Intertidal crab prey pulse export quantifies the importance of tidal wetland connectivity

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ABSTRACT

A key value of saltmarshes is their role in providing trophic subsidies, notably in the form of prey pulses of crab zoeae (CZ). No studies to date, however, have investigated quantitatively the patterns between crab zoeae pulses and saltmarsh tidal connectivity in tropical estuaries. In this study, CZ densities were examined over successive tides and months using a zooplankton sampling pump to examine links between tidal fluctuations and pulses of CZ in a tropical Australian estuary with a complex of tidal saltmarshes, mangroves, and unvegetated flats. CZ densities were linked to spatially explicit information on tidal wetland inundation that was derived from Unattended-Aerial-Vehicle (UAV) Structure from motion (SfM) photogrammetry and two-dimensional hydro-dynamic modelling. The study found that: (1) tidal connectivity is a key trigger to prey pulse export; (2) while tidal connectivity was critical in the export of CZ, not all tidal connections resulted in meaningful ecological connectivity; and (3) succulent saltmarsh was one of the tidal wetland types contributing to the export of CZ. Surprisingly, we reveal that not all succulent saltmarshes were uniformly participating in CZ export. These findings highlight the significance of quantitative eco-hydrological approaches to assess saltmarsh and tidal connectivity values. This study supports the need for management and restoration approaches to integrate a contextual understanding of the synergies between hydrology, ecology, and habitat heterogeneity. These data emphasise the need to move beyond generalisations that "similar" habitat type share similar ecological functions and should be managed equally.

1. Introduction

Understanding how saltmarsh systems work as connected and productive habitats in relation to tidal connectivity is particularly important for successful restoration and management. Tidal connectivity mediates pulses that drive ecosystem productivity at complex temporal and spatial scales (Rehage and Loftus, 2007; Matich and Heithaus, 2014) while supporting critical coastal ecosystem functions and services such as maintaining biodiversity (Friess et al., 2012; Granado et al., 2018), and dynamic coastal food webs upon which fisheries rely on (Connolly and Waltham, 2015; Nelson et al., 2015; Taylor et al., 2018; Abrantes et al., 2019). The causes and consequences of connectivity–from water movement to fish migration and export of trophic subsidies – are a complex network of physical and biological interactions linking diverse ecological units within the coastal ecosystem mosaic or the seascape (i. e., seascape connectivity) (Sheaves et al., 2006; Sheaves, 2009; Litvin

et al., 2018).

When saltmarshes co-occur with mangroves, such as in the tropics and in Australia, their position is usually high in the intertidal zone, on the landward side of mangroves in Australia (Bridgewater and Cresswell, 1999; Saintilan and Adams, 2009; Kumbier et al., 2021; Vulliet et al., 2024). In these areas, saltmarshes have recognised conservation values for their role as crustacean habitat (Mazumder, 2009; Saintilan and Mazumder, 2017; Reis and Barros, 2020; Reis et al., 2019). Saltmarsh crabs are viewed as key saltmarsh species, in part due to the monthly mass release of their zoeae (Mazumder et al., 2009; Ricardo et al., 2014). Saltmarsh crabs are known to synchronise their spawning release of zoeae with high spring tide inundation, which can become a major prey pulse for zoo-planktivorous fish in estuaries (Mazumder et al., 2006; Hollingsworth and Connolly, 2006). Zoo-planktivorous fish can take advantage of this prey pulse by switching their diet to crab zoea during these optimal times (Hollingsworth and Connolly, 2006; McPhee

et al., 2015). This process symbolises the importance of prey pulses and ecological productivity in supporting saltmarsh connectivity (Saintilan and Mazumder, 2017). However, these saltmarsh studies have occurred in sub-tropical and temperate areas, which means that applying this pattern to tropical ecosystems needs to be tested. In addition, understanding the values of tidal connectivity to upper tidal wetlands such as saltmarshes is particularly important given that tropical coastlines are expected to be particularly jeopardised by human development, climate change and sea-level rise (SLR) projections in the next few decades (Sale et al., 2014).

Temperate and subtropical studies have provided considerable knowledge on the important role of saltmarsh in the export site of crab zoea in opposition to mangroves where lower densities of crab zoeae have been recorded (Mazumder et al., 2009). The mass export of crab zoeae seems to occur almost monthly, with peaks during the coolest month of the year (Mazumder et al., 2009) and during nighttime high tides (Mazumder et al., 2009; Ricardo et al., 2014). In addition, dietary studies have found that the consumption of crab zoea by estuarine fish did not coincide with the day of the highest spring tide, but indeed highest occurrence in the fish stomachs occurred following the day of the first tide inundating the marsh (Mazumder et al., 2006; Hollingsworth and Connolly, 2006) – suggesting a crab reproductive strategy to maximise crab zoeae export on successive tides (Hollingsworth and Connolly, 2006). However, to date, no studies have quantitatively described the links between the variability in tidal connectivity – measured as the variability in tidal height and the spatial extent of saltmarsh and adjacent wetland inundation – and ecological connectivity – measured as the variability in patterns of prey pulse export. This contextual and quantitative understanding of both hydrological and ecological connectivity is, nevertheless, necessary to move towards a more holistic, process and pattern-based understanding of the values of tropical saltmarshes (Weinstein et al., 2014). In addition, given the ongoing trend of coastal development, ecosystem fragmentation and degradation (Gedan, 2009; Waltham and Sheaves, 2015; Henderson et al., 2020; Gilby, 2020), understanding how saltmarsh systems work as connected and productive habitats in relation to tidal inundation is particularly important for successful restoration and management.

Management and restoration decisions are thought to be often based on "outdated restoration techniques" (*sensu* Liu et al., 2016) and "pseudoscientific paradigms" (*sensu* Sheaves et al., 2020), which misdirect decisions and lead to economic and ecological loss. Among these restoration techniques are focusing on only one physical attribute, such as restoring tidal hydrology via the removal of barriers (Liu et al., 2016; Abbott et al., 2020). Focusing only on the removal of barriers risks assuming automatic restoration of ecological connectivity and, therefore, the expected values (e.g., fishery values) of a system back. However, studies in both rivers (Fullerton et al., 2010) and coastal ecosystems (Davis et al., 2014b) have highlighted that organisms such as fish and crabs do not respond linearly to hydrological connectivity and that other contextual variables (e.g., reproductive strategies, food availability, type of substrate, plant community structure) (Davis et al. 2012, 2014b; Luk and Zajac, 2013) participate in achieving ecological, or realised connectivity (*sensu* Davis et al., 2014b). The second is that, as postulated by Sheaves (2017) but for mangroves, the values and functions of saltmarshes may also be generalised, assumed to be uniform and transferable across estuaries due to the presence of similar habitat, often defined by broad vegetation categories (e.g., saltmarshes or mangroves). These generalisations and extrapolated paradigms may misdirect management decisions to focus only on one process or habitat, thereby potentially missing central contextual factors that are important for influencing the functionality and values of a system and, hence, restoration success (Sheaves et al., 2021).

The present study aims to develop a contextual understanding of the value of saltmarshes and connectivity in the export of crab zoea from a tropical estuary composed of mangroves, unvegetated flats and saltmarshes. Specifically, this study investigated the extent to which (1) the

crab zoea export was related to tidal fluctuations, diel period, the number of days before and after the highest spring tide, and the sampling month; and (2) the effects of the extent of tidal wetland inundation (consisting of saltmarsh, mangrove, and unvegetated flats) were related to the export. The influence of these variables on the densities of copepods was also investigated. Copepods are considered in this research as these taxa were the dominant zooplankton in the samples and could be used as a sampling control (i.e., whether the sampling system was successful at pumping zooplanktonic organisms). Additionally, copepods can provide important information on the functioning and variability of seascape connectivity due to copepods being "sink organisms" - coming from estuarine, open waters - in opposition to "pulsed organisms" (i.e., crab zoea, coming from upper tidal systems) (Mazumder et al., 2009; Qin et al., 2015). By investigating these research questions, the importance of integrating both hydrological and ecological connectivity in assessing the value of saltmarshes and tidal connectivity is explored. In addition, the need for management and restoration actions to reflect tidal wetland habitat values from a more holistic, process-based (e.g., hydrological and ecological connectivity) perspective rather than an individual habitat or vegetation-focused approach is discussed. Innovative methods that integrate remotely sensed and hydrodynamic modelling data on prey pulses, tidal cycles, and local habitat characteristics are important for coastal managers to develop a contextual understanding of saltmarsh function and processes.

2. Methods

2.1. Study area

This study was conducted at Blacksoil Creek (−19.297867, 147.021333), a saltmarsh-mangrove-saltpan complex typically observed in the dry tropics of north Queensland, Australia (Fig. 1). The study area (82.5 ha) is the upstream area of the larger Blacksoil Creek system (>300 ha). The site has been split from the remaining system by a concrete road, which has a multi-pipe culvert (1-m in diameter) as well as smaller culverts along its southern side. Tidal exchanges between the study site and the downstream portion of the system are via the main tidal creek (the main channel) that connects the site to the coastal waters. The tidal regime is meso-tidal with semi-diurnal tides, with two sets of spring tides during the month, one having higher amplitudes than the other (Vulliet et al. 2023, 2024).

The tidal wetland cover consists of 63.9% of saltpans and mudflats, 15.8% of herbaceous saltmarsh, 9.2% of succulent saltmarsh, 7.4% of *Ceriops* spp. (yellow mangrove, *Ceriops tag*al and *Ceriops austral*is), 3.1% of other mangroves (principally the grey mangrove, *Avicennia mari*na), and 0.6% of the main channel (the main tidal creek which drains the study site) (Vulliet et al., 2024). *Ceri*ops spp are mangrove species that generally dominate high intertidal zones in tropical northern Australia, Robert et al. (2015).The main channel is bordered by the red mangrove, *Rhizophora stylo*sa, transitioning to *A. mari*na and *Ceriops* spp. at the highest elevation (Vulliet et al., 2024). The saltmarsh vegetation community is dominated by succulent marsh, notably the bead weed, *Sarcocornia quinquefl*ora, with isolated patches of glasswort, *Tecticornia* spp.; grey samphire, *Tecticornia australasi*ca; pigweed, *Portulaca* spp.; pigface, *Carpobrotus glauces*cens.; prickly saltwort, *Salsola austral*is; and Seablite, *Suaeda austral*is. The herbaceous saltmarsh community is principally composed of the salt couch, *Sporobolus virginic*us with some green couch, *Cynodon dactyl*on, and jointed rush, *Juncus krauss*ii. Although there is an overall transition from mangroves to succulent saltmarsh and herbaceous saltmarsh with increasing elevation, mosaic distribution patterns characterised by overlapping distribution of different wetland types across similar elevations were also identified (Vulliet et al., 2024). Further details on the study site vegetation, configuration and hydrology can be found in Vulliet et al. (2024).

Pilot studies were conducted to identify and quantify crab species in saltmarsh areas. Fyke nets (1-mm mesh panels, 5-m opening) placed
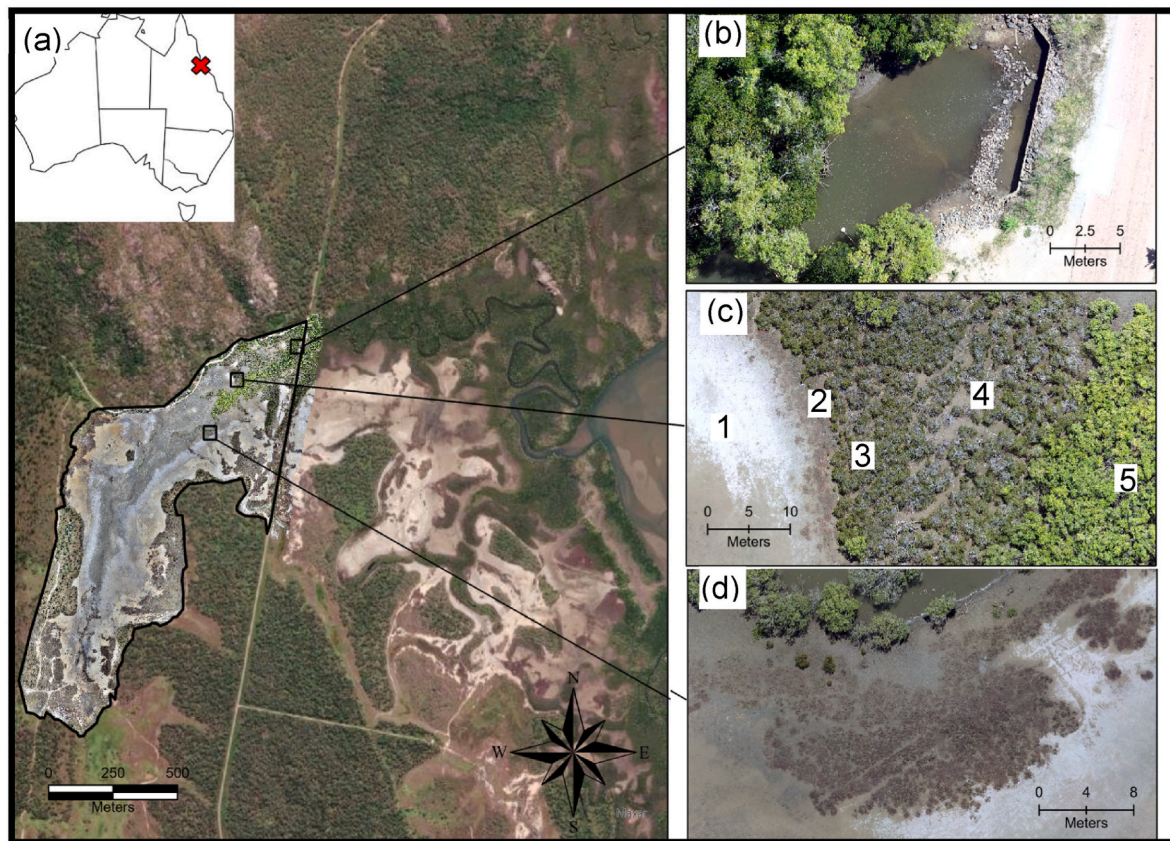
Fig. 1. Map of the study area showing (a) the study site (UAV-SfM-derived orthophoto map) within the estuarine complex of Blacksoil Creek (Landsat Imagery) in Queensland, Australia. The boxes show: (b) the location of the zooplankton sampling system upstream of the road culvert (the white float in which the bilge pump is lodged is apparent on the bottom left part of the box); (c) the mosaic structure of tidal wetland habitats characterised by (1) saltpans; (2) patches of succulent saltmarshes along (3) the *Ceriops* spp. forest; (4) patches of mudflat within the *Ceriops* spp. forest; and (5) mangrove forest dominated by *Avicennia mari*na; (d): patches of succulent saltmarshes bordering the main channel with mudflats. The destructive effects of 4-wheel driving on the saltmarsh is noticeable. Note that the scale bar differ in each boxes.

across draining channels and directly on the saltmarsh captured *Metograspus latifr*ons (Graspidae), *Paracleistostoma wa*rdi (Graspidae), *Parasesarma erythrodacty*la (Graspidae), *Australoplax triden*ta (Ocypodidae), and *Uca sign*ata (Ocypodidae). Other species are likely found at the study site (e.g., Vermeiren and Sheaves, 2014; Vermeiren and Sheaves, 2015). The catch is therefore a subset of the total species possible in the study area.

2.2. Sample collection and processing

Traditional zooplankton sampling methods (e.g., zooplankton nets, Mazumder et al., 2009) could not be used due to the high risk of saltwater crocodile (Crocodylus porosus) encounters at the study site. Therefore, a zooplankton pumping system was designed and operated using a programmed timer switch (Fig. 2), which meant that samplers did not have to enter the water or be near the creek edge at night during high tides. The sampling system consists of a 1000L intermediate bulk container (IBC) linked to a 750 GPH bilge pump attached to a float at the end of a 4-m-length swimming pool telescope pole (Fig. 2c). The bilge pump was linked to a 12V battery and activated by a timer switch (Fig. 2e) programmed to power the battery when the study site starts draining. The IBC had a float switch to stop the pump when the tank was full. The end of the pole near the float was attached via two ropes extended at two extremities to prevent the pole from retracting toward the bank edge during ebbing and flooding tides (Fig. 2d). The battery was placed in a toolbox to prevent damage from rain or tidal water. The timer switch was placed in a small container to prevent additional damage from humidity, rain, and rodent damage.

Pilot tests revealed that the tank was filled after 200 min. To sample crab zoea export over the entire ebbing tide draining the study site (which was estimated from visual observations during pilot surveys to take approximately 5–7 h), pumping was divided into five sessions of 40 min, starting 2 h after the predicted high water (HW, referring to the time at which tide is at its highest point) at Cape Ferguson tidal gauge (19.277208; 147.060908). The tank was positioned directly upstream of the main culvert (i.e., the downstream boundary of the study area) (Figs. 1b and 2b). This was a strategic placement to explicitly sample the export pulse of crab zoea from the upstream wetland area.

The system successfully sampled ebbing tides over 90 days, totalling 490 h of pumping (Table 1). Timer switch issues (rain and timer switch failure) and a rodent damaging the wiring caused unsuccessful sampling days in September, January–February, and February–March. Fish dietary studies in temperate and subtropical saltmarshes have suggested that tides that first inundate saltmarshes, rather than necessarily the highest spring tide, trigger crab spawning (Hollingsworth and Connolly, 2006; Mazumder et al., 2006). Therefore, the neap and spring tides are sampled over several consecutive days to decipher the crab zoea pattern between tidal height and export. The first deployments were over 21 nights in August 2021, 23 nights in September, and 24 days in December 2021 (Table 1). Subsequently, due to consistently negligible crab zoea densities during neap tides (presumably because the wider vegetated study area had not been inundated by tidal flow connection), the sampling system was deployed over ten days in January–February 2022, six days in February–March 2022, and seven nights in June 2022 to coincide for several days before and after the spring tide.

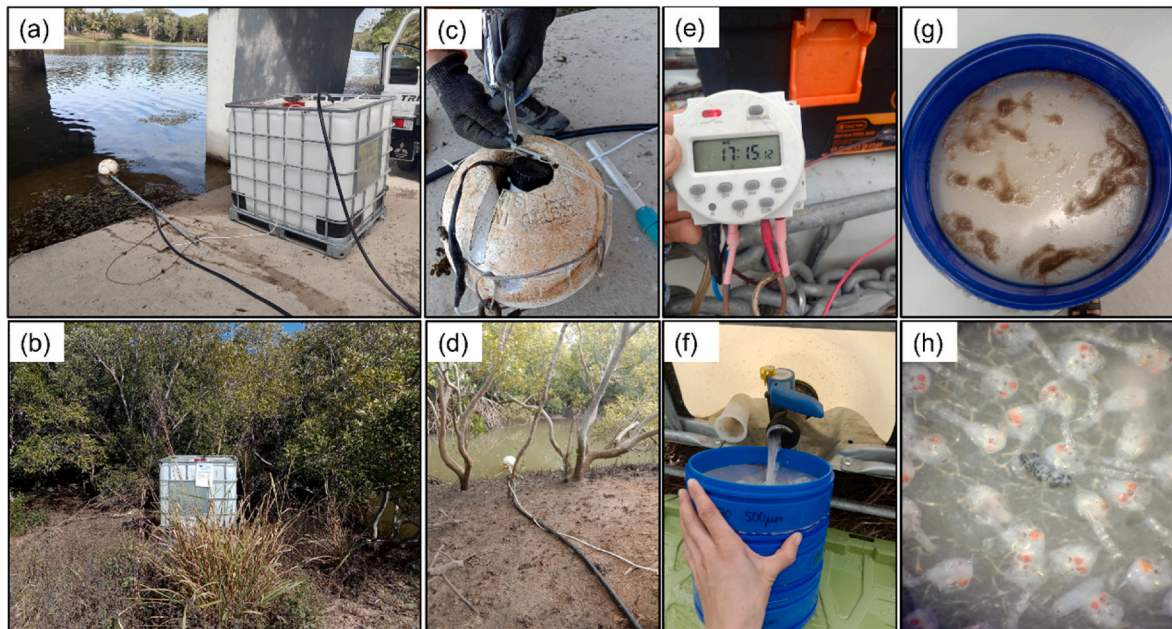The IBC tank was emptied at low tide every morning (austral winter)

Fig. 2. Description of the pumping sampling system showing: (a) the intermediate bulk container (IBC) linked to the hose with the telescope pole and the float where the bilge pump is attached; (b) the sampling system deployed at the study site; (c) close view of the 750 GPH bilge pump attached to the pole and the float; (d) the pump deployed at the study site with the pole attached to two ropes; (e) the timer switch linked to the 12V battery in the tool box; (f) example of sampling where the water from the IBC is released through a 500 μm and 250 μm sieve at the sampling site; (g) pulse of crab zoeae on the 250 μm sieve (after cleaning) in the laboratory; (h) stereo-microscope view of crab zoeae.

Table 1
Number of sampling days per sampling period along with the number that occurred during the day or the night and the number of tides preceding and succeeding the highest spring tide of the spring tide cycle. The latter is denoted by T0 (High Water), while previous day by -T1, -T2, -T3, and subsequent days by T1, T2, and T3.

Sampling period	Days	Night	Day	Neap	T-3	T-2	T-1	T0	T1	T2	T3	T4
August P1	7	6	1	5	0	0	0	0	0	1	1	0
August P2	14	14	9	8	1	1	1	1	1	1	1	0
September P1	11	11	0	4	1	1	1	1	1	1	1	0
September P2	12	12	0	5	1	1	1	1	1	1	1	0
December P1	12	3	9	5	1	1	1	1	1	1	1	0
December P2	12	1	11	7	0	1	1	1	1	1	0	0
January–February	9	0	9	1	1	1	1	1	1	1	1	1
February–March	6	0	6	1	1	1	0	1	1	1	0	0
June	7	7	0	1	1	1	1	1	1	1	0	0

or every afternoon (austral summer) after the high tide had flooded the site area by filtering the water through a 500 μm to remove larger debris and prevent damage from water pressure on crab zoea and copepods and 250 μm filter sieves (Fig. 2f), leading to one sample per sampling session. The material remaining on both sieves was transferred into a flask with water and ethanol until processing in the laboratory. The filtered content (Fig. 2g) was cleaned and transferred into a beaker in the laboratory. Copepods, consisting principally of calanoid copepod *Acartia sinjiensis*, and crab zoeae were counted in five replicates on a Bogorov tray under a stereomicroscope following subsampling and enumeration procedures (Alden III et al., 1982; Wiebe et al., 2017). The densities of copepods and crab zoea in the 1000 L (full IBC tank) (individuals/m³) were computed by counting individuals in a 6 ml subsample taken from a 150–1000 ml subsample, and then scaling up based on the proportion of the full tank volume (100,000 ml).

2.3. UAV land cover and hydrodynamic modelling data

The two-dimensional hydrodynamic model developed in Vulliet et al. (2023), utilising digital terrain and land cover information derived from an unoccupied aerial vehicle (UAV) survey, was used to report the export of crab zoea as a proportion of the tidal wetland inundated area

following each inundation. The same land cover and tidal wetlands classification described in Vulliet et al. (2024) were used, where land cover was categorised as Main Channel (MC), *Ceriops* spp. (C); *A. marina/R. stylosa* (abbreviated as M for other mangroves than *Ceriops* spp.) Mudflat/Saltpan (MS); Succulent Saltmarsh (SS); and Herbaceous Saltmarsh (HS). Inundation simulations were set to cover each sampling period following the same procedure and parameters described in Vulliet et al. (2023). The categories Woodland/Terrestrial and Manmade as well as the land cover area downstream of the main concrete road (Fig. 1) were not included in the analysis.

To quantify the extent of inundation of tidal wetland type when the pump was deployed, simulations were run for each inundation time surveyed. To obtain the extent of inundation for each night/day of sampling, mapping outputs were computed every 10 min and added to cover the time the pump commenced until it had stopped. This technique allowed the calculation of the maximum boundary extent over the study site per sampling night/day rather than over the entire simulation period. The raster mapping outputs were exported to ArcGIS Pro 2.8.6 (Esri) and overlaid with the raster land cover layer to obtain a spatial dataset with tidal wetland type inundation area for each sample collection.

The final environmental multivariate datasets also contained: 1) the

maximum observed tidal height (m) recorded at Cape Ferguson tidal gauge; 2) whether sampling was conducted at day or night; and 3) the number of tides preceding and succeeding the highest spring tide of the spring tide cycle (DayNum). The latter consisted of denoting HW by T0, previous day by -T1, -T2, -T3, and subsequent days by T1, T2, and T3. The length and high amplitude of the spring tides occurring in January–February 2022 led to adding a T4 tide. The remaining sampling days were denoted as neap tides (N) (Fig. 3c).

2.4. Data analyses

Univariate classification and regression trees (CARTs) (De'Ath, 2002) (see Davis et al. (2014a) for an application of CARTs in ecological studies) were used to observe the influence of the extent of tidal wetland inundation, diel period (i.e., day or night sampling), days before/after HW, and observed HW (HWobs) on crab zoea density. Crab zoea and copepod density data were $\log_{10}(x+1)$ transformed to reduce skewness (due to zeros and extreme values) and decrease non-normality (see Figs. S1–S2 in the Supplement for residual normality plots and Table S1 for Shapiro-Wilk tests).

Classification and regression trees are a robust and unbiased constrained multivariate technique used to investigate relationships between explanatory and response variables in ecology (De'ath and Fabricius, 2000). Classification and regression trees use a binary algorithm that grows the tree by splitting data into distinct homogenous

groups according to thresholds in the explanatory variables (Ouellette et al., 2012). The splitting process continues separately on each node (i. e. homogenous group), forming distinct community composition responding to a given threshold of environmental variables at each tree leaf (De'ath and Fabricius, 2000). The tree cross-validated (CV) error represents the average test error over the k cross-validations. A CV error ≥ 1 means that the selected tree has no predictive power, while a CV error = 0 means that the selected tree has a perfect predictive power (De'ath and Fabricus, 2000). The selected tree should have a CV relative error within 1 SE of the minimum relative error (De'ath and Fabricius, 2000). The "mvpart" function (De'ath, 2014) was used to create CARTs using the function default settings (downloaded from the devtool package (Wickham et al., 2022), formerly in the CRAN repository), applied in RStudio Desktop Version 2022.12 (Team, 2020).

The distribution of copepods and crab zoea across all sampling periods was analysed using non-metric multidimensional scaling (nMDS) on Bray-Curtis dissimilarities of $\log_{10}(x+1)$ of crab zoea and copepods densities. The BIO-ENV function (vegan package in R (Oksanen et al., 2013)) was used to find the subset of environmental variables that best correlates with the community data by calculating the Spearman rank correlation between the Euclidian distance (environmental variables) and the Bray-Curtis dissimilarity (community data) matrices. Following Clarke and Gorley (2015), environmental data were first individually normalised using the sqrt(x) function (see Figs. S3–S4 in the Supplement for residual normality plots and Table S2 for Shapiro-Wilk tests). No
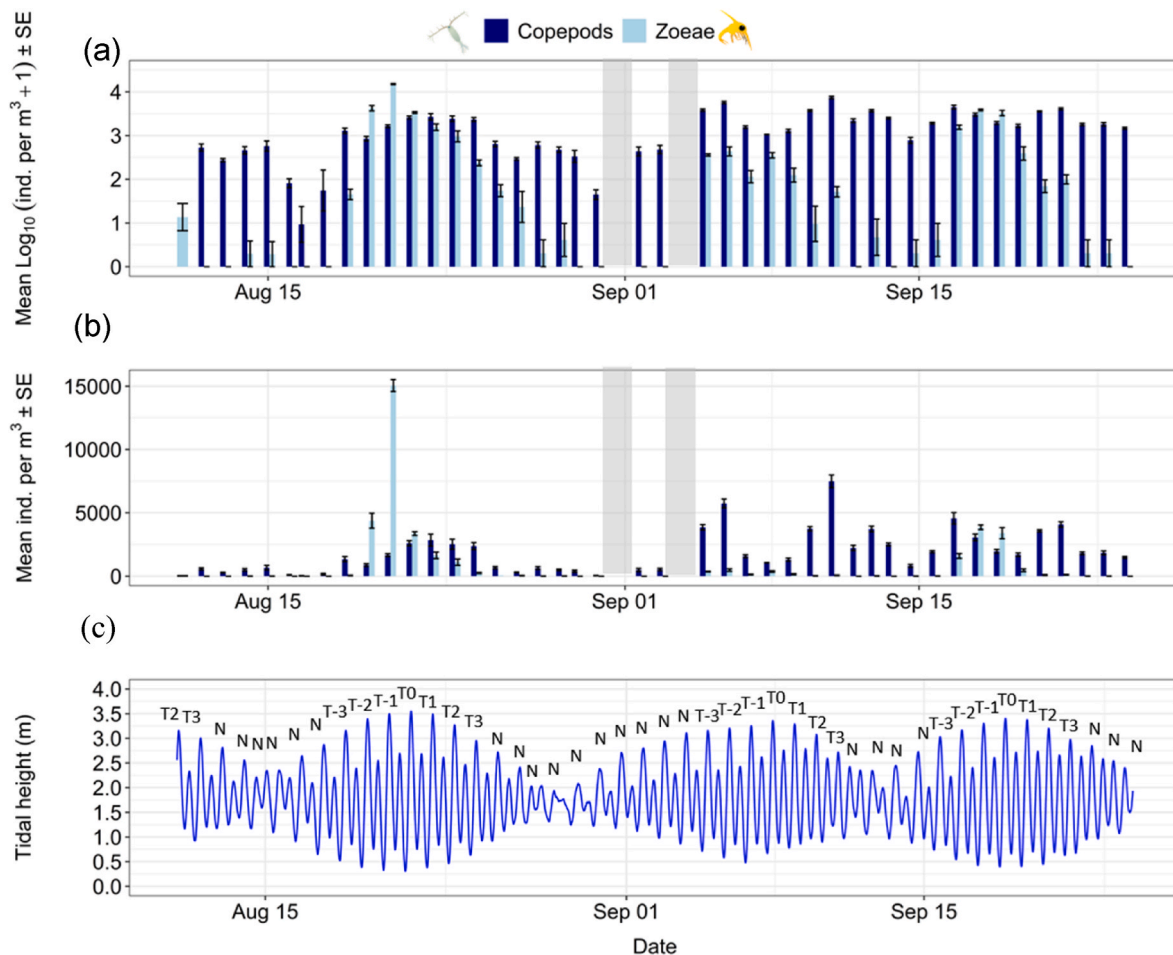

Fig. 3. Crab zoea and copepod densities per sampling day (i.e., per samples of 5 replicates of 6 ml – the mean and standard error (SE) are the sample mean and standard error) over August and September 2021 showing (a) mean $\log_{10}$(individual per m^3+1) $\pm$ SE, (b) mean individual per m^3 $\pm$ SE, and (c) corresponding observed water height (HW) recorded at Cape Ferguson tidal gauge. DayNum" = The number of tides preceding and succeeding the highest spring tide of the spring tide cycle, where days are described as T-3; T-2; T-1; T0 (Highest Spring Tide); T1; T2; T3; T4, and N (Neap tide). The shaded areas were not sampled (planned or sampling issues).

transformation was conducted on the variables Observed High Water (HWObs), *A. marina/R. stylosa*, *Ceriops* spp., and Main Channel as transformations increased heteroscedasticity. Variables that were highly auto-correlated ($R^2 > 0.95$) were removed for the analyses (Table S3 in the Supplement) (i.e., only Total boundary inundation area was removed). Individual Kruskal-Wallis tests (non-parametric alternative to

ANOVA) were conducted to observe whether there were statistically significant differences in crab zoea and copepod density respectively between DayNum, months (average of T3 to T4 tides – not including N tides as these were not consistently sampled across months), and the diel periods (Night, Day, Day/Night (Down) and Night/Day (Dusk). Note that when two high spring tides of the same month were sampled, such
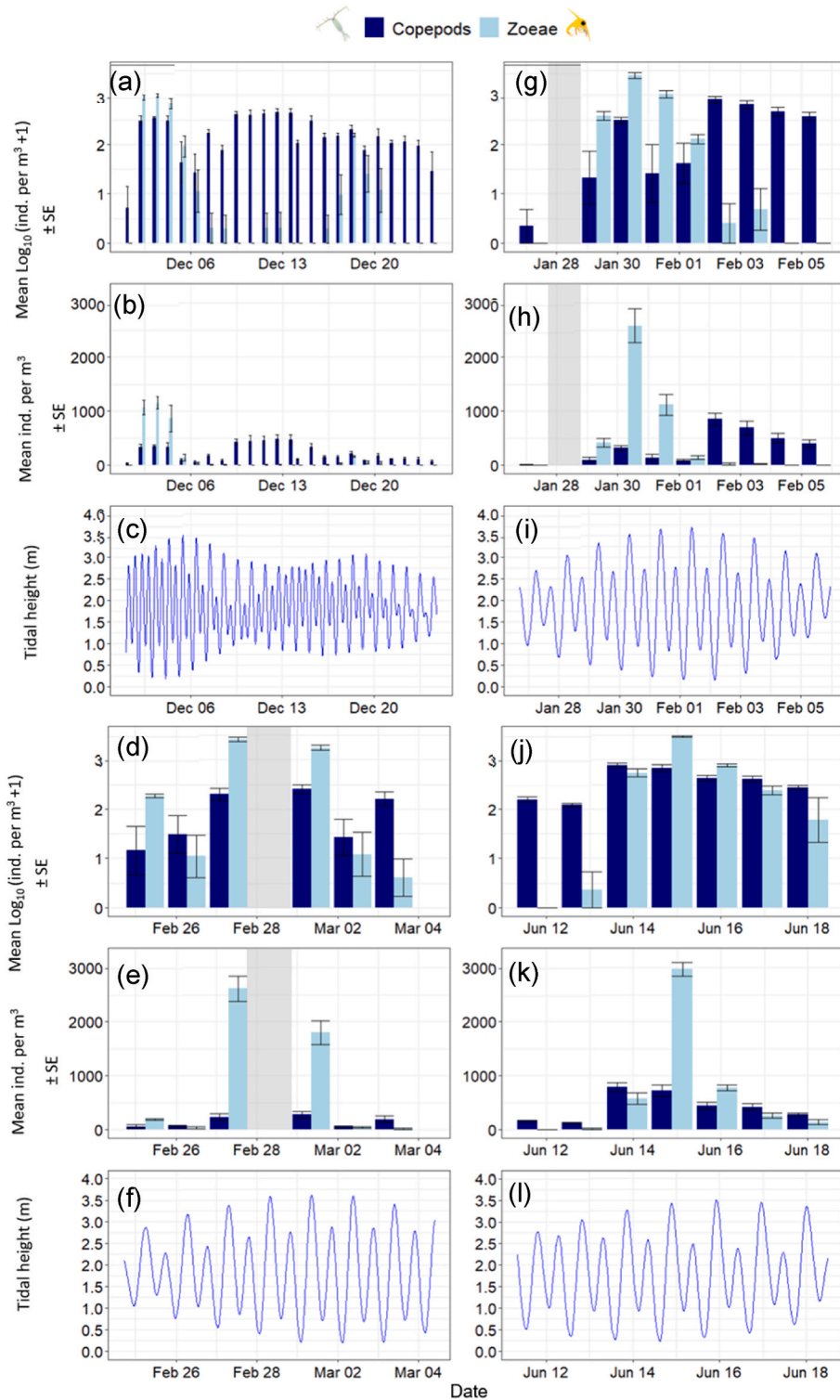

Fig. 4. Crab zoea and copepod densities per sampling day (i.e., per samples of 5 replicates of 6 ml where the mean and standard error (SE) are the sample mean and standard error) showing (a, d, g, j) mean $\log_{10}$(individual per m^3+1) ± SE, (b, e, h, k) mean count of individuals per m^3 ± SE, and (c, i, f, l) corresponding observed water height (HW) recorded at Cape Ferguson tidal gauge for (a–c) December 2021, (g–i) January–February, (d–f) February–March, and (j-l) June 2022. The rodent damage occurred in February–March, T-1 tide (shaded area in d,e).

as in September, the month was denoted as SeptP1 and SeptP2, referring to the first and second spring tides, respectively). Multiple pairwise comparisons were run using the Wilcoxon rank Sum Test (using the Benjamini-Hochberg Procedure (false discovery rate) as the p-adjustment method) to observe statistically significant groups. Unless otherwise stated, all density data are given in $\log_{10}(x+1)$ transformed.

3. Results

3.1. Patterns of crab zoea density in relation to tidal fluctuations, timing, and diel period

The greatest crab zoeae density sampled over the entire study period was in August at T-1 (4.17 ± 0.01 individuals (ind.) m^{-3} (log-transformed) or 15060 ± 479.98 ind. m^{-3} (untransformed)) (Fig. 3) where HW was 3.50 m – which was not the highest tide recorded over the sampling period (3.71 m in February) (Fig. 4). The lowest densities were recorded during neap tides and when observed HW did not exceed 3.16 m (Fig. 4), such as in the second spring tides of December.

There was a strong correlation between the crab zoea density and tidal fluctuations (Figs. 3 and 4). This was characterised by a primary split in the univariate CART of crab zoea density (Fig. 5). The split was determined by mean observed high water (MeanHWobs) of 3.16 m, where observed HW $\geq$ 3.16 m resulted in mean $\log_{10}$ (crab zoea density + 1) of 2.45 ind. m^{-3} compared to 0.49 ind. m^{-3} ($\log_{10} x +1$) in HW $\leq$ 3.16 m (Fig. 5). The secondary split shows that crab zoea density was not only related with HW height, but also with the variable DayNum (i.e., neap tides and day before and after the highest spring tide of the spring tide cycle), where the highest densities were recorded before HW (T-3 to T-1) and at the highest spring tide (T0) rather than days after T0. Over the sampling period, the greatest mean crab zoea density (3.14 ± 0.25 (SE) ind. m^{-3} (log-transformed) or 3383 ± 1734 ind. m^{-3}

(untransformed)) was observed at T-1, followed by T0 (2.82 ± 0.24 ind. m^{-3} or 1343 ± 484 ind. m^{-3} untransformed)), and T-2 (2.71 ± 0.29 ind. m^{-3} or 1342 ± 529 ind. m^{-3} (untransformed)) (Fig. 6a).

The relative statistical importance of DayNum and diel period to crab zoeae and copepods densities were further tested using the Kruskal-Wallis tests, which showed no statistically significant difference in densities of crab zoeae between day, night, dawn (transition from day to night: day/night), and dusk (transition from night to day: night/day) (Kruskal-Wallis $\chi^2 = 5.33$, df = 3, p = 0.149), but significant difference in copepod density (Kruskal-Wallis $\chi^2 = 40.98$, df = 3, p = 0.001). By opposition, copepods densities were not statistically significant different between DayNum (Kruskal-Wallis $\chi^2 = 5.75$, df = 8, p = 0.70). However, this term was statistically significant for crab zoea (Kruskal-Wallis $\chi^2 = 62.52$, df = 8, p < 0.001). Post-hoc pairwise comparisons using the Wilcoxon rank Sum Test showed that the location of median densities between DayNum was statistically significant between neap tides and T-3 (p = 0.006), T-2 (p < 0.001), T-1 (p < 0.001, T-0 (p < 0.001), T1 (p < 0.001) and T2 (p < 0.001). Neap tides were not statistically different compared with T3 (p = 0.117) and T4 (p = 0.519).

Although no significant differences in crab zoea densities were revealed among diel periods, mean crab zoea densities were higher during the night (1.64 ± 0.18 (ind. m^{-3} (log-transformed) compared to the day (1.41 ± 0.20 ind. m^{-3}); and at dawn (day/night) (0.30 ± 0.30 ind. m^{-3}) compared to dusk (night/day) (0 ind. m^{-3}) (Fig. 6b). This difference was higher when adding night/day to the day (1.37 ± 0.20 ind. m^{-3}) and day/night to the night category (1.56 ± 0.17 ind. m^{-3}). Diel differences remained not statistically significant for crab zoea even when pooling those terms (Kruskal-Wallis $\chi^2 = 0.52$, df = 1; p = 0.471).

There were also statistically significant differences in densities among months in the data here (without the N tides samples) for both crab zoea (Kruskal-Wallis $\chi^2 = 21.28$, df = 9; p = 0.0114) and copepod populations (Kruskal-Wallis $\chi^2 = 47.40$, df = 9; p < 0.001) (Fig. 6c).
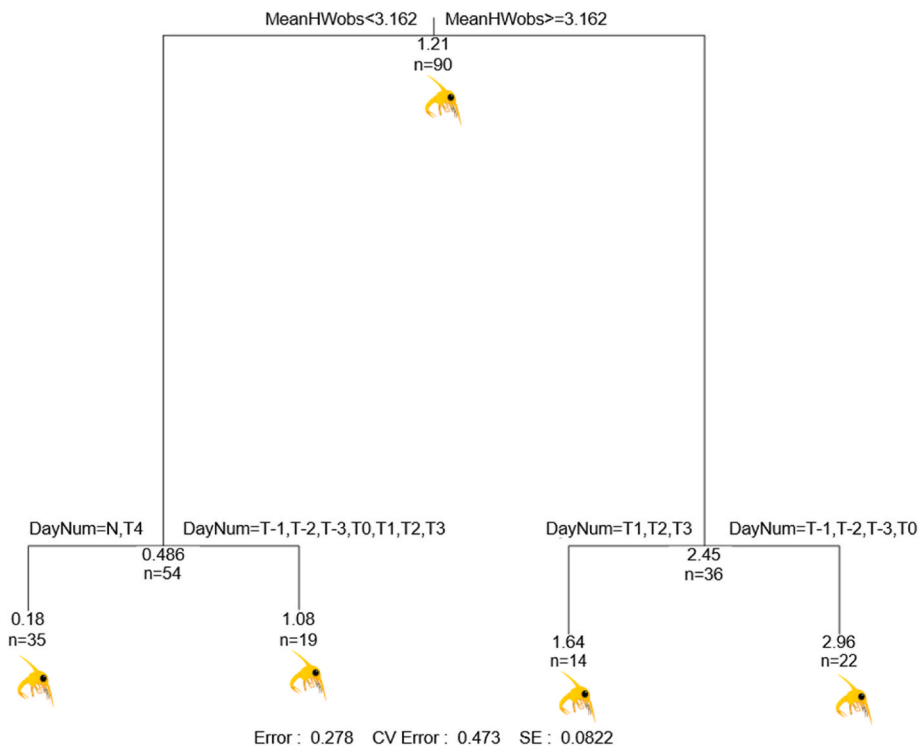

Fig. 5. Univariate classification and regression tree representing the distribution of crab zoea densities, based on $\log_{10}$(Individuals per m^3 +1). Mean densities are shown at each terminal node with the sample size in bracket. Each node represents the split based on the environmental variables that best explained variability in crab zoeae densities across samples. "MeanHWobs": MeanHigh Water observed at Cape Ferguson tidal gauge; "DayNum" = The number of tides preceding and succeeding the highest spring tide of the spring tide cycle, where days are described as T-3; T-2; T-1; T0 (Highest Spring Tide); T1; T2; T3; T4, and N (Neap tide). "Error": The total relative error of the tree, where R^2 of the model is 1. "CV error": Cross-validation error of the tree; "SE": Standard error of the cross-validation statistic (i.e., cross-validation error).
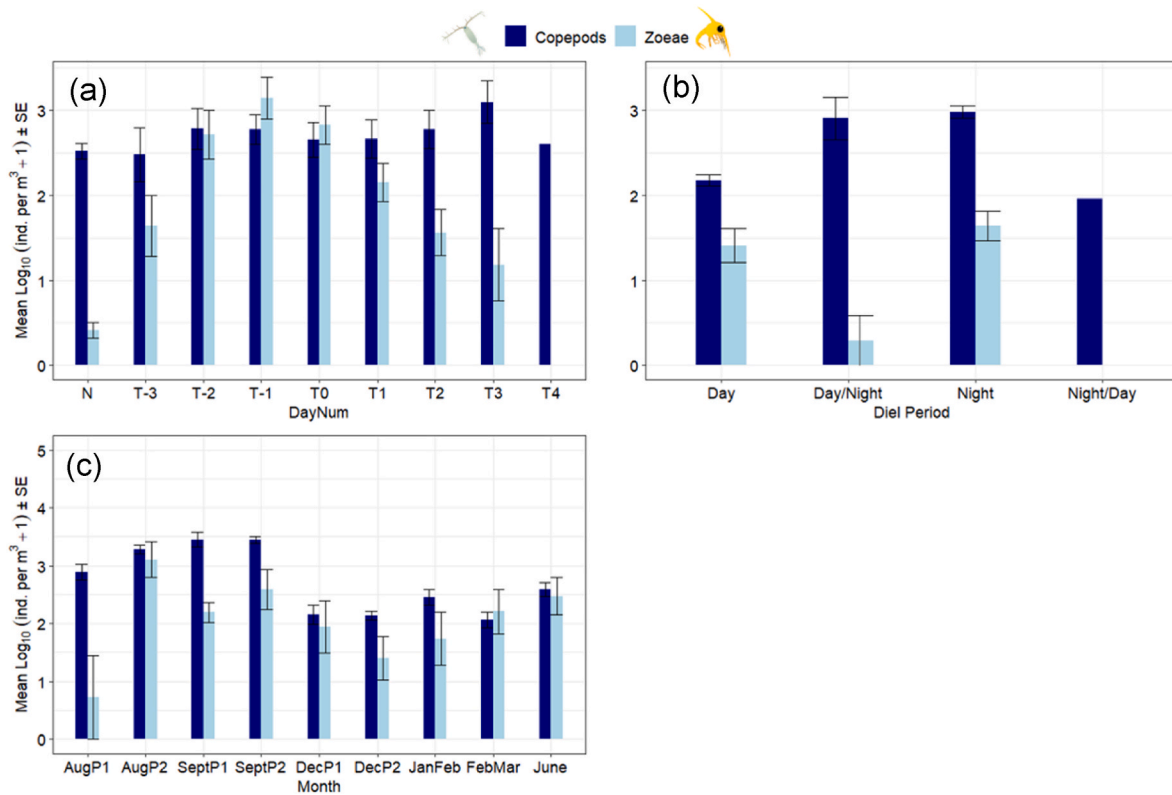
Fig. 6. Mean copepod and crab zoea densities ($\log_{10}$(individual per $m^3 + 1$) $\pm$ standard error (SE) grouped by (a) DayNum = The number of tides preceding and succeeding the highest spring tide of the spring tide cycle, where days are described as T-3; T-2; T-1; T0 (Highest Spring Tide); T1; T2; T3; T4, and N (Neap tide) and (b) diel period at which HW occurred; and (c) months (i.e., all samples of the spring tide phase without neap tide samples). "P" next to Sept and Dec refers to the first spring tide period of the month (P1) and second spring tide period of the month (P2).

Although the post-hoc pairwise comparisons using the Wilcoxon rank Sum Test identified not statistically significant groups.

3.2. Ordination of crab zoeae and copepods densities

Ordination of the samples based on Bray-Curtis dissimilarities of crab zoeae and copepods densities (Fig. 7) indicated a distinct pattern in sample structure. Samples principally characterised by spring tides, notably T-3 to T0 tides, were situated in the left part of the ordination space, with which crab zoea was highly correlated. By opposition, copepods were correlated to the right part of the ordination space, where mostly N and T2-T3 samples were ordered. This part of the ordination space was also opposed to the upper left part, where many day samples were situated.

3.3. Relationships with tidal wetland inundation

The BIO-ENV routine identified succulent saltmarsh, mudflats and *Ceriops* spp inundation area as environmental variables explaining 45% of the variability in the zooplankton structure. The vectors referring to the inundation extent of succulent saltmarsh, mudflat/saltpan, and *Ceriops* spp. were correlated with the upper left part of the ordination space in the same direction as the crab zoeae vector and in the opposite direction of copepods (Fig. 7). These results are consistent with the relationships between HWobs and the extent of upper tidal wetland inundation (Fig. 8a), where the inundation above *A. marina/R. stylosa* and *Ceriops* spp. (i.e., mangrove-saltmarsh ecotone) is predominately triggered with tides above 3 m (Fig. 8a).

Mudflat/saltpans, succulent saltmarsh, and herbaceous saltmarsh remain dry during neap tides in opposition to some expanses of *A. marina/R. stylosa* (<50% of total area) and *Ceriops* spp. (<25% of total

area) (Fig. 8b). The extent of their inundation increases from T-3 to T0 and decreases after T0 (Fig. 7b). During the study period, no more than 56% of the succulent saltmarsh became inundated, corresponding to 3.55 ha (Fig. 8c) of succulent saltmarsh. The mean percentage of inundation of succulent saltmarsh at T-1 (when the highest export of crab zoea was usually observed) was 20.6 $\pm$ 5.20 %, corresponding to a mean of 1.31 $\pm$ 0.33 ha of succulent saltmarsh inundated. Very few herbaceous saltmarshes became inundated during the study periods (<12.5% at maximum tidal height in February) (Fig. 8a).

4. Discussion

4.1. Tidal connectivity triggers prey pulse export

The findings demonstrate the key role of tidal connectivity in regulating the transfer of upper tidal tropical wetland habitat production to wider coastal ecosystems – probably in much the same way as they are importantly connected in temperate and sub-tropical regions. Specifically, for this study, crab zoeae pulse exports were triggered by tides exceeding 3.2 m, corresponding to the inundation threshold above the mangrove-marsh ecotone. This study adds more evidence to support existing eco-hydrological models that emphasise the importance of tidal connectivity patterns in supporting the functional value of upper tidal wetland habitats such as saltmarshes (Odum, 1980; Thomas and Connolly, 2001; Minello et al., 2012; Baker et al., 2013). In addition, these data support that tidal connection to upper tidal wetlands, and the export of crab zoeae, is a vector of energy export away from tidal saltmarsh areas, and could be supporting fisheries production more broadly, aligning to studies in temperate and subtropical saltmarshes (Saintilan and Mazumder, 2017; Raoult et al., 2018).
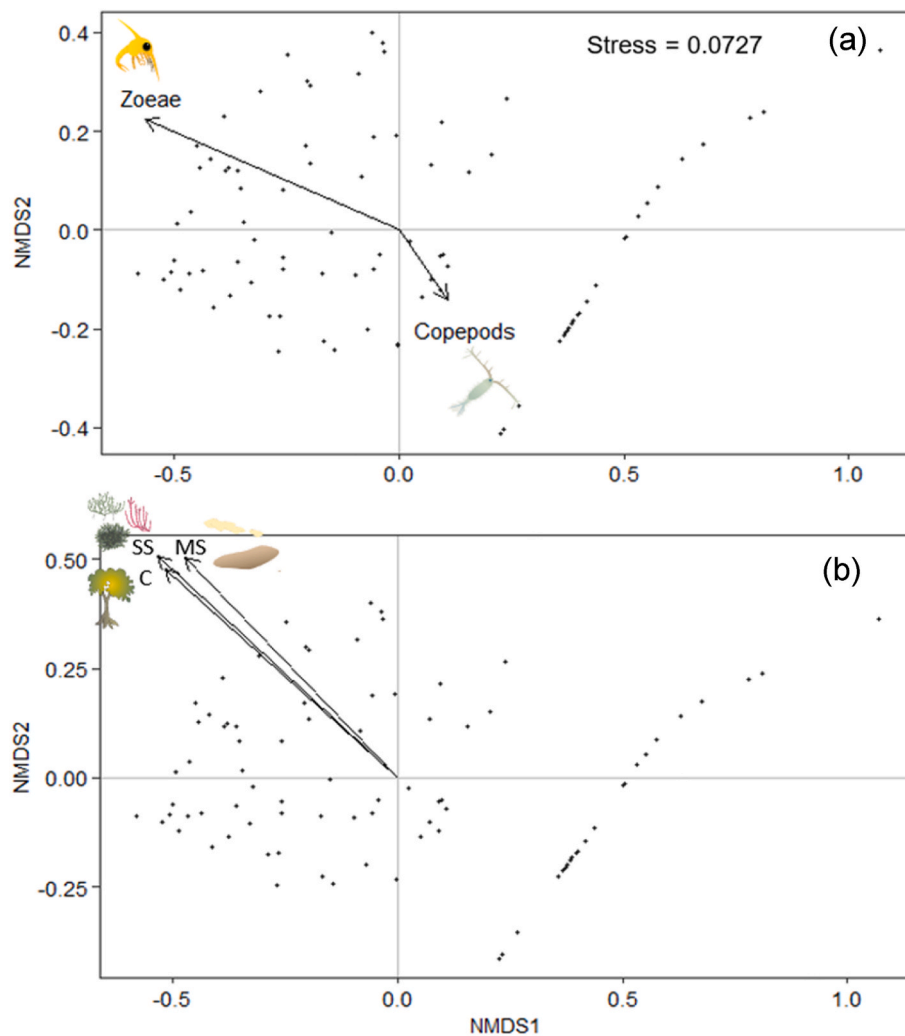
Fig. 7. Non-metric multidimensional scaling (nMDS) ordination of the samples based on Bray-Curtis dissimilarities of zooplankton density data ($\log_{10}$(individual per m^3 +1)). The vectors in (a) show the direction in the ordination space to which the zoeae and copepods are the most correlated. The environmental variables identified by the BIO-ENV routine are also shown in (b) ("SS" = Succulent saltmarsh; "MS" = Mudflats/Saltpan; "C" = *Ceriops* spp.). The direction and length of the vector is proportional to the strength of the correlation with the ordination space.

4.2. Tidal connectivity is critical for ecological connectivity

Tidal connectivity patterns undoubtedly play a key role in mediating prey pulse export, but the synchrony among suitable hydrological, biological and environmental factors and conditions must also be considered (Baker and Sheaves, 2007; Davis et al., 2014b). The model showed that once the threshold in tidal height of 3.2 m was reached, the amplitude of the peaks in prey pulse export was not proportional to tidal height or the extent of tidal inundation to upper tidal habitats. Rather, the distinct peaks in prey pulse aligned with the reproductive strategies of intertidal crabs, a notion reported in studies elsewhere (Christy and Stancyk, 1982; Mazumder et al., 2009). Crab reproductive behaviour has been shown to be influenced by additional contextual environmental and biological factors beyond tidal connectivity (Christy, 1978; Christy, 1986; D'Incao et al., 1992; Ituarte et al., 2006). For example, many crab species coordinate their spawning during the coolest month of the year (August in the present study) to reduce extreme environmental exposure (e.g., high summer temperatures) (Mazumder et al., 2009). They also often spawn at dusk and night to avoid diurnal predators (Christy, 1986; Ricardo et al., 2014). The data also indicates that synchronising spawning the day before the highest spring tide may be a key reproductive strategy, likely to maximise crab zoeae export by subsequent tides (Christy and Stancyk, 1982; Hollingsworth and Connolly, 2006).

Therefore, our data support the theory that the relationship between tidal connectivity and positive ecological outcomes is not linear (Montalto and Steenhuis, 2004; Yin et al., 2020) and contradicts a commonly applied restoration paradigm which suggests that tidal connectivity equals ecological connectivity (Hilderbrand et al., 2005; Liu et al., 2016). Consequently, in addition to maintaining tidal connectivity patterns, recognising contextual processes and patterns beyond tidal connectivity, such as life cycle histories and species requirements, should be an integrated part of coastal wetland management or restoration campaign (Weinstein et al., 2014; Nagelkerken et al., 2015).

4.3. Similar "habitat types" do not imply similar ecological values

The importance of considering contextual processes and patterns to determine the values of saltmarshes was apparent from the data. Specifically, the inundation of succulent saltmarshes, along with unvegetated flats (mudflats and saltpans) and *Ceriops* spp. inundation, was identified as a contributing component to the export of crab zoeae. However, an average of only approximately 25% of succulent saltmarshes were tidally connected when the highest peaks in prey pulse export were recorded (in T-1 tides). This suggests that the remaining succulent saltmarshes were unlikely to be important contributors to prey pulse export, unlike the most connected saltmarshes that are slightly
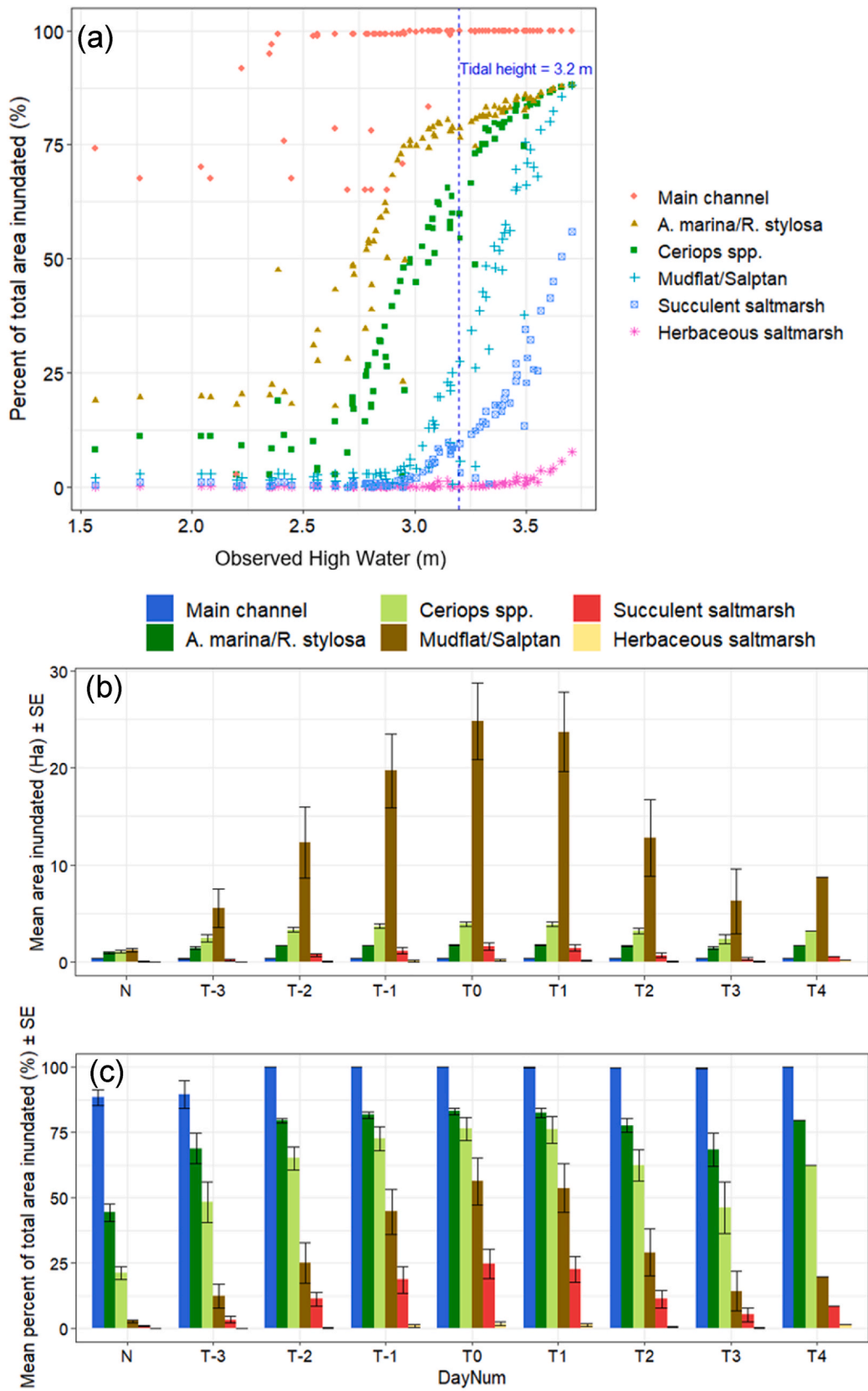
Fig. 8. (a) Relationships between the maximum percentage of wetland inundation and the observed High Water corresponding to the day of zooplankton sampling. The vertical line shows the treshold height for crab zoeae export determined by CART; (b) Mean area inundated (hectares) and (c) Mean percentage of total wetland area inundated of the given land cover (± standard error) pooled by DayNum" = The number of tides preceding and succeeding the highest spring tide of the spring tide cycle, where days are described as T-3; T-2; T-1; T0 (Highest Spring Tide); T1; T2; T3; T4, and N (Neap tide).

lower in the elevation gradient. This result emphasises that "similar" habitat types may indeed have different habitat functions due to contextual variability in factors such as tidal connectivity, spatial arrangements and anthropogenic disturbances that operate at even small spatial scales (Rogers and Krauss, 2019; Bradley et al., 2020; Ziegler et al., 2021), such as within the same location (Davis et al., 2012). Therefore, the finding highlights the importance of avoiding generalisations on the values of saltmarshes based on a vegetation-focused approach or "basic structural criteria" (*sensu* Weinstein et al., 2014). Instead, the study suggests that saltmarsh values should be defined by considering the physical and ecological contexts that influence their functions rather than generalisations and extrapolation of broader models. This shift towards a context-driven understanding of saltmarsh values should enable management and restoration strategies to align more effectively with the specific characteristics of each location (Bradley et al., 2020; Ziegler et al., 2021), which would ultimately increase the much needed overall success of restoration and management efforts (Waltham et al., 2021).

4.4. Copepods as a stable food resource for fish

The stable densities of copepods across months and tidal fluctuations indicate copepods provide a reliable food resource for fish, unlike crab zoea. The abundance of copepods in tidal creeks is attributed to the high chlorophyll *a* concentration (Zhou et al., 2009) and terrestrial particulate organic matter (Harfmann et al., 2019) that copepods are actively following (Mazumder et al., 2009; Qin et al., 2015) and that are found in tidal wetlands and creeks (Robertson and Blaber, 1992; Chew and Chong, 2011). While copepod densities remained also consistent across tidal types (N, T-3 to T-4), supporting that copepod density patterns are independent from tide succession (Chew and Chong, 2011), a slight peak in densities during T-3 tides may be attributed to tidal flushing which enhances primary productivity (Chew and Chong, 2011; Thong et al., 1993) and enhances copepod grazing activity in tidal creeks (Robertson et al., 1988). Copepods are mobile organisms, capable of actively swimming through the water column (Svetlichny et al., 2020). Conversely, crab zoea, although also mobile and able to swim vertically (Caracappa and Munroe, 2019), are more importantly subject to the influence of hydrodynamic processes for dispersion (Jiang et al., 2024). It also demonstrates the diversity of ecological connectivity: while crab zoeae exhibit a pulsed export pattern from upper tidal wetland habitats related to their reproductive strategies, copepods show a more sustained presence influenced by their feeding strategies.

4.5. Challenges and future directions

While temperate and subtropical studies have associated crab zoeae export from saltmarshes (Hollingsworth and Connolly, 2006; Mazumder et al., 2009), the mosaic distribution patterns and the tidal connectivity of succulent saltmarsh, mudflats, and *Ceriops* spp. made it challenging to isolate succulent saltmarsh from the inundation of these other high intertidal vegetated and unvegetated covers in the present study. Nevertheless, as highlighted by Sheaves et al. (2012), it is possible that the complex physical and ecological interactions that link tidal wetland components make efforts to isolate the importance of individual components in supporting critical functions not necessarily informative. Correlative studies isolating a process to a single habitat may potentially misdirect restoration efforts to focus on this particular habitat or ecosystem (e.g., saltmarshes) without considering broader contextual functioning (Sheaves et al., 2021). For instance, this may motivate increasing the area of targeted habitats without considering additional factors that may lead to restoration success (Peng et al., 2016). Consequently, in the context of whole-of-system management, it may be more relevant to understand how the patterns in the configuration of tidal wetland components (Connolly et al., 2005) and their synergies (Sheaves et al., 2012) support prey pulse export rather than attempting

to assign a specific process to a specific habitat type using correlational approaches. These observations do not intend to underestimate the role of saltmarshes in providing crab habitats (Mazumder, 2009) but rather highlight the importance of considering the integrity of the coastal ecosystem mosaic and the ecological and physical (e.g., tidal connectivity) interactions among different components (Sheaves et al., 2012; da Silva et al., 2022) in our understanding of the values of saltmarsh to crabs and the export of crab zoeae.

4.6. Implications for management and restoration

Overall, the findings add further evidence of the importance of managing saltmarshes from a whole-of-system approach (Queensland, 2016; Weinstein and Litvin, 2016; Waltham et al., 2020) and not in isolation to the remaining coastal ecosystem mosaic (Weinstein and Litvin, 2016). Recognising the ecological linkages within the coastal ecosystem mosaic is a key aspect of coastal ecosystem resilience and productivity (Bernhardt and Leslie, 2013; Carr et al., 2017; O'Leary et al., 2017; Scapin et al., 2022). Understanding current linkages (e.g., hydrological and ecological) within the coastal ecosystem mosaic is also important to improve our ability to predict tidal wetland responses to climate change and anthropogenic modification of the coastal landscape (Sheaves, 2009). Changes in the current patterns of the coastal ecosystem mosaic and its tidal connectivity patterns due to SLR, such as a shift from shallower saltmarsh and mudflats habitats to deeper mangrove-dominated systems (Kelleway et al., 2017), are likely to have important effects on current connectivity patterns, which may alter predator-prey dynamics (Davis et al., 2022). In addition, human adaptation strategies to climate change, often involving barriers to connectivity such as seawalls, have the potential to alter physical and ecological linkages among habitats (Sheaves et al., 2016), which may negatively impact the overall ecological functioning of tidal wetlands (Gilby et al., 2021). Therefore, management approaches should take into consideration the many ecological linkages that interconnected tidal wetland components hold, including prey pulses from tidal wetland habitat occurring much higher in the intertidal zone.

The results increase evidence that saltmarsh habitats should not be managed following a "one-size-fits-all" approach (Neal et al., 2018; Waltham et al., 2021). Scientists now widely accept that the context in which habitats occur is more important for defining the functions and values of tidal wetland habitats than the presence of "a type of habitat" (Bradley et al., 2020; Ziegler et al., 2021). Consequently, efforts to understand and define environmental contexts, such as tidal connectivity, should be prioritised over habitat-based management actions. The eco-hydrological workflow used in this study may be useful for coastal managers elsewhere, to assist with monitoring key contextual aspects of tidal wetland functioning, such as tidal connectivity and prey pulse exports.

5. Conclusion

The results not only highlight the importance of maintaining tidal connectivity patterns within a burgeoning modified coastal seascape (Waltham et al., 2021), but also underscore the need to consider how organisms interact with and respond to variability in their environment when planning tidal wetland restoration projects (Weinstein and Litvin, 2016). This suggests that evaluating restoration success goes beyond monitoring tidal connectivity and should include a comprehensive understanding of additional physical and ecological processes and patterns underpinning ecological functioning (Sheaves et al., 2021), such as the prey pulses described here. This is particularly important because the multifaceted and pervasive nature of connectivity (Sheaves, 2009) suggests that not incorporating less conspicuous aspects (e.g., prey pulses and trophic links) of ecological connectivity may potentially have unforeseen consequences on wider faunal community structures (Yang et al., 2008; Weinstein and Litvin, 2016). Not including this may

ultimately negatively affect key coastal ecosystem values such as fishery productivity (Weinstein et al., 2014).

CRediT authorship contribution statement

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecss.2024.108986.

Data availability

Data will be made available on request.

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