



# 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

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## 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

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.

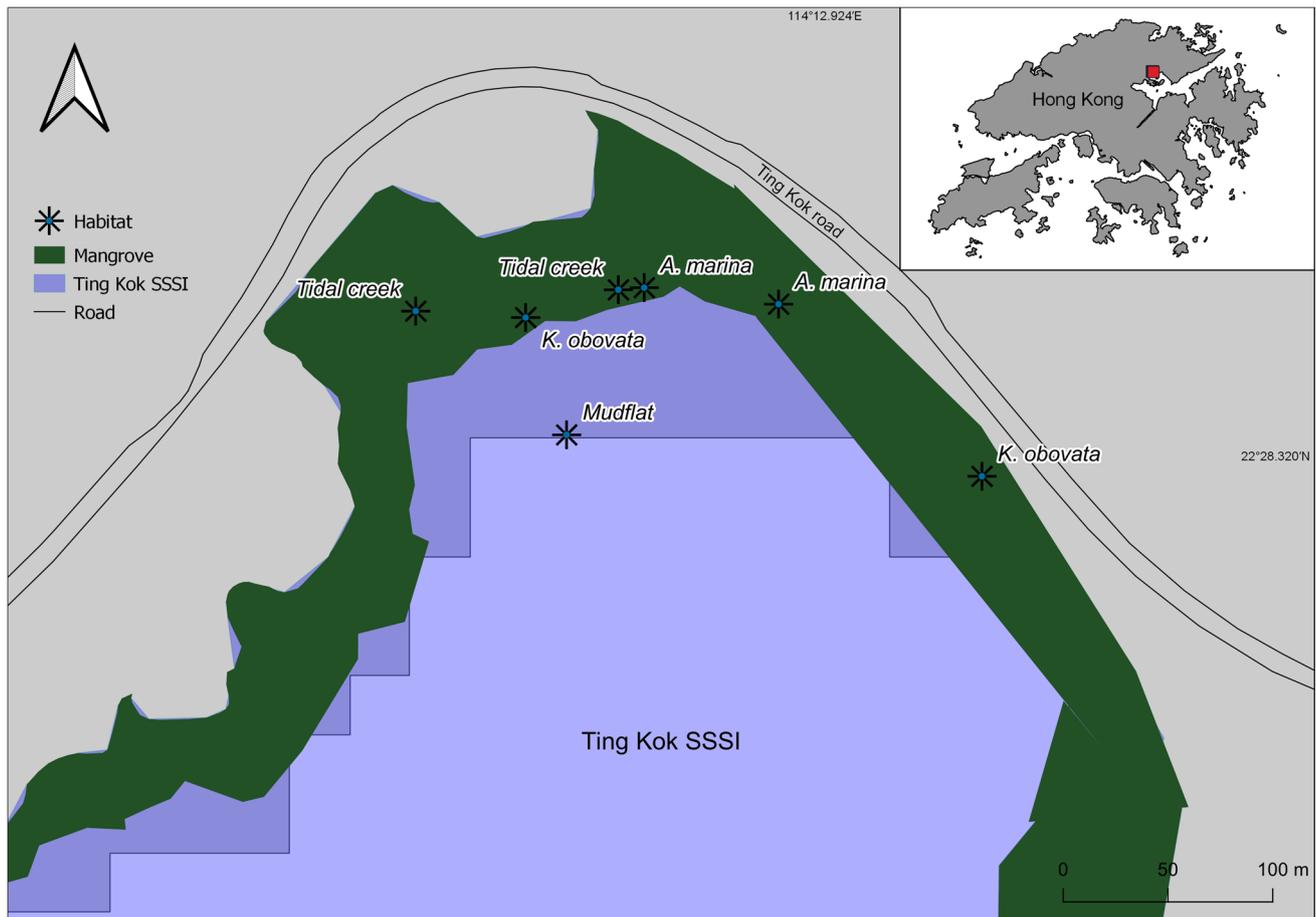
The present study aimed to improve our understanding of processes that drive community structure and physiological performance of larval invertebrates in reference

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  $\times$  3 experimental habitats + (2 light traps at the mudflat))  $\times$  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- $\mu$ m 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- $\mu$ m 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, post-larvae (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  $\mu$ l, 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  $\text{nmol O}_2 \text{ min}^{-1} \text{ ind}^{-1}$ .

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).

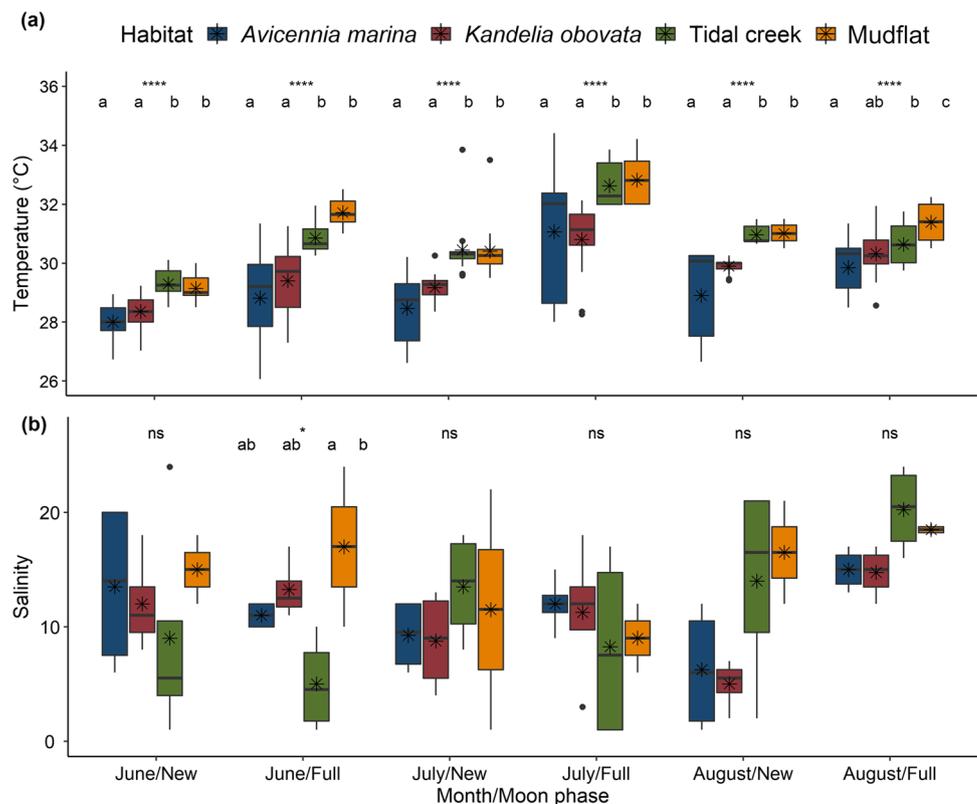
Variable numbers of individuals of each taxon were tested at all experimental water temperatures and habitats (Table S2). Hence, separate GLMs were run to test for differences in *MO2* within and among taxa and habitats at 28 °C. Additionally, GLMs were run to test for differences in *MO2* among water 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= $p > 0.05$



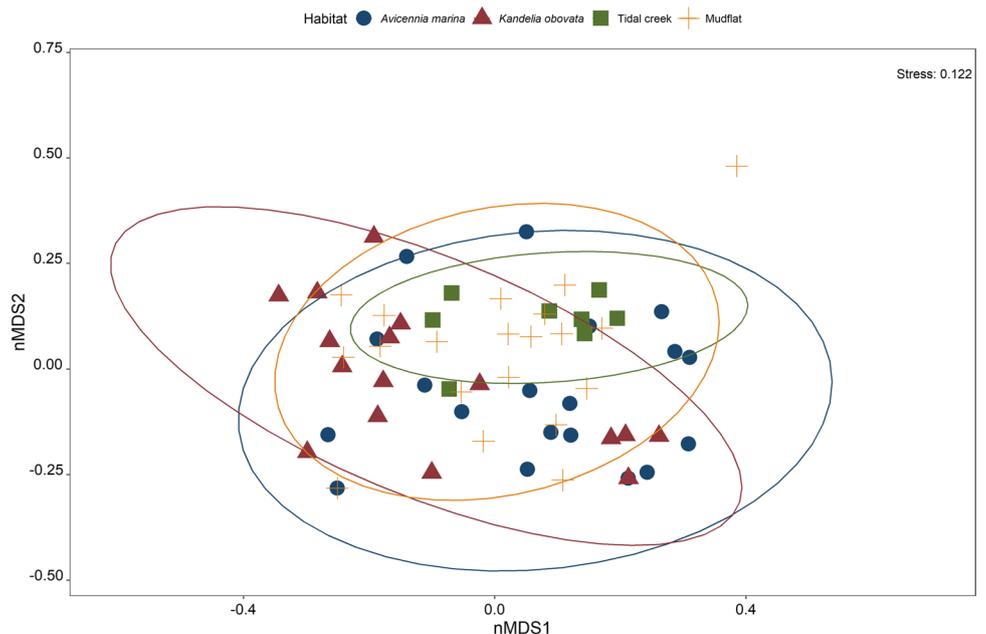
Approximately 13,700 individuals from 15 taxa were collected throughout the study period (Table 1). The *A. marina* habitat was numerically dominated by *Etisus laevimanus* and *Scopimera intermedia* zoeae. *Scopimera intermedia* zoeae and *Penaeus merguensis* juveniles dominated the *K. obovata* community, while the mudflat was mostly occupied by zoeae of *Pinnixa* sp. and *Parasesarma bidens*. Furthermore, *Pinnixa* sp. zoeae and *Laomedea* 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 (%)	<i>A. marina</i> (%)	<i>K. obovata</i> (%)	Mudflat (%)	Tidal creek (%)
Zoea	<i>Etisus laevimanus</i>	785	223 (2.9)	562 (9.3)	192 (37.5)	0	71 (9.4)	522 (4.3)
	<i>Parasesarma bidens</i>	1348	903 (11.8)	445 (7.4)	24 (4.7)	11 (2.5)	151 (20)	1162 (9.7)
	<i>Pinnixa</i> sp.	3669	2479 (32.3)	1190 (19.7)	25 (4.9)	2 (0.5)	369 (48.9)	3273 (27.3)
	<i>Scopimera intermedia</i>	394	74 (1)	320 (5.3)	179 (35)	206 (46.9)	8 (1.1)	1 (<0.1)
	<i>Upogebia</i> 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)
	<i>Tmethypocoelis ceratophora</i>	8	8 (0.1)	0	1 (0.2)	1 (0.2)	5 (0.7)	1 (<0.1)
	<i>Metapograpsus frontalis</i>	41	40 (0.5)	1 (<0.1)	0	0	9 (1.2)	32 (0.3)
Post larva	<i>Acetes</i> sp.	1126	278 (3.6)	848 (14)	7 (1.4)	25 (5.7)	12 (1.6)	1082 (9)
	<i>Bezelbub</i> sp.	45	42 (0.5)	3 (<0.1)	0	0	45 (6)	0
	<i>Laomedea</i> sp.	5745	3205 (41.8)	2540 (42)	26 (5.1)	4 (0.9)	44 (5.8)	5671 (47.2)
Juvenile	<i>Penaeus monodon</i>	80	49 (0.6)	31 (0.5)	9 (1.8)	31 (7.1)	0	40 (0.3)
	<i>Penaeus latisulcatus</i>	84	75 (1)	9 (0.1)	3 (0.6)	24 (5.5)	8 (1.1)	49 (0.4)
	<i>Penaeus merguensis</i>	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 multi-dimensional 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., *Laomedea* 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 *Laomedea* 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. merguensis* 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 sesarimid 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 sesarimid 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 sesarimid ( $F_{(2,137)} = 4.21, p = 0.016$ ) zoeae  $MO_2$  differed significantly among water temperatures, with *Pinnixa* sp. and sesarimids having greater  $MO_2$  at 33 °C than 28 °C (Fig. 4b). Sesarimid 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 sesarimid larvae increased with average to high water temperatures common in summer, with sesarimids exhibiting metabolic depression at the highest experimental temperatures (36 °C), which will be regularly experienced by 2050, according to current climate projections.

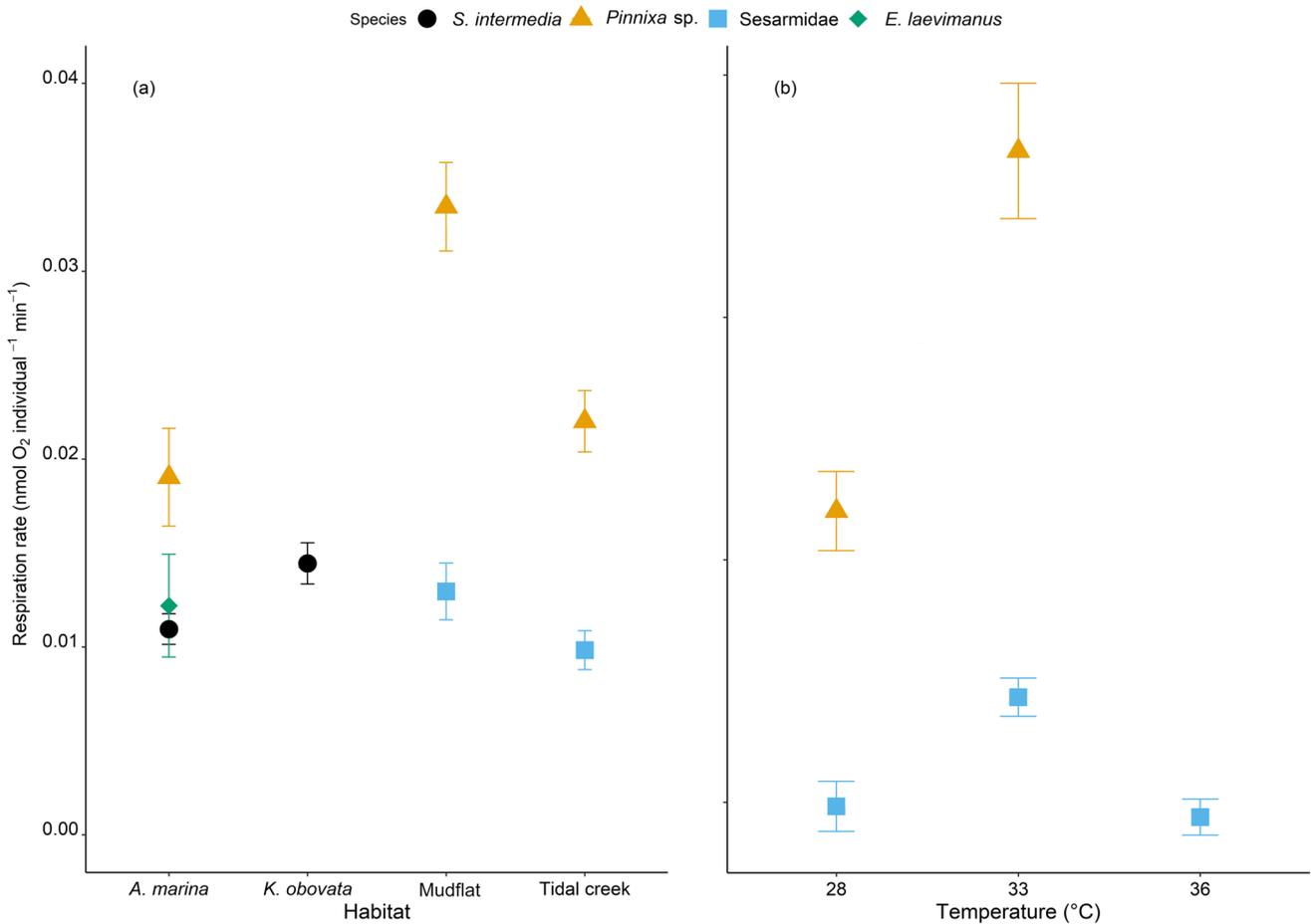
## Environmental drivers of larval community structure

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

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)



**Fig. 4** Oxygen consumption rates expressed as mean  $\pm$  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	<i>p</i>	Posthoc
<i>Scopimera intermedia</i>	6.778	1	<b>0.013</b>	<i>K. obovata</i> <sup>a</sup> , <i>A. marina</i> <sup>b</sup>
<i>Pinnixa</i> sp.	10.406	2	<b>&lt;0.001</b>	Mudflat <sup>b</sup> , <i>A. marina</i> <sup>a</sup> , Tidal creek <sup>a</sup>
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 sub-optimal 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 microscale (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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