Maternal influence on the larval morphometry of the brush-clawed shore crab *Hemigrapsus takanoi* (Decapoda: Brachyura)

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Summary: The morphology of larvae is a key factor influencing their behaviour, performance and ultimately their survival. There is evidence indicating a significant morphological variability among broods, and that this may be related to the size or conditions of the mother. However, this maternal influence is not consistent across decapod crustaceans. Using 35 broods from different mothers of the crab *Hemigrapsus takanoi* collected in the same locality of inner Tokyo Bay and at the same time, we tested the hypothesis that there is a positive relationship between the size of the mother and the progeny's morphology. Our results indicate that different patterns in the length of the lateral, rostral and dorsal spines differentiated two distinct morphogroups of larvae. These morphogroups were linked to the size of the mother, showing that larger mothers produced bigger larvae with longer carapace spines. It is possible that larger size and longer spines can influence swimming performance and predator avoidance, respectively. These relationships should be tested in future experimental studies.

Keywords: brood; life history; phenotype; size; spines; zoea.

Influencia materna en la morfometría larvaria del cangrejo de pinzas pincel *Hemigrapsus takanoi* (Decapoda: Brachyura)

Resumen: La morfología larvaria es un factor clave que influencia el comportamiento, rendimiento y en último lugar la supervivencia larvaria. Hay evidencias que indican una variabilidad morfológica significativa entre puestas, y que esto puede estar relacionado con la talla y condición de la madre. Sin embargo, la influencia materna no es consistente para todos los crustáceos decápodos. Usando 35 puestas de diferentes madres del cangrejo *Hemigrapsus takanoi*, recolectadas en la misma localidad en el interior de la Bahía de Tokio, y al mismo tiempo, testeamos la hipótesis de que hay una relación positiva entre la talla de la madre y la morfología de la progenie. Nuestros resultados indican que diferentes patrones de longitud de las espinas laterales, rostrales y laterales diferencian dos morfogrupos distintos de larvas. Esos morfogrupos se asociaron a la talla de la madre, mostrando que aquellas madres grandes producían larvas de mayor tamaño con espinas más largas. Es posible que un tamaño mayor y espinas más largas puedan influenciar la capacidad natatoria y la evasión de predadores respectivamente. Estas relaciones deberían ser testeadas en futuros estudios experimentales.

Palabras clave: progenie; ciclo de vida; fenotipo; tamaño; espinas; zoea.

INTRODUCTION

Most marine organisms produce a larva that develops for a certain time period in the water column. During this planktonic period, larval size and morphology are key life-history traits that can affect all aspects of performance and survival (Pettersen et al. 2015). For many taxa, bigger larvae facilitate the access of a wider prey size range, store higher endogenous reserves and avoid predators (Pepin 1989, Park et al. 2004, Bashevkin et al. 2020).

Variation in progeny size among species, and among populations within species, was initially attributed to variation in natural selection (Fox and Czesak 2000). However, this variability is more and more viewed as a physiological constraint that prevents mothers from producing homogeneous progeny size (Marshall et al. 2008). In decapod crustaceans, variations in progeny size and morphology have been associated with maternal size (or age) and/or the environmental conditions experienced by the mother during the embryonic development (Anger 2001). For instance, lower temperature at higher-latitude populations is related to the production of larger crab larvae in the Pacific sub-Arctic/Arctic sector (*Chionoecetes opilio*; Landeira et al. 2017), NE Pacific (*Metacarcinus magister*; Shirley et al.1987), SE Pacific (*Cancer setosus*; Weiss et al. 2010) and NE Atlantic (*Macropodia rostrata*; Marco-Herrero et al. 2012). It has also been observed that seasonal changes in temperature, salinity, and food availability can influence the production of different larval phenotypes throughout the year (Urzúa and Anger 2013; González-Ortegón and Giménez 2014). In some caridean shrimps these environmental factors are linked to maternal size, as carapace length also varies significantly between breeding seasons (González-Ortegón et al. 2018; Oliphant and Thatje 2021). Despite the growing body of evidence supporting the maternal influence in the larval phenotype, few studies have reported this effect extracting the environmental factors. Maternal influence on larval morphology has been seen in the coconut crab, *Birgus latro* (Sato and Suzuki 2010), the European lobster, *Homarus gammarus* (Moland et al. 2010), the kuruma prawn, *Marsupenaeus japonicus* (Sato et al. 2017), and the blue crab, *Callinectes sapidus* (Caracappa and Munroe 2018). However, other species such as the red king crab, *Paralithodes camtschaticus*, and the shore crab, *Hemigrapsus crenulatus*, have shown no such relationship (Swiney et al. 2013, Urzúa et al. 2018), suggesting that the consistency of the pattern across the different crustacean groups is not well supported yet.

The brush-clawed shore crab, *Hemigrapsus takanoi* Asakura and Watanabe, 2005, is a common brackish and estuarine invertebrate found under intertidal boulders in its native distribution range of the northwest Pacific (Asakura and Watanabe 2005). Multiple introductions, likely by shipping lines, have facilitated the expansion of *H. takanoi* along the northern European coasts from the Bay of Biscay to the Baltic Sea (Makino et al. 2018). *Hemigrapsus takanoi* is an active predator and its large populations are modifying the popu-

lation dynamics of native mussels (Nour et al. 2020). As a euryhaline species, *H. takanoi* is an excellent osmoregulator, which allows it to colonize variable-salinity environments (Shinji et al. 2009). During the larval phase, this crab develops through five zoeal stages and one megalopal stage (Landeira et al. 2019). The zoeal stages of *H. takanoi* are not euryhaline and need to be exported from the brackish water (spawning grounds) into the marine environment for larval development and to recolonize brackish water in the megalopal stage (Mingkid et al. 2006). The first zoeal stage is especially vulnerable since survival, swimming performance and feeding behaviour are compromised under low-salinity conditions (Landeira et al. 2020).

The present study aimed to evaluate the morphological variability among broods in *Hemigrapsus takanoi* zoea I and the effect of the size of the mother on the size and morphology of the progeny. To this end, we performed morphometrics on the carapace of the larvae and their mother. We hypothesized that there is a positive relationship between the size of the mother and the progeny's morphometrics.

MATERIALS AND METHODS

Sampling and study area

Crabs were collected in Daiba Park (35°38'04"N; 139°46'26"E), located in the inner part of Tokyo Bay, where *H. takanoi* is the dominant intertidal crab. On 26 May 2017, ovigerous crabs ($N = 120$) were collected during the low-tide period from the intertidal zone (approx. 3 m² area) by hand flipping cobbles. In the field, the specimens were identified following the key characters of pigmentation pattern on the abdominal somites and on the cephalothorax described by Asakura and Watanabe (2005). Only crabs with embryos in an advanced stage of development (eyes visible) were used for the experiment. The crabs were selected to cover the widest size range possible (carapace length ranged from 8 to 15 mm). After collection, the crabs were transported to the aquarium facilities of the Tokyo University of Marine Science and Technology at Shinagawa Campus.

Culture and maintenance

Inside a temperature-controlled room, the crabs were placed individually in 1 L plastic buckets containing 0.8 L of 20°C and 25 salinity seawater (field conditions at time of collection) with aeration and under natural daylight. Every morning, the water was changed, and the crabs were fed pieces of the wakame seaweed, *Undaria pinnatifida* (Harvey) Suringar 1873. Before that, the buckets were checked to collect newly hatched larvae. Then, both the larvae and the mother were preserved in 80% ethanol for morphometric analysis. To minimize the potential effect of long-term maintenance conditions, we used only 35 broods of larvae from crabs that released the larvae within four days of incubation. The rest of the crabs were discarded and returned to the field.

Morphometric analysis

We applied morphometric measurements of 35 ovigerous crabs and 20 preserved larvae (zoea I) from their broods. Females were placed next to a scale for calibration and photographed. Then, the carapace length was measured on the digitalized images using ImageJ 1.50i software (http://rsb.info.nih.gov/ij/). The larvae were processed using a stereomicroscope with a calibrated eye-piece graticule, and the following measurements were obtained: carapace length (CL) measured from the base of the rostral spine to the posterior dorsal margin of the carapace; length of dorsal spine of carapace (DSL); length of lateral spine of carapace (LSL); rostral spine length (RSL); rostral-dorsal spine distance (RDSD), measured from the tip of the rostral spine to the tip of the dorsal spine; lateral spine distance (LSD), measured from the tip of the lateral spines of the carapace. All larval measurements were completed within one month after specimen preservation.

Statistical analysis

Multivariate statistical analysis was used to identify morphological patterns. In a first step, to classify the individual larvae of all broods, hierarchical clustering analysis was performed using the log-formed morphometric data of each measurement for each larva in a Euclidean distance matrix. After this, two one-way analysis of similarity (ANOSIM) tests were performed to evaluate differences between morphogroups of larvae and between broods (Clarke and Gorley 2015). The morphometric measurements contributing most to the differences between morphogroups were identified with the similarity percentage (SIMPER) procedure. Using the same Euclidean distance matrix, a principal component analysis (PCA) was used to examine patterns in larval morphometry among broods and to characterize which morphometric measurements were driving them. To link larval morphometric patterns among broods with the size of the mother, the PCA ordination was represented by superimposing circles of increasing size related to the CL of the female crabs. Moreover, for an easier pattern visualization, cluster morphogroups were also overlaid (Clarke and Gorley 2015). To analyse inter-brood differences for each morphometric measurement, the nonparametric Kruskal-Wallis ANOVA test was used, because of the non-normal and heteroscedastic nature of the data set (Kruskal and Wallis 1952). Parametric tests were not used because most of the variables did not meet the underlying conditions of normality (Kolmogorov-Smirnov) and homogeneity of variances (Levene's test). Simple linear regressions were carried out to ascertain the extent of the effect of mother size on the morphometry of zoea I larvae. The statistical analyses were carried out using the PRIMER v7 software and the IBM SPSS Statistics package v27.

RESULTS

The classification of individual larvae by dendrogram, based on morphometric variables, revealed clear grouping patterns. Indeed, two main morphogroups of larvae (Group A and Group B) were categorized by a Euclidean distance of 0.5 (Fig. 1A). The ANOSIM test supported the classification, since these
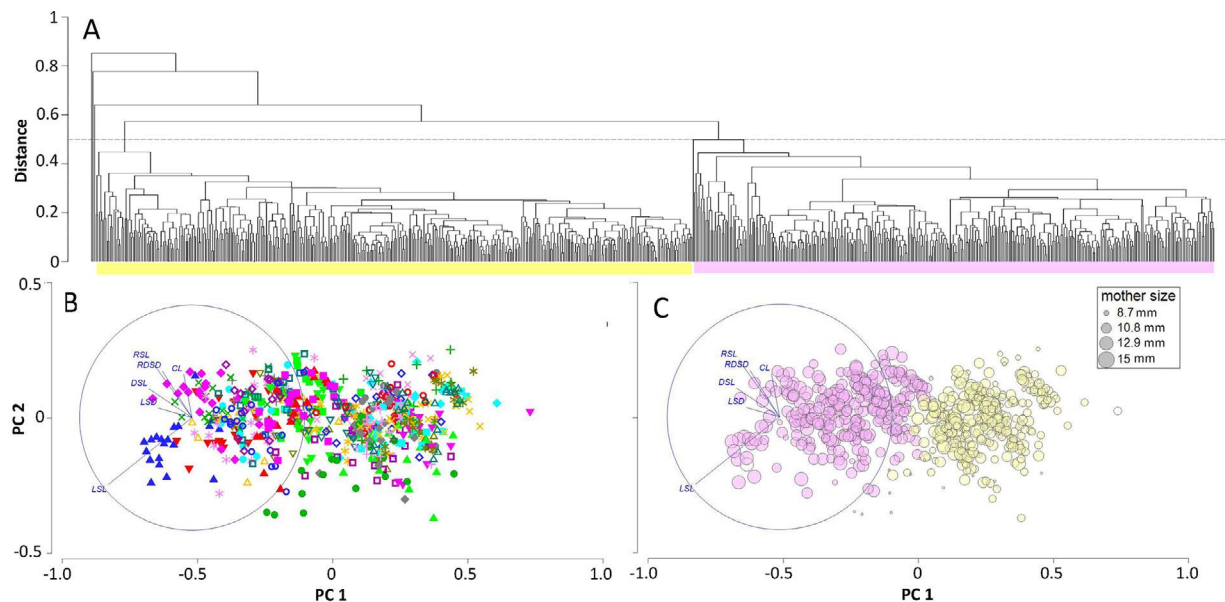

Fig. 1. – Dendrogram of *Hemigrapsus takanoi* zoeae associations by Euclidean distance similarity analysis based on a similarity matrix of log-transformed data for each morphometric measurement (A). Principal component analysis examining patterns in larval morphometry among broods and characterizing which morphometric measurements are driving the patterns (B). The same PCA ordination is represented by superimposing circles of increasing size related to the carapace length of the female crabs (C). Broods of each female are indicated with different colours and the symbols indicated in B. In plots A and C, pink and yellow colours are used to show morphogroups A and B, respectively. Abbreviations for morphometric measurement: RSL rostral spine length; LSL, length of lateral spine of carapace; RDSD, rostral-dorsal spine distance; DSL, length of dorsal spine of carapace; LSD, lateral spine distance; CL, carapace length.
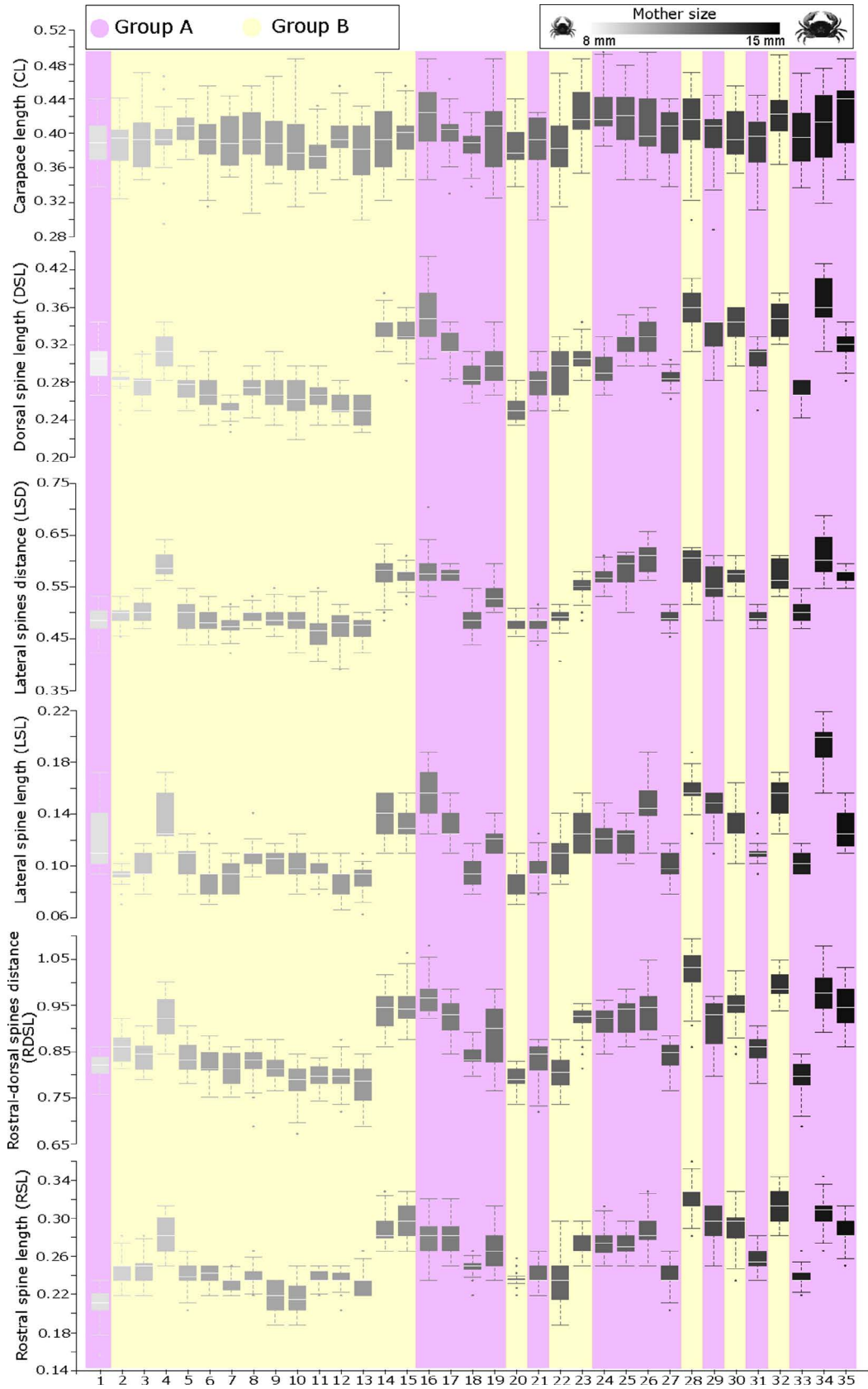
Fig. 2. – Box plots showing the distribution of each morphometric measurement (RSL, rostral spine length; LSL, length of lateral spine of carapace; RDSD, rostral-dorsal spines distance; DSL, length of dorsal spine of carapace; LSD, lateral spines distance; CL, carapace length) for all 35 broods of *Hemigrapsus takanoi*. Note that the broods are displayed according to the size of the mother, and the grey colour intensity of the box plot indicates the proportional size of their mother. Pink and yellow colours are used to show morphogroups A and B, respectively. In each box plot, the median (solid line) values are indicated in the centre of the box and the edges of the box are the 25th and 75th percentiles.

Table 1. – Summary of the minimum (min), maximum (max) and mean values obtained in each measurement (RSL, rostral spine length; LSL, length of lateral spine of carapace; RDSD, rostral-dorsal spines distance; DSL, length of dorsal spine of carapace; LSD, lateral spine distance; CL, the carapace length) in each morphogroup of *Hemigrapsus takanoi* larvae.

	Morphogroup A			Morphogroup B		
	min	max	mean	min	max	mean
CL	0.29	0.49	0.41 ± 0.04	0.29	0.50	0.39±0.04
LSD	0.42	0.69	0.54 ± 0.05	0.39	0.64	0.51±0.05
RDSD	0.69	1.08	0.89 ± 0.07	0.67	1.09	0.86±0.08
DSL	0.23	0.41	0.31 ± 0.03	0.22	0.39	0.29±0.04
RSL	0.16	0.34	0.26 ± 0.03	0.19	0.36	0.25±0.03
LSL	0.08	0.22	0.13 ± 0.03	0.06	0.19	0.11±0.03

Table 2. – Simple linear regression results evaluating the relationship between the mother size and each morphometric variable measured in *Hemigrapsus takanoi* larvae (zoea I): RSL, rostral spine length; LSL, length of lateral spine of carapace; RDSD, rostral-dorsal spines distance; DSL, length of dorsal spine of carapace; LSD, lateral spines distance; CL, carapace length.

		Correlations		Linear regression model			ANOVA	
	N	Pearson	P	r^2	intercept	slope	F	p
DSL	35	0.475	0.002	0.226	0.188	0.01	9.64	0.004
RSL	35	0.551	$<10^{-4}$	0.302	0.148	0.01	14.311	0.001
LSL	35	0.468	0.002	0.219	0.039	0.007	9.247	0.005
RDSD	35	0.451	0.003	0.204	0.661	0.019	8.449	0.006
LSD	35	0.438	0.004	0.192	0.383	0.013	7.848	0.008
CL	35	0.879	$<10^{-4}$	0.772	0.314	0.011	111.638	$<10^{-4}$

morphogroups were statistically different (R=0.79; P<0.1%). The SIMPER procedure identified that LSL, RSL and DSL were the variables contributing most to the dissimilarities between morphogroups, with 47.2%, 15.0% and 14.6%, respectively. The PCA ordination allowed larval morphometric variability to be reduced to two principal components (Fig. 1B), which explained 85.6% of the cumulative variation (PC1, 75.5% and PC2, 10.1%). Broods showed a patchy distribution (with certain overlapping), suggesting high morphological similarity among the larvae of the same brood. Differences between broods were confirmed by the ANOSIM test (R=0.58; P<0.1%). Eigenvectors of morphometric measurements pointed towards the same direction in the PC1, indicating a similar effect in the ordination pattern (Fig. 1B). The superimposition of the mother carapace size on the PCA plot showed no clear pattern among broods, but the smallest crabs were mainly located on the negative side of the PC2 axis, towards the direction of the LSL eigenvector (Fig. 1C). Correlations between maternal size and each PC axis showed a moderate significant correlation with PC1 (Pearson's correlation, r=0.457, P<0.001), but no correlation with PC2 (Pearson's correlation, r=0.127, P<0.01). However, when the morphogroups were coded with colours in the PCA, a clear separation of the larvae was visible, showing larvae from Group A located on the negative side of PC1 and those of Group B on the positive side (Fig. 1C).

Inter-brood variability was visible by observing them independently (Fig. 2) and statistically different (KW-ANOVA, P<0.001) for most of the morphometric measurement (CL, DSL, LSL, RDSL, and RSL), but LSD showed no significant trend (KW-ANOVA, P=0.192). We also found significant inter-brood differences between morphogroups for each morphometric measurement (KW-ANOVA, P<0.001), because larvae of morphogroup A were bigger and had longer spines than those of morphogroup B (Table 1, Supplementary Table 1, 2). When the broods were arranged according to the mother CL, a pattern came out which relates the mother size and the larval morphometry by brood (Fig. 2). Thus, smaller females tended to produce larvae of morphogroup B, whereas larger females tended to produce larvae of morphogroup A.

To determine whether maternal body size can predict the size of the larvae, we performed linear regressions (Fig. 3). We found significant positive correlations between the CL of the female crab and each morphometric variable measured in the zoea I larvae (Table 2). This correlation was particularly strong between the CL of the zoea I and the mother (Pearson, r=0.879). This regression model predicted 77% of the variance and showed a good fit for the data (F=111.638, P<10^{-4}).

DISCUSSION

Variations in the larval morphology of decapod crustaceans have been accepted as a common phenomenon,
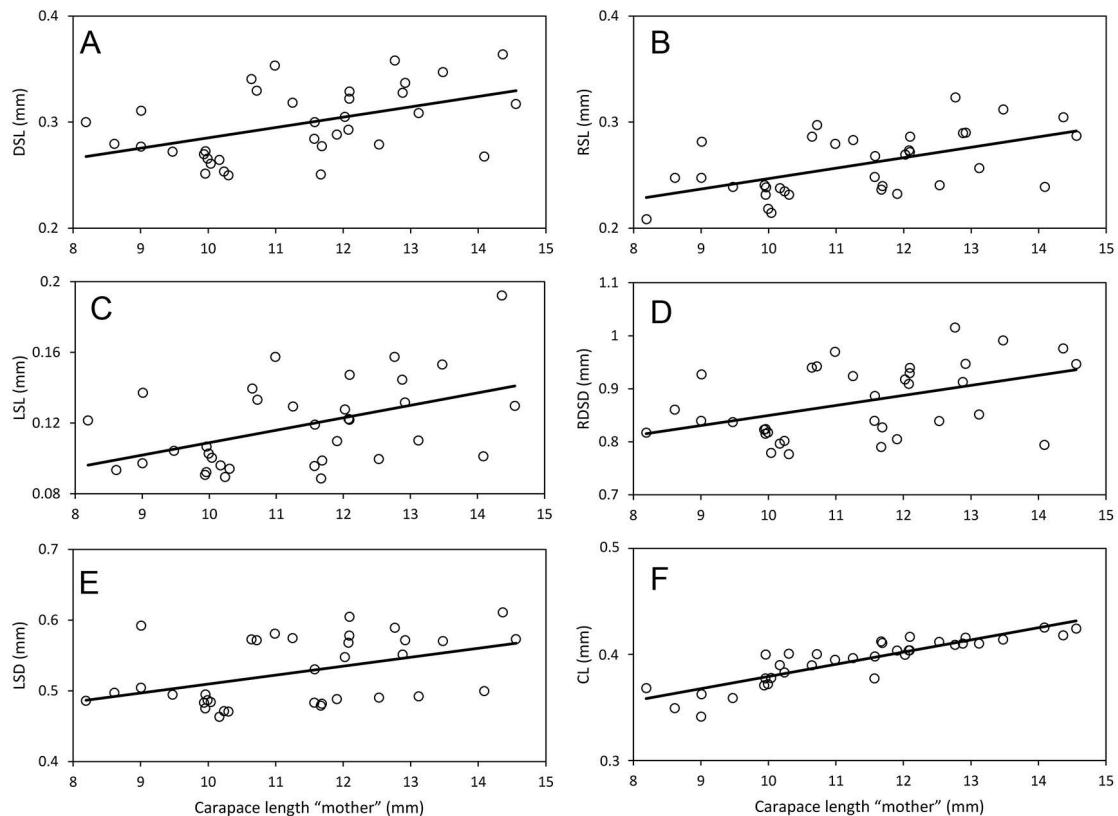
Fig. 3. – Relationship between mother size (carapace length) and larval size (zoea I) in *Hemigrapsus takanoi* measured using the rostral spine length (RSL), length of lateral spine of carapace (LSL), rostral-dorsal spine distance (RDSD), length of dorsal spine of carapace (DSL), lateral spine distance (LSD) and carapace length (CL). See Table 2 for the regression results.

though only a few experiments have tried to explain the mechanisms behind them. Using the first zoeal stage of *H. takanoi* hatched in the laboratory from ovigerous crabs collected at the same location and time, we found differences in the larval morphology between broods. Interestingly, our results also showed a consistent positive relationship between the size of the larvae and the crab mother.

Our results support the initial hypothesis that bigger mothers produce bigger larvae in the crab *H. takanoi*. Interestingly, previous results with a sibling species, *Hemigrapsus crenulatus*, reported that offspring size was not related to female body size (Urzúa et al. 2018). In this case, it is possible that the narrow size range (22-26 mm carapace width) of the female crabs used in that experiment masked the maternal influence on the progeny. In caridean shrimps, this pattern seems more consistent and it has been suggested that larger mothers may provision offspring more efficiently than smaller mothers (Oliphant and Thatje 2021). In fact, González-Ortegón et al. (2018) demonstrated the importance of diet on offspring provisioning. These authors found that larger female *Palaemon serratus* feed at higher trophic levels, which was related to the production of bigger eggs with higher content of carbon and nitrogen. In our case, it is not easy to find this diet-mediated relationship, but it is possible that bigger *H. takanoi* females can benefit from the high densities of crabs occurring in the sampling loca-

tion at Tokyo Bay. Thus, under these conditions there may occur a density-dependent regulation, in which the big females prey more frequently on juveniles and new recruits, as observed in other cannibalistic crab species (Eggleston and Armstrong 1995).

After hatching as larva, swimming to the upper layers of the water column is a key behaviour that facilitates the offshore exportation into the marine environment (Queiroga and Blanton 2005), since the zoea stages cannot develop under low-salinity conditions (Mingkid et al. 2006, Landeira et al. 2020). Few studies deal with the morphology and swimming during the larval stages of decapod larvae. However, Caracappa and Monroe (2019) reported interesting variability in the swimming behaviour among broods of blue crab *Callinectes sapidus* zoeae. For example, they found that larger zoeae also displayed faster vertical pathways, spent more time swimming upward, and spent more time in motion. Our data cannot support that bigger zoeae of *H. takanoi* can also perform a better transport offshore than smaller ones. However, swimming has a higher energy demand, and bigger larva can benefit from a better energy allocation due to a maternal influence. In any case, future experiments testing this size-swimming performance relationship would help to understand the maternal influence in this topic.

We also found a positive allometric relationship between the size of the larvae and the length of the cara-

pace spines. It is known that the rostral, dorsal and lateral spines of the carapace are involved in controlling the position and orientation of the zoea while swimming (Smith and Jensen 2015). In relation with this, Caracappa and Monroe (2019) found that zoeae with longer spines were also more likely to swim upward. In our case it is likely that longer spines could help keep zoeae oriented upward, maximizing the propulsive thrust while swimming vertically towards the upper layer of the water column. Moreover, the development of long spines may help to defend the larva from gape-limited planktivorous fishes (Bashevkin et al. 2020). Predation pressure seems to be an important driver for morphological plasticity, since fish kairomones may induce spine elongation during the development of crab larvae (Charpentier et al. 2017).

The present study adds new insights to understanding the morphological variability of crustacean larvae and how these patterns can be linked to maternal size. In the context of reproducibility of animal research, morphological differences between broods should be considered for future experimental designs.

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SUPPLEMENTARY MATERIAL

Table S1. – Summary of the size (carapace length, mm) of each *Hemigrapsus takanoi* female (n=35) and the morphological data of its batch of larvae (n=20 zoea 1) shown as mean values (µm) and standard deviation (SD). Measurements: DSL, length of dorsal spine of carapace; RSL, rostral spine length; LSL, length of lateral spine of carapace; RDSD, rostral-dorsal spine distance; LSD, lateral spine distance; CL, carapace length.

mother size	DSL mean	DSL SD	RSL mean	RSL SD	LSL mean	LSL SD	RDSD mean	RDSD SD	LSD mean	LSD SD	CL mean	CL SD
14.37	364.1	24.3	304.7	18.2	192.2	18.9	975.8	42.9	610.9	41.8	407.0	46.4
10.99	353.5	31.0	279.7	20.3	157.4	18.0	969.5	36.0	580.9	36.8	416.3	36.2
12.09	322.3	15.2	271.9	13.2	121.9	11.7	929.3	35.8	578.1	35.5	415.2	34.5
12.77	358.2	20.4	323.4	18.6	157.4	13.1	1015.2	64.4	589.1	36.8	413.6	40.8
10.64	340.6	17.5	286.3	17.5	139.5	15.7	939.8	43.9	572.7	39.1	392.9	41.7
12.92	337.1	20.3	290.2	21.4	131.6	14.7	946.9	44.4	571.5	25.3	399.5	29.9
13.48	347.3	20.6	312.1	20.1	153.1	13.6	991.0	30.2	570.3	28.9	421.6	36.2
12.10	328.9	19.9	286.3	19.8	147.3	18.7	939.5	48.5	604.7	26.2	404.2	42.8
9.01	310.9	19.9	281.6	20.7	137.1	21.5	927.0	44.3	592.2	25.3	394.4	37.0
11.25	318.4	18.0	283.2	18.0	129.3	10.3	923.8	40.8	574.6	12.7	402.3	28.6
14.56	317.2	17.2	287.1	16.9	129.7	16.3	946.5	44.8	573.0	14.0	422.2	41.0
10.72	329.7	16.5	297.3	18.4	133.2	11.4	942.2	42.0	571.5	20.9	395.2	27.0
12.88	327.7	21.6	289.8	22.9	144.5	13.4	912.5	48.1	551.2	40.2	394.9	37.9
12.02	305.1	15.7	269.5	12.0	127.7	16.4	917.6	36.8	547.7	22.8	423.0	34.5
11.58	300.0	23.6	268.0	22.9	119.1	9.2	886.3	63.2	530.5	26.0	398.4	49.2
12.08	293.0	16.8	273.4	17.6	122.3	13.1	909.0	34.3	568.0	18.5	422.6	26.5
9.94	269.9	19.4	240.6	9.1	90.6	13.2	822.7	34.2	483.2	22.4	392.1	30.1
12.53	278.9	13.1	240.6	13.7	99.6	10.4	839.1	36.0	490.2	12.6	399.5	28.8
8.61	279.7	15.7	247.7	15.2	93.4	10.9	860.5	35.2	497.3	20.3	383.2	31.0
9.01	277.0	15.9	247.7	16.8	97.3	10.6	839.5	32.4	504.3	21.2	394.8	34.4
9.47	272.3	14.9	239.1	14.3	104.3	13.6	837.1	36.8	494.5	32.9	405.8	17.3
9.99	269.9	21.7	218.4	15.3	102.7	8.7	817.6	31.1	486.7	19.2	389.3	30.0
13.12	308.6	16.8	256.6	11.4	110.2	11.8	851.2	34.7	492.2	12.6	385.9	36.7
11.91	288.3	26.8	232.4	27.0	109.8	14.9	804.7	39.0	488.3	23.2	364.0	34.4
11.69	277.3	17.6	239.8	11.6	98.8	11.7	827.0	44.1	481.6	17.2	389.8	31.5
11.57	284.4	14.3	248.4	11.7	95.7	10.7	839.5	26.0	483.2	25.2	386.6	23.9
10.04	260.9	21.7	214.5	16.8	100.4	11.4	778.9	41.6	484.0	22.3	383.5	40.6
10.30	250.0	12.8	231.6	11.1	94.1	9.7	776.6	43.9	470.7	23.2	374.9	37.3
10.17	264.5	15.1	237.9	8.4	96.1	8.9	796.5	25.8	463.3	36.8	374.1	27.7
9.96	272.7	14.6	238.7	11.2	106.6	10.0	823.8	45.0	494.9	15.5	392.5	40.1
8.19	300.0	20.1	208.6	22.0	121.5	24.9	817.2	31.0	485.9	28.0	388.6	26.2
14.09	267.6	11.3	239.1	9.4	101.2	7.6	794.1	37.8	499.6	22.6	397.5	35.9
9.96	251.6	10.4	231.6	8.7	92.2	11.7	815.2	33.4	475.0	20.8	392.0	29.6
11.67	250.8	13.0	236.3	9.5	88.7	10.8	790.2	24.2	478.9	14.0	383.1	24.2
10.24	253.5	12.5	234.8	10.9	89.5	10.0	801.6	34.8	471.1	30.2	393.3	24.7

Table S2. – Average values (µm) and standard deviation (SD) of the whole dataset obtained by measuring 20 larvae for each of the 35 *Hemigrapsus takanoi* females. Measurements: DSL, length of dorsal spine of carapace; RSL, rostral spine length; LSL, length of lateral spine of carapace; RDSD, rostral-dorsal spine distance; LSD, lateral spine distance; CL, carapace length.

DSL	RSL	LSL	RDSD	LSD	CL
298.0±37.8	259.7±33.3	118.2±27.9	874.4±78.7	526.0±53.6	397.0±37.1