 1 were discounted as being non-important variables. Notably, despite high correlation with ‘Secchi Disk Depth’, ‘Turbidity’ was not an important factor contributing to jellyfish occurrence in either of the latent variables (VIP score <1).

Within the Upper Estuary, more sites reported sightings of medusae at higher salinities (Fig. 1). Jellyfish were only observed at multiple sites when salinity was >10 ‰, and jellyfish were reported occurring in salinity <10 ‰ only three times across the whole dataset. With every increase of 5 ‰, roughly one additional site reported observing jellyfish across the Upper Estuary (PLSR; Table 2). Visibility in the Upper Estuary was often <1m, with only 5 reports of Secchi disk depth >1m. The average Secchi disk depth was ~0.4m, and jellyfish were observed more frequently when Secchi disk depth was deeper, i.e. the water was clearer. Most freshwater inputs occurred in the first three months of the year, and ‘Month’ and ‘Salinity’ were correlated (r=0.52, p<0.001). Both ‘O_2’ and ‘Month’ were barely relevant to the model with VIP scores just above 1 (Table 2), but each saw a slight increase in the number of sites reporting jellyfish when the water was more oxygenated, as well as later in the year.

Table 2. Important (VIP >1) and relevant (VIP 1-1.5) variables contributing significantly to the variation in the number of sites reporting jellyfish in the Upper, Mid and Lower Estuary and their associated regression coefficients.

Location	Variable	VIP - LV1	VIP - LV2	Regression Coefficient
Upper Estuary	Salinity	1.84	1.73	+0.24
	Specific Conductance at 25°C	1.84	1.73	+0.25
	Secchi Disk Depth	1.30	1.22	+0.17
	O_2	1.03	1.04	+0.14
	Month	1.07	0.99	+0.14
Mid Estuary	Salinity	1.80		+0.08
	Turbidity	1.42		-0.07
	Month	1.27		+0.06
	pH	1.17		+0.06
Lower Estuary	Year	1.45		+0.03
	Turbidity	1.39		-0.03
	Total Phosphorous	1.20		-0.03
	Total Nitrogen	1.12		-0.03
	Salinity	1.08		+0.02

In the Mid and Lower estuary, single latent variables explained 30 and 35% of the variation in the predictors respectively. However the models only accounted for 12 and 5% of the variation in the outcome variable respectively. This low amount of variation explained by the two models, combined with the small regression coefficients (<0.1), indicates that despite their significance, the actual effect of these variables on the presence or absence of *C. mosaicus* in the mid estuary was limited (Table 3). Within the Mid Estuary, medusae were only observed at salinities >10 ‰ except for one occasion, where they were observed at two sites. They were also more frequently observed when 'Turbidity' was low and from October to December. Within the Lower Estuary, medusae were more frequently observed in the latter months of the year when the waters were less turbid and more saline.

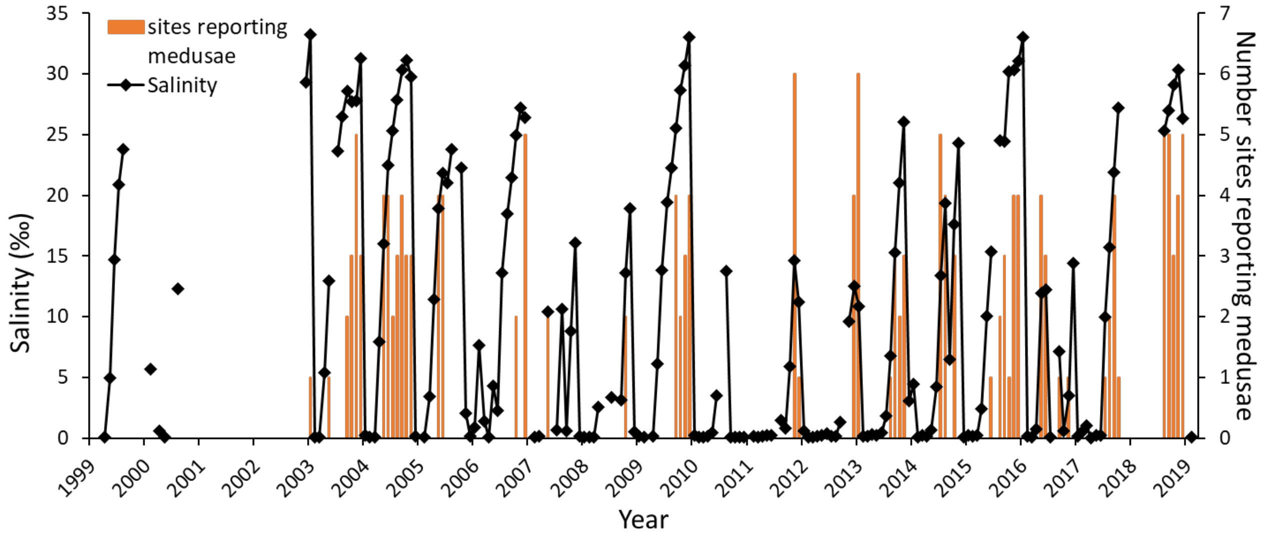

Figure 1. Salinity and number of Upper Estuary sites reporting medusae across the 20-year dataset

3.2 Barrage opening simulation

All medusae in the 34.5 (control) and 30 ‰ treatments survived and swam actively throughout the experiment. By Day 5, all of the medusae exposed to a salinity of 10 ‰ ceased to pulsate, and at 20 ‰ only one medusa was alive from Day 7 until the end of the experiment.

On Day 0 pulsation rates were similar across all treatments (p>0.05, Fig. 2). By Day 2, medusae at 10 pulsed significantly slower than the other treatments (F(3,12)=32.241, p<0.001) and on Day 3, medusae at both 10 and 20 salinity pulsed more slowly than the controls (F(3,12)=22.49, p<0.001). Pulsation rates did not differ between the control and 20 treatment at any other time during the experiment (p>0.05).

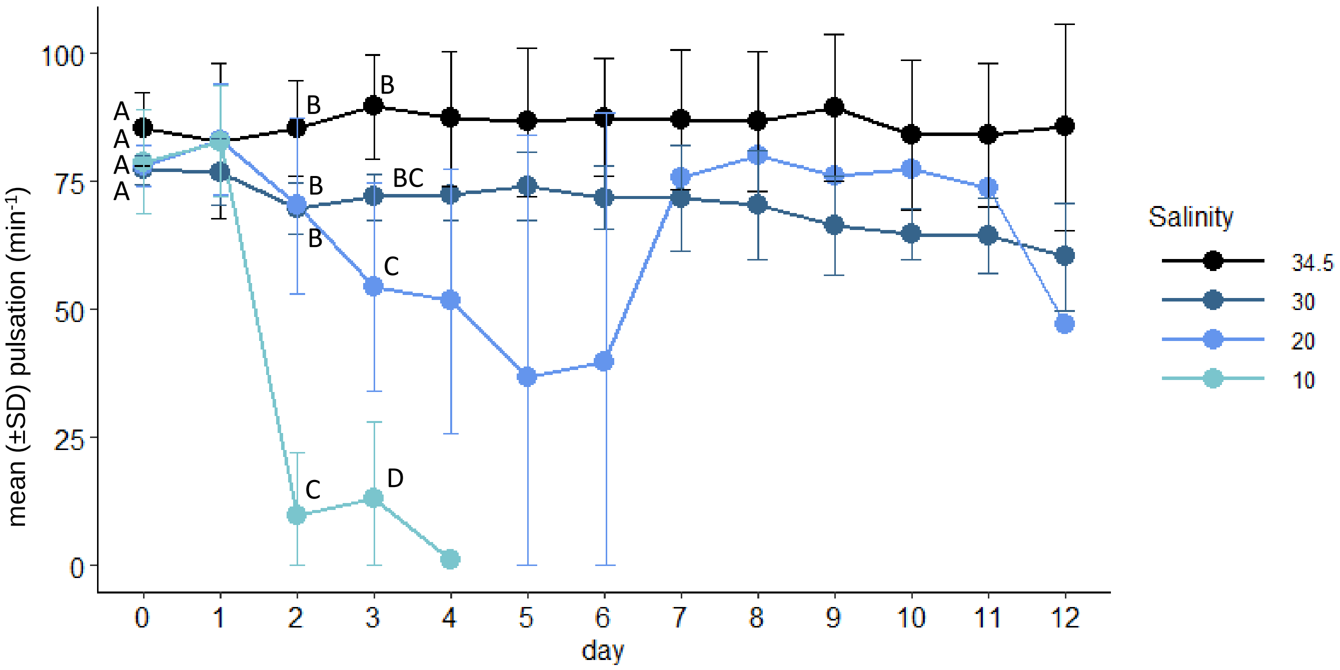

Figure 2. Mean pulsation rates across the experiment (n= 4). Salinity was reduced on Day 1 after the observation. From Day 7, only 1 medusa was alive at 20. Letters above data points indicate similarities (e.g. A, A), and differences (e.g. A, B) between treatments at single time points, as determined by post hoc tests

On Day 0 respiration rates were similar across all treatments ($p>0.05$, Fig. 3). By Day 2, medusae consumed significantly less oxygen at 10 than at control or 20 salinities ($F(3,12)=3.63$, $p<0.05$). Respiration rates were similar for medusae at 34.5 and 30 on Day 7, but by Day 12 medusae at 30 had lower respiration rates than the controls ($F(4.39)=-3.6241$, $p<0.05$).

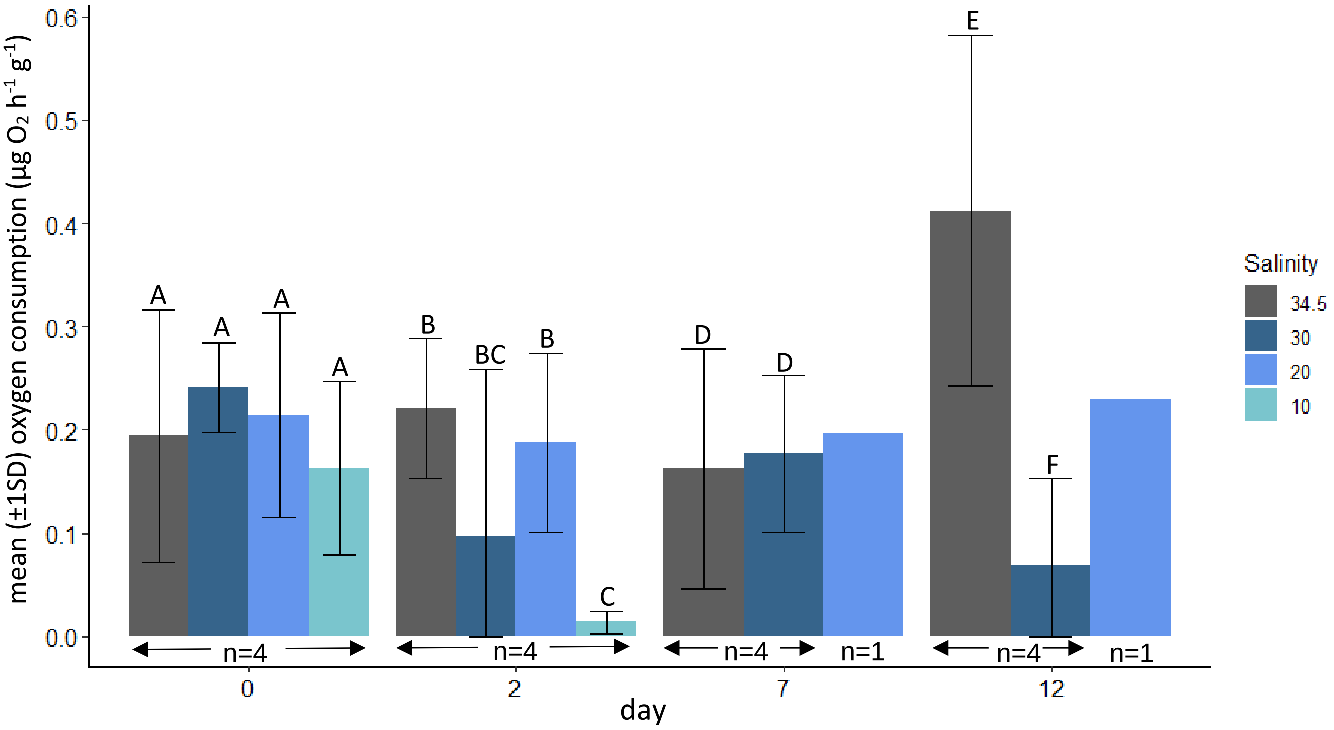

Figure 3. Mean (± SD) oxygen consumption across the experiment. Letters above data points indicate similarities (e.g. A, A) and differences (e.g. A, B) between treatments at single time points, as determined by post hoc tests

3.3 Short-term rainfall simulation

All control medusae maintained at 33 and those exposed to a temporary decrease to 20 survived to the end of the experiment. Only 50% of medusae that experienced a temporary reduction in salinity to 10 and 15 were still alive by Day 4 and Day 17 respectively.

Prior to the decrease in salinity that occurred after the observation on Day 1, pulsation rates were similar across all treatments ($p>0.05$, Fig. 4). On Day 2, all medusae in treatments that experienced a salinity decrease pulsed significantly slower than the controls ($F(3,12)=7.965$, $p<0.01$). Following the return to ambient salinity on Day 7, medusae in treatments that decreased to 15 were still pulsing significantly slower than the controls and the treatment that decreased to 20 ($F(2,4.88)=24.52$, $p<0.01$). Salinity negatively affected pulsation rates of medusae that experienced a decrease to 20, although this effect depended on the day of the experiment ($F(18,108)=2.520$, $p<0.01$). From Day 2 to Day 5 pulsation rates were significantly slower in the 20 salinity treatment compared to the controls.

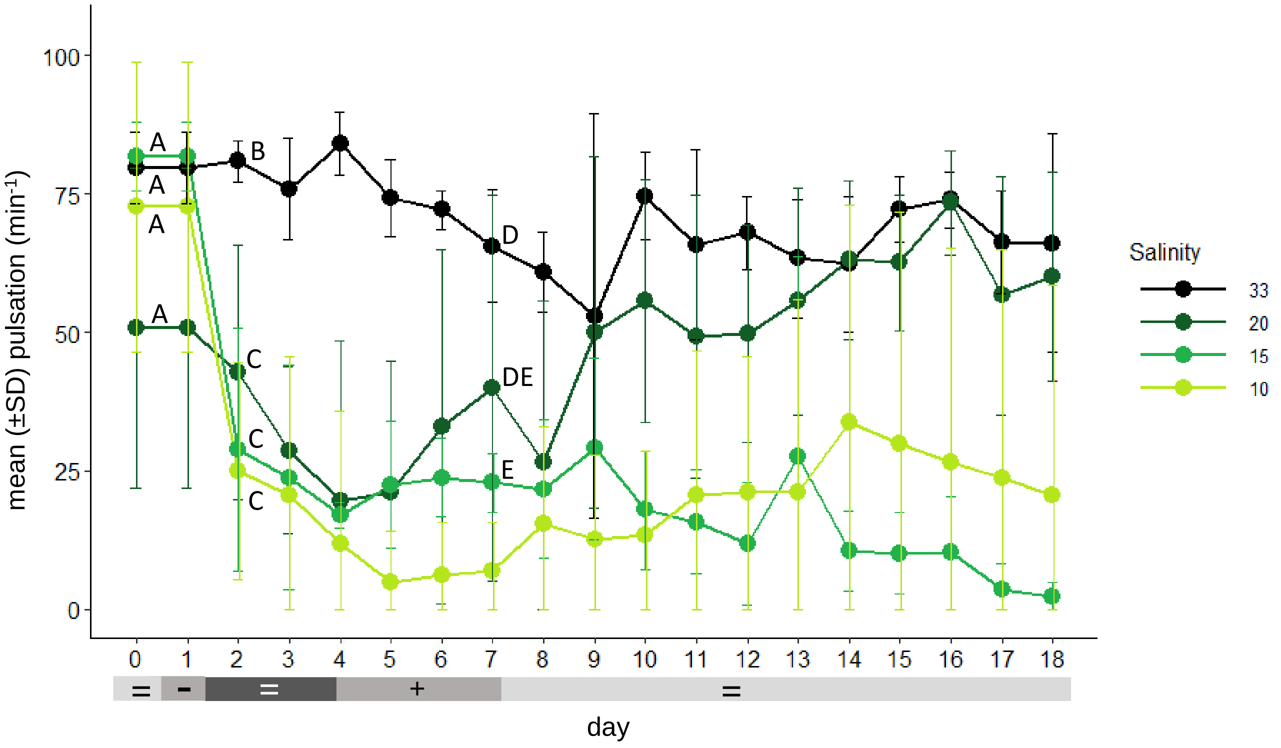

Figure 4. Mean pulsation rates across the experiment (n= 4). Letters above data points indicate similarities (e.g. A, A) and differences (e.g. A, B) between treatments, as determined by post hoc tests. The grey bar indicates the direction of salinity changes across the experiment

Oxygen consumption was similar between all treatments on Day 0, 3 and 8 (excluding 10 treatment on day 8, $p>0.05$, Fig. 5). On days 13 and 18 the controls and medusae that experienced a decrease to 20 had similar respiration rates ($p>0.05$).

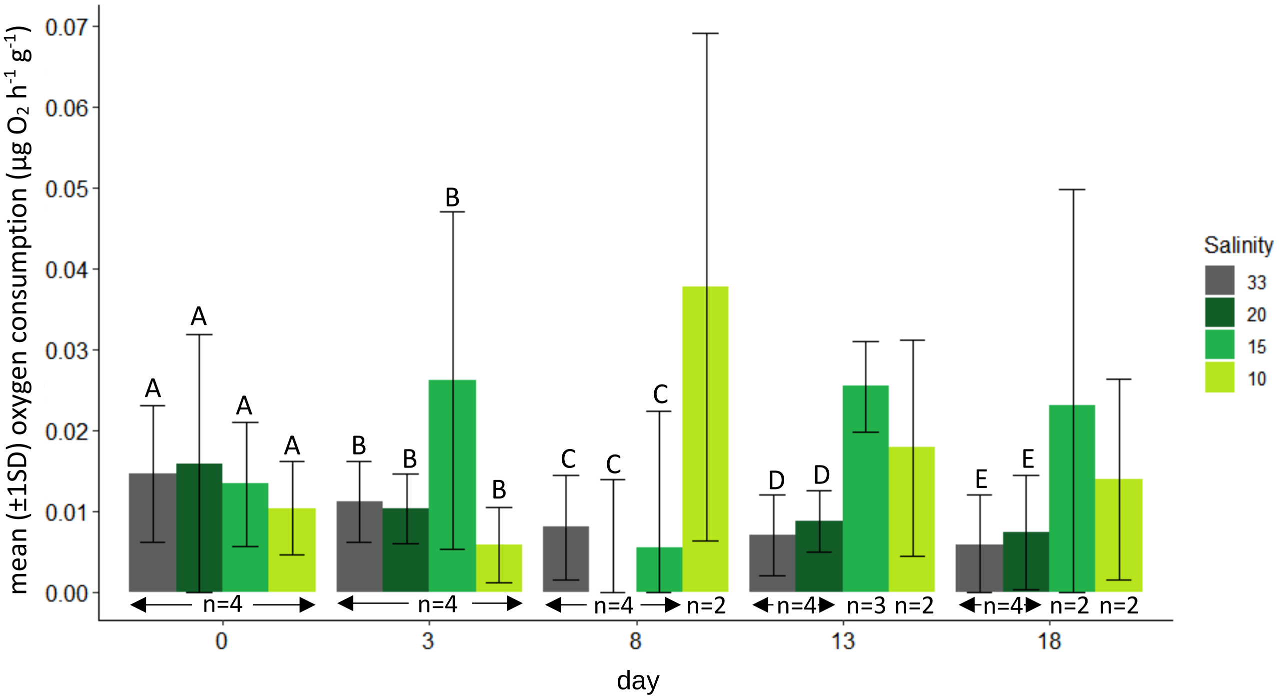

Figure 5. Mean oxygen consumption across the experiment (n=4). Letters above data points indicate similarities (e.g. A, A) and differences (e.g. A, B) between treatments, as determined by post hoc tests

4 Discussion

Barrages are commonly constructed to regulate freshwater flows in estuaries (Lehner et al., 2011; Mulligan et al., 2020). How barrages modify both the physical characters of estuaries (Ma et al., 2019; Kang and Lee, 2020), and population dynamics of estuarine animals (Gillanders and Kingsford, 2002; Amorim et al., 2018; Kim and Kim, 2020), is a key research focus with the aim of balancing societal needs with ecological impacts. Despite general investigations into how modified freshwater inputs into estuaries affect gelatinous zooplankton (Wang et al., 2016; Baumsteiger et al., 2018), we demonstrate for the first time that modification of freshwater flow by a barrage regulates the population dynamics of the estuarine jellyfish *Catostylus mosaicus*. Two studies have previously examined the effects of major dams and regulated flow on estuarine scyphozoan medusae (Xian et al., 2005; Amorim et al., 2018), but these structures differ from barrages by generating a large freshwater reservoir as well as a much larger storage buffer capacity. Medusae were unable to survive extended periods at extreme low salinities, such that they would experience when a barrage opens, but were able to survive and recover from short-term freshwater inputs such that they would experience during a rainfall event. Consequently, artificial modifications of flow that occur following the construction of barrages are likely to result in large changes to estuarine medusa population dynamics.

Jellyfish are osmoconformers, unable to respond to rapid changes in salinity without shrinking or swelling (Albert, 2014). In an estuary characterised by sudden freshwater inputs, due to seasonal heavy rainfall and barrage openings, substantial and abrupt decreases in salinity are frequent (Margvelashvili et al., 2003). The disappearance of medusae from the upper estuary coincided with a sustained reduction in salinity. It is unclear, however, whether the freshwater discharged killed the medusae or whether they may have been flushed downstream. The two experiments we conducted provided insight into the ability of *Catostylus* medusae to withstand changes in salinity. Unlike polyps, medusae can actively move away from low salinity areas to prevent injury, with *A. labiata* observed swimming vertically downwards in response to encountering low salinity surface waters (Albert, 2012). The data presented here contained monthly observations of the occurrence of medusae at sites along the estuary, so changes in distribution along the estuary at a time scale appropriate for identifying a net downstream movement could not be identified. During periods of very high flow, salinity in the Fitzroy River can be reduced to zero 30km below the barrage, halfway along the estuary towards the mouth. Fewer sites reported medusae when salinity was lower than 10 and in the laboratory, severe impairment of medusae pulsation and respiration at moderate salinities was followed by rapid death at extreme low salinities, suggesting that medusae cannot survive at extreme low salinities for more than a few days to a week. Such rapid changes probably do not allow sufficient time for medusae to escape low salinity areas before they incur irreversible damage or perish. This is in line with observations that medusae are not observed <12 salinity (Pitt and Kingsford, 2003a).

Records and anecdotal observations have reported that estuarine jellyfish are more often observed at higher salinities and disappear from estuaries following freshwater inputs (Kingsford et al., 2000; Amorim et al., 2018). Small freshwater inputs into the estuary, however, such as rainfall events, may result in less dense freshwater sitting as a lens at the surface. This may create a ‘refuge’ below the halocline in which medusae can shelter during the event (Rippingale and Kelly, 1995; Albert, 2014). Despite not having any refuge from osmotic changes in the rainfall simulation experiment, within a few days of recovery to marine conditions, all medusae at 20 survived and were able to recover to pre-input pulsation rates. This contrasts with the barrage opening simulation, where ¾ of medusae died within 7 days when continuously exposed to 20 salinity. In the lower part of the estuary, where salinity reductions may not be quite as abrupt or as dramatic as in the Upper Estuary, medusae are likely to survive rainfall events, or barrage openings if >30km downstream, by escaping to higher salinity areas or outlasting the osmotic changes. Alternatively, in response to a freshwater input, medusae may have swum vertically downwards, into deeper, more turbid areas, and not been observed during sampling (Albert, 2012).

Salinity tolerances normally constrain estuarine inhabitants to specific areas of the natural salinity gradient in an estuary (Gillanders and Kingsford, 2002). Construction of a barrage greatly narrows, and in some cases, eliminates the gradient from fresh to saltwater as these constructions primarily act as a physical barrier separating fresh river water from the marine saltwater (Kim and Kim, 2020). In the Fitzroy River, the construction of a barrage greatly shortened the extent of the estuary, reducing the available habitat for medusae (Margvelashvili et al., 2003). This is not the case for all estuaries, for example in the Yangtze River, intrusion of marine water into the estuary extended further upstream after the construction of the Three Gorges Dam facilitated the introduction of marine invasive species (Xian et al., 2005). In both cases, the artificial construction determined the timing and scale of large salinity changes in their respective estuaries by releasing freshwater. In some regions, freshwater releases from major dams, termed “freshets” have been posited as a way to control blooms of *Aurelia aurita* blooms in estuarine ecosystems (Amorim et al., 2018). Our data confirms that medusae are vulnerable to sudden, extreme salinity changes. These constructions are likely change the natural population dynamics of animals that would, under normal circumstances, be driven by natural freshwater inputs into the estuary (Gillanders and Kingsford, 2002; Amorim et al., 2018).

Within shallow semi-enclosed systems, areas of higher salinity in deep water may provide sedentary polyps with a refuge from large seasonal freshwater inputs, enabling them to repopulate the estuary with medusae in the spring (Rippingale and Kelly, 1995). However, this is unlikely to be the case when large volumes of freshwater are released into estuaries. For example most barrage openings resulted in the Upper Fitzroy estuary salinity dropping to below 5 and to 0 in many cases. Whilst polyps from coastal and estuarine species appear to be more tolerant of low salinity than their medusa counterparts, with some able to survive in salinities of 10 (Holst and Jarms, 2010; Dong et al., 2015), reduced rates of asexual budding has been reported at 5 (Purcell et al., 1999), and polyps have died when salinity was reduced to 10 and <7.5 (Holst and Jarms, 2010). Moreover, during periods of high freshwater flows following the opening of the barrage, large quantities of sediment are flushed out of the estuary (Margvelashvili et al., 2003) which is likely to be inhospitable to the establishment of polyp colonies. The reappearance of medusae in the estuary coincides with the return of marine conditions, consistent with the exchange time for the estuary water of 100 days (Dobbie et al., 2003). This observation indicates that medusae in the estuary may be restocked from coastal populations rather than from local populations of polyps. Data on sizes of medusae, however, would be needed to help interpret recruitment patterns.

The most robust test of how modification of environmental flows affects medusae populations would require comparing the population dynamics of medusae in a modified estuary with one or more control estuaries where flows were unmodified. Comparing population dynamics of medusae in the estuary before and after the construction of the barrage would also be very informative. However, no data on the population dynamics of medusae are available from before the barrage was constructed and estuaries to the north and south of the Fitzroy River lack populations of *C. mosaicus*. Hence robust controls were not available and our conclusions from the EHMP data set are essentially based on correlations. Relying solely on correlational and circumstantial evidence to support inferences risks drawing the wrong conclusions from data (Pitt et al., 2018). Nevertheless, there are two reasons we are confident in our conclusions. First was the consistency of the pattern observed over the duration of the 20-year data set. Major flow events occurred approximately 16 times over the 20-year period and medusae disappeared from the Upper estuary following every major flow event. Secondly, our observations were supported by robust laboratory experiments, replicating changes that would occur naturally (i.e. rainfall) and as a result of estuarine modifications (i.e. a barrage opening).

In conclusion, our study provides evidence that the population dynamics of the estuarine medusae *Catostylus mosaicus* are partly driven by freshwater inputs into an artificially modified and managed estuary. Medusae are unable to survive extreme low salinity such as when a barrage releases large volumes of freshwater, but are more likely to survive smaller, transient changes to salinity in the estuary that might occur following a rainfall event. Modifications of natural estuarine systems that change freshwater flows in an estuary are therefore likely to lead to significant changes in the population dynamics of estuarine medusae.

5 Appendices

Appendix 1 – Map of the Fitzroy Basin with land use and sampling points divided by area (Upper, Mid, Lower estuary). Base map sourced from the Queensland Land Use Mapping Program (Department of Environment and Science, Queensland Government).

Appendix 2 – Correlation matrixes for (a) Upper, (b) Mid, (c) Lower estuary variables

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