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ORIGINAL ARTICLE

Fine scale environmental variability and physiological tolerance influence invertebrate larval communities from a human-impacted mangrove in Hong Kong

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Abstract

Macroinvertebrates that rely on a supply of planktonic larvae for recruitment play a significant role in maintaining productivity in mangrove ecosystems. Thus, identifying the spatial distribution and physiological limitations of invertebrate larval communities within mangroves is important for targeted conservation efforts to maintain population persistence amid the threat of climate change. Here, the role of spatial, lunar, and environmental factors in structuring invertebrate larval communities in Ting Kok, the second largest mangrove forest in Hong Kong, was examined. Results indicate that, spatially, invertebrate larval communities were influenced by environmental filtering, habitat type, and the lunar tidal cycle. This indicates the fundamental role of habitat heterogeneity and connectivity for the transport, distribution, and development of crustacean larvae. Larvae of key sesarmids exhibited metabolic depression at water temperatures forecasted to be regularly experienced by the year 2050, according to current climate projections. The impacts of climate change, coupled with habitat destruction and degradation of hydrological connectivity, make larval communities increasingly vulnerable to mass-mortality and displacement. This places ecosystem productivity and functionality at risk through cascading negative effects of recruitment limitation. Further focus on this subject will help disentangle the effects of process rates and scales of transport that underlie community assemblages in mangrove systems. Furthermore, identifying physiological bottlenecks of key taxa and habitat provisioning that enhance larval survival will be helpful to prioritize strategies for conservation management in dynamic intertidal settings.

Keywords Mangroves · Larvae · Community composition · Physiology · Environmental drivers

Introduction

Mangrove systems are among the most highly productive and biologically significant ecosystems in the world (Lee et al. 2014; Medina-Contreras et al. 2020). Ecologically and commercially important benthic macroinvertebrate mangrove taxa that contribute to productivity rely on a supply of planktonic larvae that recruit into adult populations (Thorson 1950). Larvae provide a vital intermediate link between primary producers and higher trophic levels, which contribute to their high rates of mortality (Saintilan and Mazumder 2017). Climate change effects are predicted to affect larvae already developing close to their thermal limits, compounding the effects of competition for space and predation, making them increasingly vulnerable (Weiss et al. 2012). Early stage crustacean larvae are mostly passive dispersers, relying on hydrodynamics for transport; however, larval behavior enables them to actively maintain their position in

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the water column (Pineda et al. 2007; Heino 2013; Epifanio and Cohen 2016). Late-stage crustacean larvae and juveniles show strong independent mobility and actively move into preferred nursery, settlement, and juvenile habitats (Radford et al. 2007; Pilditch et al. 2015; Valanko et al. 2015). These differences in active/passive transport and habitat selection impact their coexistence in heterogeneous environments through competition-colonization trade-offs (Tilman 1994; Pineda et al. 2007). Variations in tolerances to heat stress limit crustacean larval distribution; thus, their physiological needs dictate where early development occurs (Anger and Charmantier 2000; Charmantier et al. 2002; Paula et al. 2004; Giménez 2010).

Identifying the spatial distribution and structure of invertebrate larval communities within mangroves is important to determine areas for targeted conservation efforts to maintain a healthy supply of recruits to ecologically important benthic macroinvertebrate populations that sustain productivity in mangroves (Cannicci et al. 2008, 2021). Increased environmental variability serves to enhance or limit larval survival and how multi-scale community structure and ultimately the productivity of ecosystems will adapt under different climate change scenarios (Wiens and Bachelet 2010). Furthermore, unraveling the linkages between biological and physical drivers in relation to larval community structure is essential to support conservation strategies that incorporate inclusive ecological approaches. The effects of abiotic change on the physiology of organisms have been well established (Seebacher and Franklin 2012). By incorporating physiological knowledge, conservation strategies can be better developed and tested by generating models that predict how organisms may respond to environmental change (Cooke et al. 2012). In terms of invertebrate larvae, understanding their physiological responses to acute temperature changes can inform on their vulnerability at an individual, population, and community level and can provide valuable insight into what influences larval community assembly under various environmental conditions (Small et al. 2015; Vorsatz et al. 2021d). Indeed, the metabolic responses to variable salinity have been widely addressed for embryos and larvae of mangrove and mangrove-associated crabs (Anger and Charmantier 2000; Charmantier et al. 2002; Diele and Simith 2006; Simoni et al. 2013; Simith et al. 2014). Early developmental stages of mangrove crab larvae are more vulnerable to acute thermal stress (Vorsatz et al. 2021c) when compared to later ones, i.e., the megalopae. In some species, embryos and mothers form thermal bottlenecks (Vorsatz et al. 2021a) and Marochi et al. (2021) also indicated that ocean warming will likely impact larval settlement hindering population maintenance and connectivity.

The present study aimed to improve our understanding of processes that drive community structure and physiological performance of larval invertebrates in reference to short- (tidal and seasonal) and long-term changes (under climate change scenarios) in an anthropogenically impacted mangrove forest in Hong Kong SAR, China. Here, we examined the distribution of larval invertebrates among available habitats, lunar tidal cycles, and related environmental conditions within the mangrove forest using field-based techniques (Pineda et al. 2007). We tested how environmental history might shape invertebrate physiological performance as measured through respiration rates on individuals collected from different habitats and how selected larvae adapt under already experienced and predicted water temperatures using respirometry experiments. We predicted that life history characteristics of certain taxa will dictate the physiological constraints and influence the invertebrate larval community structure in relation to lunar cycles and environmental conditions at available targeted habitats within the mangroves (Vorsatz et al. 2021d). Secondly, larvae collected from different habitats within the mangrove forest should not exhibit any differences in metabolic rate owing to the assumption that water temperature in aquatic habitats should be thermally uniform, making species equally competitive to coexist in any available habitat patch (Thompson et al. 2020). Finally, metabolic rates of larvae will increase as water temperature increases, but if maximum water temperatures surpass those already experienced, a decline in metabolic rate will be observed (Pörtner 2002, 2021; Pörtner and Farrell 2008).

Materials and methods

Study area

The Ting Kok (22° 28’ N, 114° 13’ E) mangrove site is situated on the eastern coast of Hong Kong, within the Tolo Harbour, a poorly flushed bay that regularly experiences hypoxia during the summer (Tong et al. 2006). Its mangrove cover of ~ 8.8 ha comprises seven of the eight true mangrove species occurring in Hong Kong, of which *Kandelia obovata* dominates the species composition (Morton 2016). For this study, four qualitatively distinct habitats were identified for field sampling and environmental characterization. These included pencil roots of *Avicennia marina*, buttress roots of *Kandelia obovata*, constantly inundated soft-bottomed tidal creeks (up to 50 m in length, 5 m in width), and an exposed mudflat habitat adjacent to the mangrove forest leading into the bay (Fig. 1). These habitats were chosen based on the qualitative complexity of the habitat (roots/no roots) which may contribute to variations in environmental conditions and spatio-temporal assemblages and metabolic responses of invertebrate larvae (Vorsatz et al. 2021b, c, d).

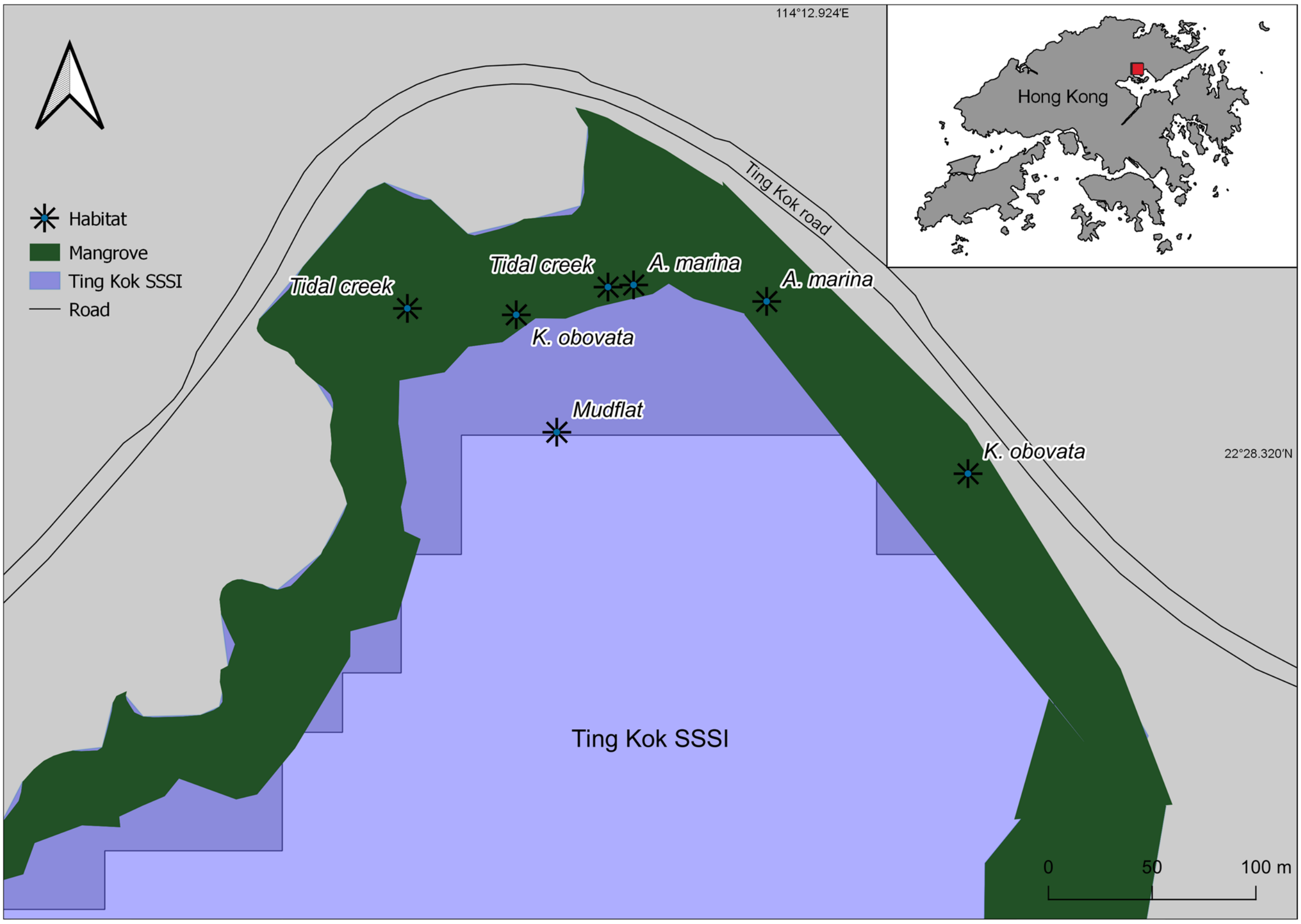

Fig. 1 Map of study area, the Ting Kok SSSI (special site of scientific interest) mangrove forest, located on the eastern coast of Hong Kong. Habitats sampled are the pneumatophores of *Avicennia marina*, the buttress roots of *Kandelia obovata*, tidal creeks, and a mudflat adjacent to the mangrove forest. Asterisks indicate the approximate area in each habitat where light traps were placed

Field sampling

Invertebrate larvae were sampled at each habitat during the new and full moon spring tides from June to August 2018 (n = 6 sampling events) using small size-selective light traps (Chan et al. 2016). To assess larval community composition, on all sampling events, two traps were deployed at least 4 m apart in each duplicated experimental habitat and two at the mudflat during low tide on each sampling event and collected approximately 24 h later. In total, 84 samples were collected with light traps for larval community analyses ((4 light traps × 3 experimental habitats + (2 light traps at the mudflat)) × 6 events). Additionally, an extra trap was deployed at each habitat to collect crab larvae for physiological experiments. Upon trap retrieval, the collected sample was transferred from the light traps into 20-L buckets and sifted through a 65-µm mesh to prevent any larval loss and to exclude any microalgae or non-targeted larvae that may be present in the sample. Samples collected for the larval assemblage analysis were preserved in 95% ethanol for identification. The content of the traps designated to collect crab larvae for physiological experiments was transferred to collection jars filled with 65-µm filtered seawater to eliminate any cross-contamination of microalgae and other organisms that may have affected the dissolved oxygen concentration in the collection jars and transported back to the laboratory within the School of Biological Sciences at the University of Hong Kong.

Environmental characteristics

Salinity measurements were taken in situ at each habitat upon each trap retrieval using a handheld optical seawater refractometer (RedSea). Water temperature was recorded at 5-min intervals for the entire duration of trap deployment at identified habitats using iButton temperature loggers (Maxim Integrated Products, ColdChain Thermodynamics). Tidal data were retrieved from the Hong Kong Observatory site (http://www.hko.gov.hk/en/tide/predtide.htm).

Larval composition

Samples collected to determine the invertebrate larval community composition were processed in the laboratory and identified to the finest possible taxonomic scale under a stereomicroscope according to published descriptive keys (Chaudhari and Jalihal 1993; Bento and Paula 2018). Organisms were ontogenetically classified as zoeae, veligers, postlarvae (stage in which juvenile characteristics appear, up to 3 mm in carapace length), and juveniles, where possible.

Physiological experimental setup

In the laboratory, larvae sampled for physiological trials were placed in separate beakers, according to habitat, filled with aerated filtered seawater and acclimated in a water bath, unfed, for at least 12 h, at the collection temperatures (28–33 °C). Following acclimation, the most consistently occurring crab larvae were separated from each sample and coarsely sorted to family level and placed back into habitat-specific beakers in the water bath. To avoid potential bias from acute heat shock, but allowing experiments to be conducted over a 10-h period to minimize bias related to endogenous circadian rhythms, the temperature of the water bath was ramped up or down by 1 °C every 15 min until the desired experimental water temperature was reached (Kelley et al. 2011). Experimental animals were then acclimated at the experimental water temperature for at least an additional hour before recording oxygen consumption.

Experimental water temperatures were selected based on the nominal average (28 °C) and maximum (33 °C) temperatures recorded based on 48 h of monitoring in June 2018. In addition, predicted maximum temperatures (36 °C), with an increase of 3 °C by 2050 (Lee et al. 2011), were selected where possible. The oxygen consumption rates (MO_2) used as a proxy for metabolic rate (Brown et al. 2004) of crab larvae from each habitat were measured within a sealed 80 µl, 24-well, glass microplate developed by Loligo Systems (Denmark), where up to a maximum of three larvae from each specific habitat were placed per well. An optical fluorescence-based oxygen meter (Sensor dish reader SDR2, PreSens, Germany) was used in conjunction with the microplate to measure respiration rates simultaneously in each of the 24 independent wells. This respirometry system provides high accuracy, throughput, sensitivity, and simplicity for individual-based measurements of marine invertebrate embryos and larvae (Szela and Marsh 2005; di Lorenzo and Galassi 2017). Larvae were kept in the dark during trials to reduce activity and equate the results to standard metabolic rates (Clarke 2004). Furthermore, to control for background bacterial respiration, four wells were filled with only filtered seawater during each trial. The oxygen consumption was recorded every 60 s at the static experimental temperature using the SDR version 4.0.0 software (PreSens, Germany) for the duration of the experimental run, which lasted for approximately an hour. The concentration of oxygen was plotted as a function of time and the first 30% linear decreases in oxygen (to avoid hypoxia) were used to calculate MO_2, corrected for background respiration and expressed as nmol O_2 min^{-1} ind^{-1}.

At the conclusion of each experimental trial, larvae were removed from the microplate and preserved individually in 95% ethanol for further identification and measurements. The zoeae of four taxa, Sesarmidae, *Pinnixa* sp., *Scopimera intermedia*, and *Etisus laevimanus*, were identified as the most numerically dominant. To correct for the volume of each experimental well and to calculate individual oxygen consumptions, the biovolume of each zoea was estimated from the volume (V) of a sphere, ($V = \frac{4}{3}\pi r^3$), where r represents the radius (Hillebrand et al. 1999; zoeal carapace radius in this case).

Statistical analysis

All data were analyzed in R for computing statistics (R Core Team 2019). To determine the variability in environmental characteristics, water temperature and salinity were assessed for normality and homoscedacity using a Shapiro–Wilk and Levene's test, respectively. A nonparametric factorial analysis of variance using an Aligned Rank Transformation of both water temperature and salinity among habitats and moon phase of each month was conducted using the *ARTool* package (Wobbrock et al. 2011). Additionally, a Kruskal–Wallis test was used to compare water temperature and salinity among habitats for each moon phase within the month sampled. Where results were significant, to detect the pairwise differences among months and habitats, comparisons using Tukey post-hoc tests with a Benjamin-Hochberg correction for multiple testing were used (Benjamini and Hochberg 1995).

The larval community data were analyzed in the *mvabund* package for model-based generalized linear models (Wang et al. 2012). The best parsimonious model was selected based on the AIC of full models by means of a single-term deletion procedure using the *drop1* function in the *MASS* package (Venables and Ripley 2002). The best fitting generalized linear model was fitted using the *ManyGLM* function with a negative binomial distribution and a 999 Monte Carlo resampling procedure to examine the effect of habitat, lunar phase, maximum tidal height, and average, minimum, and maximum water temperature on larval community composition. An offset was used to account for differences in sampling intensity among the mudflat and the remaining habitats. This analysis aids in avoiding data transformations as the negative binomial model corrects for extreme values of distribution or overdispersion (O'Hara and Kotze 2010).

In addition, this model allows to avoid confounding effects of location and dispersion and offers more predictive power than standard distance-based analyses (Warton et al. 2012). Pairwise comparisons were computed using a free stepdown resampling procedure and univariate tests in *ManyGLM* to detect differences in larval communities among habitats and moon phases and to identify which taxa were driving these differences based on their contribution to the *Sum-of-LR* (Wang et al. 2012; Warton et al. 2012). Where taxa were significantly driving differences in community composition among habitats and moon phases, univariate tests were run in the *MASS* package using the *glm.nb* and *multcomp* function to ascertain in which habitat and phase of the moon these taxa were more abundant. Additionally, abundance data were Hellinger-transformed and Wisconsin double-standardized preceding calculation of the Bray–Curtis similarity matrix (Legendre and Gallagher 2001). Communities were then visualized using non-metric multidimensional scaling (NMDS).

Variable numbers of individuals of each taxon were tested at all experimental water temperatures and habitats (Table S2). Hence, separate GLMs were run to test for differences in $MO2$ within and among taxa and habitats at 28 °C. Additionally, GLMs were run to test for differences in $MO2$ among water temperatures between Sesarmid and *Pinnixa* sp. zoeae collected at the tidal creek. Residuals were examined for normality and homoscedascity with Shapiro–Wilk and Levene's test, respectively. When violations of the assumptions of normality and homogeneity of residuals occurred, generalized linear models using a gamma-distribution with a log-link function were used. All significant results ($p < 0.05$) were followed by Tukey post-hoc tests using a Benjamini–Hochberg correction (Benjamini and Hochberg 1995).

Results

There was little variation (0.2 m) in maximum tidal height at new and full moon throughout the sampling period (Fig. S1). Water temperature significantly differed among habitats ($F_{(3,\ 320)} = 119.04$, $p < 0.001$). Consistent differences were observed among habitats within months, although the mudflat and tidal creek showed no significant difference between them ($t = -1.34$, $p = 0.53$), but were always higher than the *K. obovata* and *A. marina* habitats ($p < 0.05$, Fig. 2a), with the exception of the last sampling event. Generally, no differences were observed in salinity among habitats ($F_{(3,60)} = 0.97$, $p = 0.41$) or the interaction between habitat and moon phase of each month ($F_{(15,\ 60)} = 1.43$, $p = 0.16$). There were, however, differences in salinity among moon phases of each month ($F_{(5,\ 60)} = 3.38$, $p = 0.01$). Salinity did not vary among sampling events, with the exception of the full moon June sampling event where it was significantly higher at the mudflat than at the tidal creek (Fig. 2b).

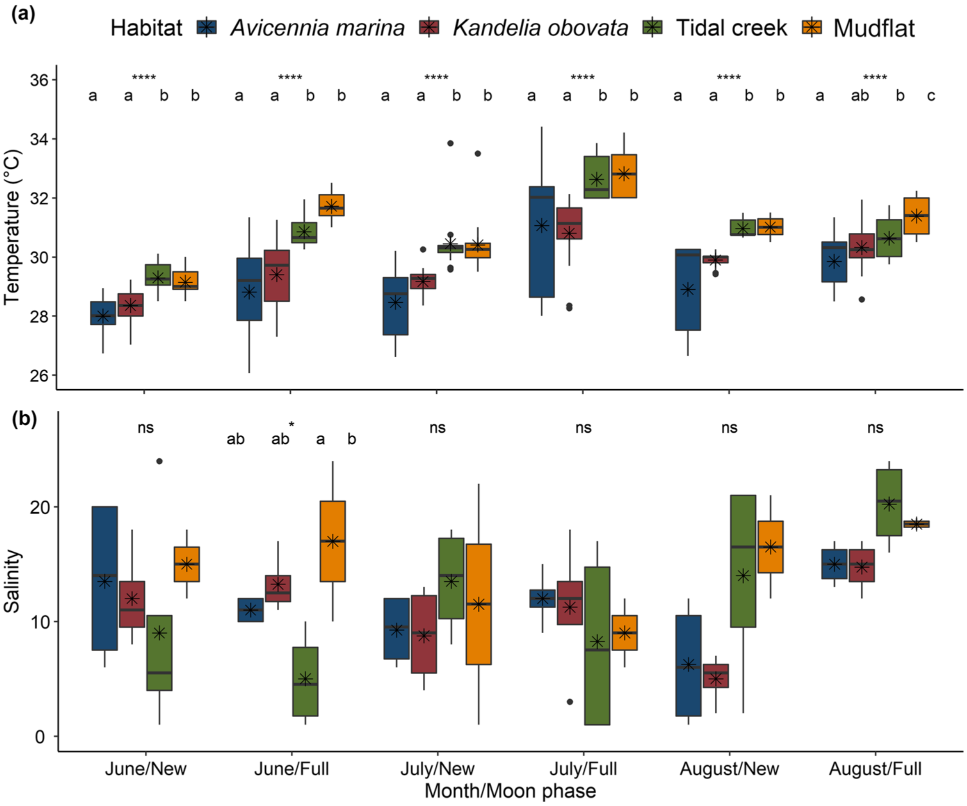

Fig. 2 Boxplots of **a** water temperature and **b** salinity at each habitat sampled at the Ting Kok mangrove forest per monthly moon phase in 2018. The 25 and 75% percentiles are represented by the lower and upper limits of each box; the horizontal line indicates the median, the vertical lines of each box indicate 1.5 × above and below the interquartile range, the asterisk (*) indicates the mean, and the dark circles (●) show outliers. Where salinity or water temperature significantly differed among habitats within each monthly moon phase, post-hoc tests indicating homogenous groups (letters) are given. **** = $p < 0.0001$; *** = $p < 0.001$; ** = $p < 0.01$; * = $p < 0.05$; ns = $p > 0.05$

Approximately 13,700 individuals from 15 taxa were collected throughout the study period (Table 1). The *A. marina* habitat was numerically dominated by *Etisus laevimanus* and *Scopimera intermedia* zoeae. *Scopimera intermedia* zoeae and *Penaeus merguiensis* juveniles dominated the *K. obovata* community, while the mudflat was mostly occupied by zoeae of *Pinnixa* sp. and *Parasesarma bidens*. Furthermore, *Pinnixa* sp. zoeae and *Laomedia* sp. post-larvae dominated the tidal creek (Fig. S2).

The NMDS indicated overlap among larval communities across habitats (Fig. 3). The multivariate generalized linear model indicated that differences occurred in larval assemblages among habitats and moon phases, while maximum tidal height and water temperature were also significant predictors (Table 2). Post-hoc tests showed that numerically and compositionally distinct assemblages occupied all habitats regardless of moon phase (Table S3). The species

Table 1 Invertebrate larval composition and abundance by number (N) and percentage (%) of total catch per moon phase and habitat at Ting Kok

Developmental stage	Taxon	N	Moon phase		Habitat			
			New (%)	Full (%)	*A. marina* (%)	*K. obovata* (%)	Mudflat (%)	Tidal creek (%)
Zoea	*Etisus laevimanus*	785	223 (2.9)	562 (9.3)	192 (37.5)	0	71 (9.4)	522 (4.3)
	Parasesarma bidens	1348	903 (11.8)	445 (7.4)	24 (4.7)	11 (2.5)	151 (20)	1162 (9.7)
	Pinnixa sp.	3669	2479 (32.3)	1190 (19.7)	25 (4.9)	2 (0.5)	369 (48.9)	3273 (27.3)
	Scopimera intermedia	394	74 (1)	320 (5.3)	179 (35)	206 (46.9)	8 (1.1)	1 (<0.1)
	Upogebia sp.	55	40 (0.5)	15 (0.2)	0	6 (1.4)	26 (3.4)	23 (0.2)
	Sesarmidae sp. 1	51	14 (0.2)	37 (0.6)	36 (7)	0	0	15 (0.1)
	Tmethypocoelis ceratophora	8	8 (0.1)	0	1 (0.2)	1 (0.2)	5 (0.7)	1 (<0.1)
	Metapograpsus frontalis	41	40 (0.5)	1 (<0.1)	0	0	9 (1.2)	32 (0.3)
Post larva	*Acetes* sp.	1126	278 (3.6)	848 (14)	7 (1.4)	25 (5.7)	12 (1.6)	1082 (9)
	Bezelbub sp.	45	42 (0.5)	3 (<0.1)	0	0	45 (6)	0
	Laomedia sp.	5745	3205 (41.8)	2540 (42)	26 (5.1)	4 (0.9)	44 (5.8)	5671 (47.2)
Juvenile	*Penaeus monodon*	80	49 (0.6)	31 (0.5)	9 (1.8)	31 (7.1)	0	40 (0.3)
	Penaeus latisulcatus	84	75 (1)	9 (0.1)	3 (0.6)	24 (5.5)	8 (1.1)	49 (0.4)
	Penaeus merguiensis	251	224 (2.9)	27 (0.4)	2 (0.4)	126 (28.7)	3 (0.4)	120 (1)
Veliger	Gastropod	32	18 (0.2)	14 (0.2)	8 (1.6)	3 (0.7)	4 (0.5)	17 (0.1)

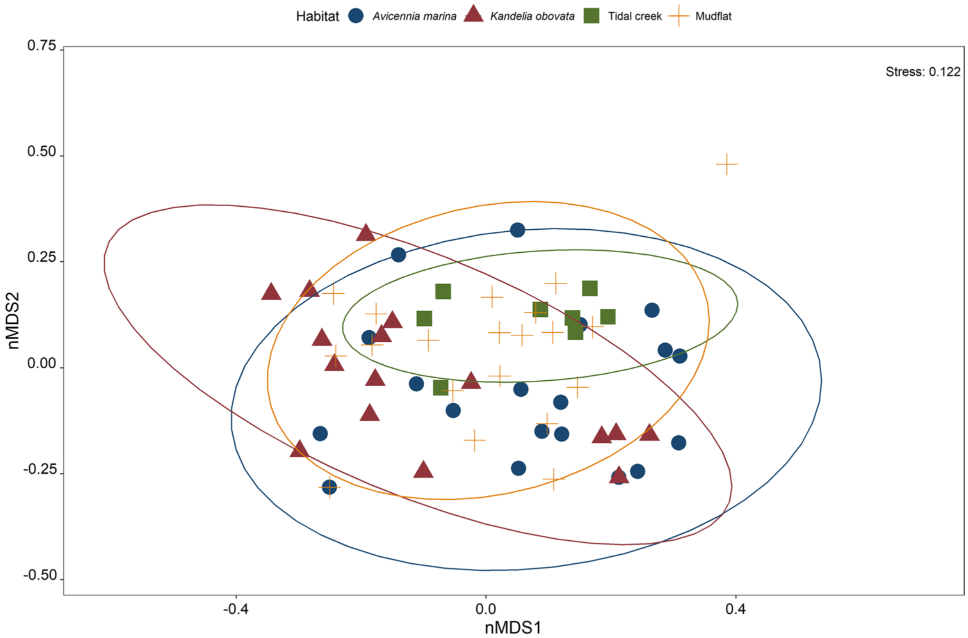

Fig. 3 Non-metric multidimensional scaling plot of invertebrate larval communities among habitats; *Avicennia marina* (blue circles), *Kandelia obovata* (red triangles), tidal creek (green squares), and the mudflat (orange crosses) at the Ting Kok mangrove forest, Hong Kong. Ellipses represent 95% confidence intervals fitted into the spatial ordination

driving the differences among habitats were *Acetes* sp., *P. bidens*, *Pinnixa* sp., *Laomedia* sp., and *S. intermedia* zoeae (Table 2). Univariate analyses of significant taxa driving differences among habitats indicated that the mean abundance of *Acetes* sp., *P. bidens*, *Pinnixa* sp., and *Laomedia* sp. zoeae was commonly significantly greater in the tidal creek and the mudflat as compared to *A. marina* and *K. obovata* (Table 1, Table S4). Alternatively, *S. intermedia* zoeae were most abundant in *A. marina* and *K. obovata.* Furthermore, *Tmethypocoelis ceratophora* and *Metopograpsus frontalis* zoeae and *P. merguiensis* and *P. latisulcatus* juveniles were driving the differences in community composition and abundance between moon phases (Tables 2 and S5).

At 28 °C, MO_2 differed among taxa and habitats (Fig. 4a, Tables 3 and S6). There was no significant difference in MO_2 among habitats for *S. intermedia* and sesarmid zoeae at 28 °C; however, MO_2 differed significantly among habitats for *Pinnixa* sp. (Table 3). Taxa collected from *A. marina* differed significantly in MO_2 ($F_{(2, 44)} = 4.68$, $p = 0.014$), where *Pinnixa* sp. MO_2 was significantly greater than *S. intermedia* and *E. laevimanus* ($p < 0.05$; Fig. 4a). Additionally, the MO_2 between sesarmid and *Pinnixa* sp. larvae collected from the tidal creek differed at 28 °C ($F_{(1, 96)} = 4.64$, $p < = 0.03$, Fig. 4a) and at 33 °C ($F_{(1, 59)} = 3.43$, $p < = 0.04$, Fig. 4b). *Pinnixa* sp. ($F_{(1, 73)} = 23.552$, $p < 0.001$) and sesarmid ($F_{(2, 137)} = 4.21$, $p = 0.016$) zoeae MO_2 differed significantly among water temperatures, with *Pinnixa* sp. and sesarmids having greater MO_2 at 33 °C than 28 °C (Fig. 4b). Sesarmid zoeae had significantly lower MO_2 at 36 °C when compared to 33 °C indicating a decrease in metabolic rate (Fig. 4b).

Discussion

Invertebrate larval communities differed in both abundance and composition at different habitats and phases of the moon at Ting Kok. Several taxa drove these differences and more frequently occupied habitats with increased potential for retention and depth such as the tidal creek or the mudflat going out into the bay. Taxa differed in their metabolic response according to which habitat they were collected, with *Pinnixa* sp. specifically exhibiting higher metabolic rates in the mudflat. The oxygen consumption of *Pinnixa* sp. and sesarmid larvae increased with average to high water temperatures common in summer, with sesarmids exhibiting metabolic depression at the highest experimental temperatures (36 °C), which will be regularly experienced by 2050, according to current climate projections.

Environmental drivers of larval community structure

The majority of larval taxa that structured the community among habitats were more abundant in the tidal creeks, while maximum tidal height was a significant predictor for the abundance of *P. merguiensis* and *P. latisulcatus* juveniles in addition to *T. ceratophora* zoeae and *Laomedia* sp. post larvae. The tidal creeks, however, undergo significant variations in salinity (0–22) indicating that larvae and post-larvae that occur in this habitat should have acclimatized to mesohaline conditions for growth and survival unhindered by saline fluctuations (Gaudy and Sloane 1981; Epifanio and Cohen 2016). Hydrological connectivity in the form of unimpaired adjacent lotic and lentic habitats also provide a critical transition zone for larvae moving through the mosaic of available habitats within the mangrove ecosystem (Lee 2008). Preserving the integrity of habitat structure and hydrological connectivity is thus imperative in providing grounds and corridors for optimal larval development and transport (Pérez-Ceballos et al. 2020). Mangroves in urban settings such as those in Hong Kong are under increasing threat of hydrological alteration due to land reclamation and construction for the growing need of infrastructure (Li and Lee 1997; Tam and Wong 2002). The effects of interrupted

Table 2 Summary results of the generalized linear model (*ManyGLM*) indicating the change in community composition and abundance with habitat (*A. marina*/*K. obovata*/tidal creek/mudflat) and moon phase (new/full) as categorical and maximum tidal height, average, maximum, and minimum water temperatures as continuous predictor variables. The percent deviance explained and coefficients are given for taxa that were driving differences among habitats and whose abundance was affected by the continuous predictor variables (% deviance explained/coefficient estimate)

Predictor variable	Deviance	*p*-value	Drivers of difference in community composition related to categorical and continuous predictor variables (% deviance explained/coefficient estimate)
Habitat	199	**0.001**	*Acetes* sp. (14.8), *P. bidens* (11.4), *Pinnixa* sp. (10.9), *Laomedia* sp. (9.1), *S. intermedia* (5.9)
Moon phase	31	**0.001**	*T. ceratophora* (28.3), *M. frontalis* (20.8), *P. merguiensis* (12.6), *P. latisulcatus* (6.3)
Maximum tidal height	448	**0.011**	*Laomedia* sp. (83.8/ − 18.3), *T. ceratophora* (2.8/618.8), *P. merguiensis* (2.6/197.2), *P. latisulcatus* (2.4/142.3)
Average water temperature	54	**0.003**	*Acetes* sp. (35.4/3.1), *Laomedia* sp. (16.1/ − 5.7)
Maximum water temperature	77	**0.001**	*Bezelbub* sp. (25.9/15.3), *Pinnixa* sp. (18.1/4.1), *P. bidens* (13.5/2.7)
Minimum water temperature	38	**0.001**	*Acetes* sp. (38.12/1.9)

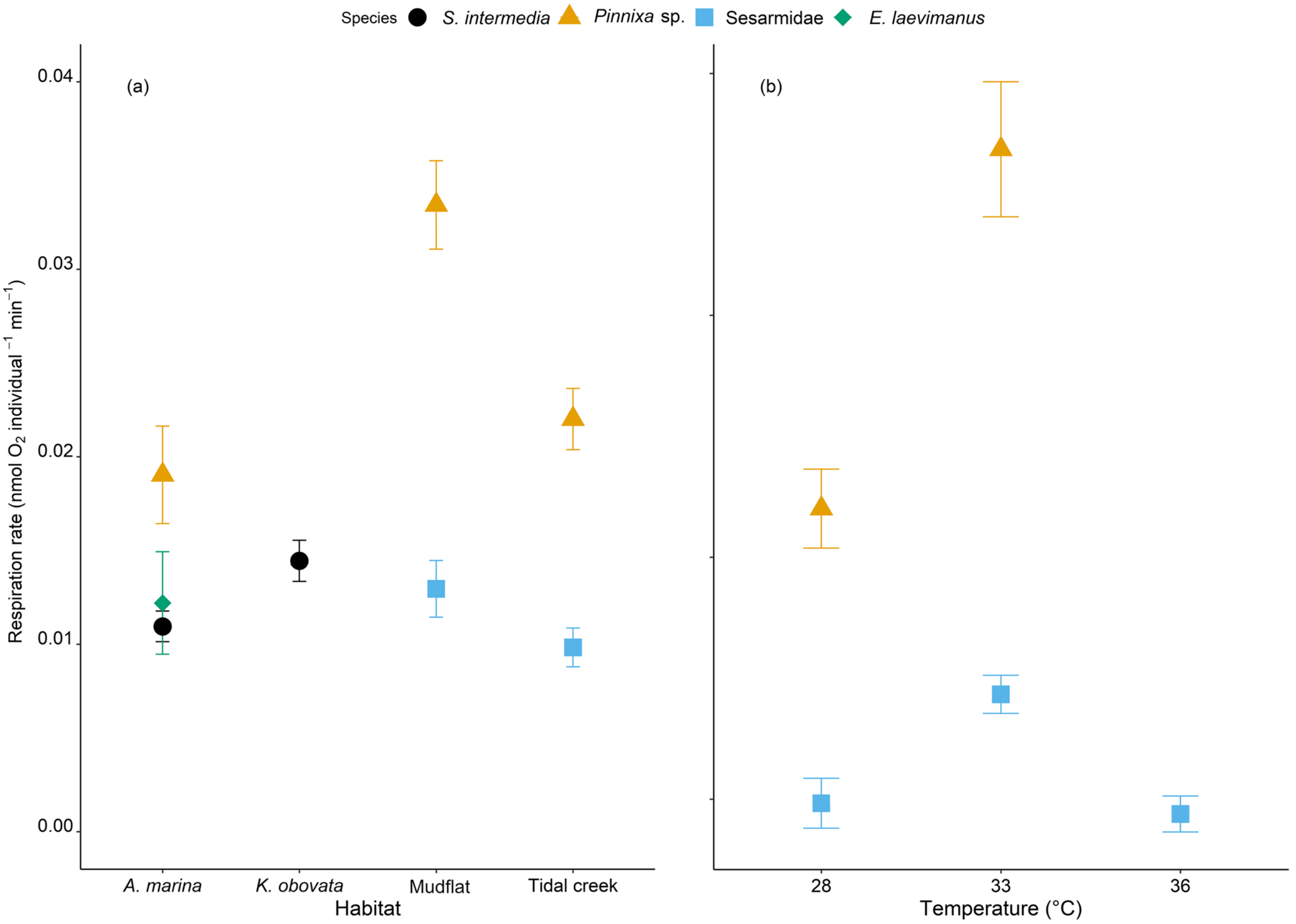

Fig. 4 Oxygen consumption rates expressed as mean ± SE of *Scopimera intermedia* (black circles), *Pinnixa* sp. (yellow triangles), sesarmidae (blue squares), and *Etisus laevimanus* (green diamonds) zoeae within the Ting Kok mangrove forest tested at **a** 28 °C, among habitats, and **b** water temperatures among taxa collected in the tidal creek

hydrodynamics due to anthropic disturbance could therefore be detrimental to larvae that rely on this connectivity throughout their ontogeny for successful development and ultimately recruitment into adult populations (Pérez-Ceballos et al. 2020).

Early and late-stage decapod larvae respond to environmental signals such as water temperature and maximum tidal height to expedite transport from spawning grounds and back to suitable nursery and settlement habitats (Little and Epifanio 1991; Gonçalves et al. 2003; Valanko et al. 2015). The significance of temperature in shaping the spatial structure of communities within mangroves argues in favor of environmental filtering, resulting in species abundances of *Acetes* sp., *Bezelbub* sp., *Pinnixa* sp., and *P. bidens* larvae that display positive relationships with higher average, maximum, and minimum water temperatures. Furthermore, these same species were responsible for ~ 46% of the variation in community assemblages among habitats and occurred more abundantly in the tidal creeks and mudflat than any other habitat. This is consistent with wide-scale larval distribution patterns that suggest that larvae are mainly concentrated in areas with environmental conditions favorable to their development, generally sought out through exogenous and endogenous signals from gravity, hydrostatic pressure, UV radiation, turbulence, salinity, and water temperature (Epifanio and Cohen 2016).

Table 3 Results of the generalized linear models testing for differences in MO_2 among habitats for each taxon at 28 °C, (*F*) Fisher statistics, (d.f) degrees of freedom, (*p*) statistical significance, and posthoc test results are indicated for each model

Taxa	F	d.f	*p*	Posthoc
Scopimera intermedia	6.778	1	**0.013**	*K. obovata*^{a}, *A. marina*^{b}
Pinnixa sp.	10.406	2	**< 0.001**	Mudflat^b, *A. marina*^{a}, Tidal creek^a
Sesarmid	2.404	1	0.125	

Spatial heterogeneity of organismal metabolism

Temperature is reflective of water exchange in intertidal areas (Rodil et al. 2017), and along with salinity are the most influential physico-chemical factors in crustacean larval survival and development (Magris and Fernandes 2011). It is thus expected that physiological temperature constraints, along with other environmental and biotic factors, shape invertebrate larval community structure and fitness of populations through either enhancing or impairing the metabolism of aquatic ectotherms (Brown et al. 2004). Here, taxa that occurred among the pneumatophores of *A. marina* and the tidal creeks had significant differences in their metabolic rate when measured at 28 °C. This is likely due to taxon-specific responses in optimized resource allocation to growth as well as directional selection (Kozłowski and Weiner 1997; Gaitán-Espitia et al. 2013). Metabolic rates differed between sesarmids and *Pinnixa* sp. zoeae collected from the tidal creek and the mudflat, likely reflecting short-term acclimation to variations in their environmental history expressed as physiological plasticity (Jimenez et al. 2015; Vorsatz et al. 2021d). Metabolic responses to temperature of ectotherms correlate with the thermal range that they experience (Gaston and Spicer 2009). This evokes an evolutionary response to short-term changes in temperature that an organism that occupies a specific habitat may have experienced, coupled with the genetic contribution to intraspecific physiological differences and capacity to cope with environmental change (Castillo and Helmuth 2005; Jimenez et al. 2015). The increase in metabolism observed in the mudflat could derive from a response to predators, as more energy is activated to elicit a flight type behavior in the presence of elevated kairomones, a likely trade-off in energy allocation between reaching neritic water offshore for further development and the increased risk of predation (Mitchell et al. 2017). Alternatively, the rise in metabolism could be an artifact of short-term acclimation to areas that are generally hotter and more exposed to UV radiation in the absence of a forest canopy (Hernández Moresino et al. 2011).

Climate change implications for key taxa

As expected, the metabolic rates of both *Pinnixa* sp. and sesarmid zoeae initially increased with an increase in temperature from 28 to 33 °C (Clarke 2004). The metabolism of sesarmid zoeae decreased at 36 °C suggesting a limitation or failure of the respiratory system at upper extreme temperatures. Metabolic depression as a response to environmental stress has been observed in virtually all known animal phyla (Guppy and Withers 1999). For marine invertebrates, metabolic depression due to thermal stress has been documented to have negative effects on feeding, growth, recruitment, survival, and ultimately population persistence (Byrne and Przeslawski 2013; Przeslawski et al. 2015). Sesarmid larvae in Hong Kong may be vulnerable to thermal stress as future climate projections indicate that mean maximum temperatures in the region could increase by 3 °C to reach 36 °C regularly by 2050 (Lee et al. 2011). The risk of thermal stress of these larvae may only be minimally reduced by physiological plasticity due to the low acclimation in thermal tolerance of ectotherms (Gunderson and Stillman 2015). Furthermore, negative climate impacts may intensify in Ting Kok and the wider Tolo Harbor area, consequent to historical anthropic interruption of hydrodynamics likely resulting in regular hypoxic and thermally stressful conditions in the summer due to poor tidal flushing and suboptimal water exchange (Tong et al. 2006).

Conclusions

Here, we propose that larvae of mangrove taxa have associations with environmental factors that indicate the extent of habitat use and larval transport across the complex intertidal mangrove microscape (Laprise and Dodson 1994). Larvae of key taxa show metabolic depression at 36 °C indicating their vulnerability to thermal stress. Environmental change and species-sorting will play a large role in how communities will be structured in the future if warming trends are not curbed, elevating the risk of local extinction-debt of vulnerable taxa (Urban 2015; Lancaster et al. 2017). More research is however needed to disentangle the effects of process rates, scales of transport, and disturbance events to infer how they might affect the patterns and processes that underlie community assemblages in urbanized mangrove systems. Furthermore, identifying the ontogenetic and environmental physiological bottlenecks of key taxa will be helpful in recognizing key areas for conservation management in dynamic intertidal settings going forward (Madliger et al. 2017).

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Author contribution LDV, FP, and PP conceptualized the study; LDV, FP, and SC designed the research; LDV, FP, and SC collected the data; and LDV analyzed the data and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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References

Anger K, Charmantier G (2000) Ontogeny of osmoregulation and salinity tolerance in a mangrove crab, *Sesarma curacaoense* (Decapoda: Grapsidae). J Exp Mar Bio Ecol 251:265–274. https://doi.org/10.1016/S0022-0981(00)00223-9

Benjamini Y, Hochberg Y (1995) Controlling the false discovery rate: a practical and powerful approach to multiple testing. J R Stat Soc Ser B 57:289–300. https://doi.org/10.1111/j.2517-6161.1995.tb02031.x

Bento M, Paula J (2018) Keys and bibliography for the identification of zoeal stages of brachyuran crabs from the Western Indian Ocean. West Indian Ocean J Mar Sci 17:13–51

Brown JH, Gillooly JF, Allen AP, Savage VM, West GB (2004) Toward a metabolic theory of ecology. Ecology 85:1171–1789. https://doi.org/10.1890/03-9000

Byrne M, Przeslawski R (2013) Multistressor impacts of warming and acidification of the ocean on marine invertebrates' life histories. Integr Comp Biol 53:582–596. https://doi.org/10.1093/icb/ict049

Cannicci S, Burrows D, Fratini S, Smith TJ, Offenberg J et al (2008) Faunal impact on vegetation structure and ecosystem function in mangrove forests: a review. Aquat Bot 89:186–200. https://doi.org/10.1016/j.aquabot.2008.01.009

Cannicci S, Lee SY, Bravo H, Cantera-Kintz JR, Dahdouh-Guebas F et al (2021) A functional analysis reveals extremely low redundancy in global mangrove invertebrate fauna. Proc Natl Acad Sci 118:e2016913118. https://doi.org/10.1073/pnas.2016913118

Castillo KD, Helmuth BST (2005) Influence of thermal history on the response of *Montastraea annularis* to short-term temperature exposure. Mar Biol 148:261–270. https://doi.org/10.1007/s00227-005-0046-x

Chan BKK, Shao KT, Shao YT, Chang YW (2016) A simplified, economical, and robust light trap for capturing benthic and pelagic zooplankton. J Exp Mar Bio Ecol 482:25–32. https://doi.org/10.1016/j.jembe.2016.04.003

Charmantier G, Giménez L, Charmantier-Daures M, Anger K (2002) Ontogeny of osmoregulauon, physiological plasticity and larval export strategy in the grapsid crab *Chasmagnathus granulata* (Crustacea, Decapoda). Mar Ecol Prog Ser 229:185–194. https://doi.org/10.3354/meps229185

Chaudhari KJ, Jalihal DR (1993) A field key to the seed of penaeid prawns along the Konkan coast (west coast of India). Crustaceana 65:318–335. https://doi.org/10.1163/156854093X00757

Clarke A (2004) Is there a universal temperature dependence of metabolism? Funct Ecol 18:252–256. https://doi.org/10.1111/j.0269-8463.2004.00842.x

Cooke SJ, Hinch SG, Donaldson MR, Clark TD, Eliason EJ et al (2012) Conservation physiology in practice: how physiological knowledge has improved our ability to sustainably manage Pacific salmon during up-river migration. Philos Trans R Soc B Biol Sci 367:1757–1769. https://doi.org/10.1098/rstb.2012.0022

di Lorenzo T, Galassi DMP (2017) Effect of temperature rising on the stygobitic crustacean species *Diacyclops belgicus*: does global warming affect groundwater populations? Water 8:951. https://doi.org/10.3390/w9120951

Diele K, Simith DJB (2006) Salinity tolerance of northern Brazilian mangrove crab larvae, *Ucides cordatus* (Ocypodidae): necessity for larval export? Estuar Coast Shelf Sci 68:600–608. https://doi.org/10.1016/j.ecss.2006.03.012

Epifanio CE, Cohen JH (2016) Behavioral adaptations in larvae of brachyuran crabs: a review. J Exp Mar Bio Ecol 482:85–105. https://doi.org/10.1016/j.jembe.2016.05.006

Gaitán-Espitia JD, Bruning A, Mondaca F, Nespolo RF (2013) Intraspecific variation in the metabolic scaling exponent in ectotherms: testing the effect of latitudinal cline, ontogeny and transgenerational change in the land snail *Cornu aspersum*. Comp Biochem Physiol - A Mol Integr Physiol 165:169–177. https://doi.org/10.1016/j.cbpa.2013.03.002

Gaston KJ, Spicer JI (2009) Physiological diversity: ecological implications. John Wiley & Sons

Gaudy R, Sloane L (1981) Effect of salinity on oxygen consumption in postlarvae of the penaeid shrimps *Penaeus monodon* and *P. stylirostris* without and with acclimation. Mar Biol 65:297–301. https://doi.org/10.1007/BF00397125

Giménez L (2010) Relationships between habitat conditions, larval traits, and juvenile performance in a marine invertebrate. Ecology 95:1401–1413. https://doi.org/10.1890/09-1028.1

Gonçalves F, Ribeiro R, Soares AMVM (2003) Comparison between two lunar situations on emission and larval transport of decapod larvae in the Mondego estuary (Portugal). Acta Oecologica 24:S183–S190. https://doi.org/10.1016/S1146-609X(03)00036-5

Gunderson AR, Stillman JH (2015) Plasticity in thermal tolerance has limited potential to buffer ectotherms from global warming. Proc R Soc B Biol Sci 282:20150401. https://doi.org/10.1098/rspb.2015.0401

Guppy M, Withers P (1999) Metabolic depression in animals: physiological perspectives and biochemical generalizations. Biol Rev 74:1–40. https://doi.org/10.1111/j.1469-185X.1999.tb00180.x

Heino J (2013) Does dispersal ability affect the relative importance of environmental control and spatial structuring of littoral macroinvertebrate communities? Oecologia 171:971–980. https://doi.org/10.1007/s00442-012-2451-4

Hernández Moresino RD, Gonçalves RJ, Helbling EW (2011) Sublethal effects of ultraviolet radiation on crab larvae of *Cyrtograpsus altimanus*. J Exp Mar Bio Ecol 407:363–369. https://doi.org/10.1016/j.jembe.2011.07.019

Hillebrand H, Dürselen CD, Kirschtel D, Pollingher U, Zohary T (1999) Biovolume calculation for pelagic and benthic microalgae. J Phycol 35:403–424. https://doi.org/10.1046/j.1529-8817.1999.3520403.x

Jimenez AG, Jayawardene S, Alves S, Dallmer J, Dowd WW (2015) Micro-scale environmental variation amplifies physiological variation among individual mussels. Proc R Soc B Biol Sci 282:2152273. https://doi.org/10.1098/rspb.2015.2273

Kelley AL, de Rivera CE, Buckley BA (2011) Intraspecific variation in thermotolerance and morphology of the invasive European green crab, *Carcinus maenas*, on the west coast of North America. J Exp Mar Bio Ecol 409:70–78. https://doi.org/10.1016/j.jembe.2011.08.005

Kozłowski J, Weiner J (1997) Interspecific allometries are by-products of body size optimization. Am Nat 149:352–380. https://doi.org/10.1086/285994

Lancaster LT, Morrison G, Fitt RN (2017) Life history trade-offs, the intensity of competition, and coexistence in novel and evolving communities under climate change. Philos Trans R Soc B Biol Sci 372:20160046. https://doi.org/10.1098/rstb.2016.0046

Laprise R, Dodson JJ (1994) Environmental variability as a factor controlling spatial patterns in distribution and species diversity of zooplankton in the St Lawrence Estuary. Mar Ecol Prog Ser 107:67–82. https://doi.org/10.3354/meps107067

Lee SY (2008) Mangrove macrobenthos: assemblages, services, and linkages. J Sea Res 59:16–29. https://doi.org/10.1016/j.seares.2007.05.002

Lee TC, Chan KY, Ginn WL (2011) Projection of extreme temperatures in Hong Kong in the 21st century. Acta Meteorol Sin 25:1–20. https://doi.org/10.1007/s13351-011-0001-3

Lee SY, Primavera JH, Dahdouh-Guebas F, Mckee K, Bosire JO et al (2014) Ecological role and services of tropical mangrove ecosystems: a reassessment. Glob Ecol Biogeogr 23:726–743. https://doi.org/10.1111/geb.12155

Legendre P, Gallagher ED (2001) Ecologically meaningful transformations for ordination of species data. Oecologia 129:271–280. https://doi.org/10.1007/s004420100716

Li MS, Lee SY (1997) Mangroves of China: a brief review. For Ecol Manage 96:241–259. https://doi.org/10.1016/S0378-1127(97)00054-6

Little KT, Epifanio CE (1991) Mechanism for the re-invasion of an estuary by two species of brachyuran megalopae. Mar Ecol Prog Ser 68:235–242

Madliger CL, Franklin CE, Hultine KR, van Kleunen M, Lennox RJ et al (2017) Conservation physiology and the quest for a 'good' Anthropocene. Conserv Physiol 5:1–10. https://doi.org/10.1093/conphys/cox003

Magris RA, Fernandes LFL (2011) Diversity and distribution of assemblages of estuarine decapod larvae (Crustacea: Decapoda: Anomura, Brachyura) in tropical southeastern Brazil. Zootaxa 29:1–13. https://doi.org/10.11646/zootaxa.2758.1.2

Marochi MZ, Costa TM, Buckley LB (2021) Ocean warming is projected to speed development and decrease survival of crab larvae. Estuar Coast Shelf Sci 259:107478. https://doi.org/10.1016/j.ecss.2021.107478

Medina-Contreras D, Arenas-González F, Cantera-Kintz J, Sánchez-González A, Giraldo A (2020) Food web structure and isotopic niche in a fringe macro-tidal mangrove system, Tropical Eastern Pacific. Hydrobiologia 847:3185–3199. https://doi.org/10.1007/s10750-020-04295-x

Mitchell MD, Bairos-Novak KR, Ferrari MCO (2017) Mechanisms underlying the control of responses to predator odours in aquatic prey. J Exp Biol 220:1937–1946. https://doi.org/10.1242/jeb.135137

Morton B (2016) Hong Kong's mangrove biodiversity and its conservation within the context of a southern Chinese megalopolis. A review and a proposal for Lai Chi Wo to be designated as a World Heritage Site. Reg Stud Mar Sci 8:382–399. https://doi.org/10.1016/j.rsma.2016.05.001

O'Hara RB, Kotze DJ (2010) Do not log-transform count data. Methods Ecol Evol 1:118–122. https://doi.org/10.1111/j.2041-210x.2010.00021.x

Paula J, Mendes RN, Mwaluma J, Raedig C, Emmerson W (2004) Combined effects of temperature and salinity on larval development of the mangrove crab *Parasesarma catenata* Ortman, 1897 (Brachyura: Sesarmidae). West Indian Ocean J Mar Sci 2:57–63. https://doi.org/10.4314/wiojms.v2i1.28429

Pérez-Ceballos R, Zaldívar-Jiménez A, Canales-Delgadillo J, López-Adame H, López-Portillo J et al (2020) Determining hydrological flow paths to enhance restoration in impaired mangrove wetlands. PLoS One 15:e0227665. https://doi.org/10.1371/journal.pone.0227665

Pilditch CA, Valanko S, Norkko J, Norkko A (2015) Post-settlement dispersal: the neglected link in maintenance of soft-sediment biodiversity. Biol Lett 11:20140795. https://doi.org/10.1098/rsbl.2014.0795

Pineda J, Hare JA, Sponaugle S (2007) Larval transport and dispersal in the coastal ocean and consequences for population connectivity. Oceanography 27:22–39. https://doi.org/10.5670/oceanog.2007.27

Pörtner HO (2002) Climate variations and the physiological basis of temperature dependent biogeography: systemic to molecular hierarchy of thermal tolerance in animals. Comp Biochem Physiol - A Mol Integr Physiol 132:739–761. https://doi.org/10.1016/S1095-6433(02)00045-4

Pörtner HO (2021) Climate impacts on organisms, ecosystems and human societies: integrating OCLTT into a wider context. J Exp Biol 224:1–17. https://doi.org/10.1242/jeb.238360

Pörtner HO, Farrell AP (2008) Physiology and climate change. Science 322:690–692. https://doi.org/10.1126/science.1163156

Przeslawski R, Byrne M, Mellin C (2015) A review and meta-analysis of the effects of multiple abiotic stressors on marine embryos and larvae. Glob Chang Biol 21:2122–2140. https://doi.org/10.1111/gcb.12833

Radford CA, Jeffs AG, Montgomery JC (2007) Directional swimming behavior by five species of crab postlarvae in response to reef sound. Bull Mar Sci 80:369–378

R Core Team (2019) R: A language and environment for statistical-computing. Version 3.6.3. R Foundation for Statistical Computing, Vienna

Rodil IF, Lucena-Moya P, Jokinen H, Ollus V, Wennhage H et al (2017) The role of dispersal mode and habitat specialization for metacommunity structure of shallow beach invertebrates. PLoS One 12:e0172160. https://doi.org/10.1371/journal.pone.0172160

Saintilan N, Mazumder D (2017) Mass spawning of crabs: ecological implications in subtropical Australia. Hydrobiologia 803:239–250. https://doi.org/10.1007/s10750-017-3150-2

Seebacher F, Franklin CE (2012) Determining environmental causes of biological effects: the need for a mechanistic physiological dimension in conservation biology. Philos Trans R Soc B Biol Sci 367:1607–1614. https://doi.org/10.1098/rstb.2012.0036

Simith DJB, Pires MAB, Abrunhosa FA, Maciel CR, Diele K (2014) Is larval dispersal a necessity for decapod crabs from the Amazon mangroves? Response of *Uca rapax* zoeae to different salinities and comparison with sympatric species. J Exp Mar Bio Ecol https://doi.org/10.1016/j.jembe.2014.03.021

Simoni R, Giomi F, Spigoli D, Pörtner HO, Cannicci S (2013) Adaptations to semi-terrestrial life in embryos of East African mangrove crabs: a comparative approach. Mar Biol 160:2483–2492. https://doi.org/10.1007/s00227-013-2243-3

Small DP, Calosi P, Boothroyd D, Widdicombe S, Spicer JI (2015) Stage-specific changes in physiological and life-history responses to elevated temperature and pCO2 during the larval development of the European lobster *Homarus gammarus* (L.). Physiol Biochem Zool 88:494–507. https://doi.org/10.1086/682238

Szela TL, Marsh AG (2005) Microtiter plate, optode respirometry, and inter-individual variance in metabolic rates among nauplii of *Artemia* sp. Mar Ecol Prog Ser 296:281–289. https://doi.org/10.3354/meps296281

Tam NF, Wong Y (2002) Conservation and sustainable exploitation of mangroves in Hong Kong. Trees - Struct Funct 16:224–229. https://doi.org/10.1007/s00468-001-0149-z

Thompson PL, Guzman LM, De Meester L, Horváth Z, Ptacnik R et al (2020) A process-based metacommunity framework linking local and regional scale community ecology. Ecol Lett 23:1314–1329. https://doi.org/10.1111/ele.13568

Thorson G (1950) Reproductive and larval ecology of marine bottom invertebrates. Biol Rev 25:1–45. https://doi.org/10.1111/j.1469-185X.1950.tb00585.x

Tilman D (1994) Competition and biodiversity in spatially structured habitats. Ecology 75:2–16. https://doi.org/10.2307/1939377

Tong YF, Lee SY, Morton B (2006) The herbivore assemblage, herbivory and leaf chemistry of the mangrove *Kandelia obovata* in two contrasting forests in Hong Kong. Wetl Ecol Manag 14:39–52. https://doi.org/10.1007/s11273-005-2565-0

Urban MC (2015) Accelerating extinction risk from climate change. Science 348:571–573. https://doi.org/10.1126/science.aaa4984

Valanko S, Heino J, Westerbom M, Viitasalo M, Norkko A (2015) Complex metacommunity structure for benthic invertebrates in a low-diversity coastal system. Ecol Evol 5:5203–5215. https://doi.org/10.1002/ece3.1767

Venables WN, Ripley BD (2002) Modern applied statistics with S, 4th edn. Springer, New York

Vorsatz LD, Mostert BP, McQuaid CD, Cannicci S, Porri F (2021) Thermal sensitivity in dual-breathing ectotherms: embryos and mothers determine species' vulnerability to climate change. Limnol Oceanogr Lett 7:251–260. https://doi.org/10.1002/lol2.10225

Vorsatz LD, Pattrick P, Porri F (2021) Quantifying the in situ 3-dimensional structural complexity of mangrove tree root systems: biotic and abiotic implications at the microhabitat scale. Ecol Indic 121:107154. https://doi.org/10.1016/j.ecolind.2020.107154

Vorsatz LD, Pattrick P, Porri F (2021) Ecological scaling in mangroves: the role of microhabitats for the distribution of larval assemblages. Estuar Coast Shelf Sci 253:107318. https://doi.org/10.1016/j.ecss.2021.107318

Vorsatz LD, Pattrick P, Porri F (2021) Fine-scale conditions across mangrove microhabitats and larval ontogeny contributes to the thermal physiology of early stage brachyurans (Crustacea: Decapoda). Conserv Physiol 9:1–14. https://doi.org/10.1093/conphys/coab010

Wang Y, Naumann U, Wright ST, Warton DI (2012) Mvabund- an R package for model-based analysis of multivariate abundance data. Methods Ecol Evol 3:471–474. https://doi.org/10.1111/j.2041-210X.2012.00190.x

Warton DI, Wright ST, Wang Y (2012) Distance-based multivariate analyses confound location and dispersion effects. Methods Ecol Evol 3:19–101. https://doi.org/10.1111/j.2041-210X.2011.00127.x

Weiss M, Heilmayer O, Brey T, Lucassen M, Pörtner HO (2012) Physiological capacity of *Cancer setosus* larvae - adaptation to El Niño Southern Oscillation conditions. J Exp Mar Bio Ecol 413:100–105. https://doi.org/10.1016/j.jembe.2011.11.023

Wiens JA, Bachelet D (2010) Matching the multiple scales of conservation with the multiple scales of climate change: special section. Conserv Biol 24:51–62. https://doi.org/10.1111/j.1523-1739.2009.01409.x

Wobbrock JO, Findlater L, Gergle D, Higgins JJ (2011) The alignedrank transform for nonparametric factorial analyses using onlyanova procedures. In Proceedings of the SIGCHI conference onhuman factors in computing systems. Association for Computing Machinery, New York, pp. 143–146