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INTERPOPULATION COMPARISON OF REPRODUCTION OF THE ATLANTIC SHRIMP *HIPPOLYTE OBLIQUIMANUS* (CARIDEA: HIPPOLYTIDAE)

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ABSTRACT

The genus *Hippolyte* is represented by typically small shrimps with intriguing mechanisms of reproduction. In order to study possible variability in reproductive aspects among different populations, we conducted an exhaustive comparative study of *H. obliquimanus* from South (Brazil) and Central American (Costa Rica) waters. The study focuses on fecundity and reproductive output. Mean size of ovigerous females was significantly larger, and both mean reproductive output and mean fecundity were significantly higher in specimens from Costa Rica then in those collected in Brazil. Embryo volume was significantly smaller in the Costa Rican population, and in both populations embryos doubled their volume during embryogenesis. We discuss and compare our findings with the information available regarding *H. obliquimanus* and other hippolytid shrimp. The reproductive traits of both populations of *H. obliquimanus* show some important differences which may reflect adaptations to local environmental conditions, demonstrating a high plasticity of reproductive features of the species in Brazilian and Costa Rican waters.

KEY WORDS: Brazil, Costa Rica, fecundity, gonochoric, *Hippolyte obliquimanus*, reproductive output

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INTRODUCTION

Reproduction is one of the central features in the life history of any organism. Decapod crustaceans are not only highly diverse (Martin and Davis, 2001), but also exhibit an enormous variability of reproductive strategies which can be considered as strategic adaptations to optimize lifetime fitness (Hadfield and Strathmann, 1996; Yoshino et al., 2002).

Considerable efforts have been undertaken to document and study the intraspecific plasticity of reproductive features in marine (Jones and Simons, 1983; Clarke, 1987; Wehrtmann and Kattner, 1998; Hernáez, 2001; Lardies and Wehrtmann, 2001; Brante et al., 2003; Ituarte et al., 2006; Castilho et al., 2007; Lardies et al., 2008) and freshwater decapods (Mashiko, 1987; Yam and Dudgeon, 2005; Ituarte et al., 2007). The underlying mechanisms responsible for these variations are currently the subject of debate (Berrigan and Charnov, 1994; Blanckenhorn and Demont, 2004), but evolutionary forces as well as regional and local environmental conditions seem to exert an important influence in shaping life-history traits along a species' geographical distribution (Vernberg, 1962).

Species covering a wide range of geographical distribution are especially suited to study interpopulational variability (Wehrtmann and Kattner, 1998; Ituarte et al., 2006; Castilho et al., 2007; Mantelatto et al., 2010). The present study concerns *Hippolyte obliquimanus* Dana, 1852 with a known geographic distribution comprising the western Atlantic coast, from the Caribbean and along the north-south Brazilian coast from the states of Ceará to Santa Catarina (Fausto-Filho, 1975; Udekem d'Acoz, 1997; Young, 1998). As observed in other members of Hippolytidae, *H. obliquimanus* can be found in shallow water associated with both seagrass and seaweed habitats (Bauer, 2004). To date, apart from its taxonomy (see below), the biological data available deal with the records of parasites (Tsukamoto, 1981, as *H. curacaoensis* Schmitt, 1924), recruitment (Bauer, 1989, as *H. curacaoensis*), description of its sexual system (Terossi et al., 2008), ecological aspects such as population features (Terossi and Mantelatto, 2010), and larval morphology (Terossi et al., in press). However, published information concerning the embryo production of the species is restricted to isolated studies in Puerto Rico (Bauer, 1991, as *H. curacaoensis*) and southern Brazil (Mantelatto et al., 1999).

Udekem d'Acoz (1997) revised the current taxonomy of this species of the genus *Hippolyte*, and postulated, based only on adult morphology, that *H. curacaoensis* from Curaçao is a junior synonym of *H. obliquimanus* from Brazilian waters. Recent genetic studies, using 16Smt and COI genes, have corroborated this hypothesis (Terossi and Mantelatto, unpublished data). In view of these findings, *H. obliquimanus* is a species covering a wide geographical range (from 38°N to 28°S), which makes it an ideal candidate to study in a comparative way life-history patterns in different populations along its geographical distribution.

Here we analyze several reproductive features (embryo number and volume; reproductive output) of *H. obliquimanus* collected in Brazil and Costa Rica, and compare the results obtained with those available for the same species from other regions. Such an interpopulational approach might provide valuable insights into the possible plasticity in reproductive aspects of a species with a wide

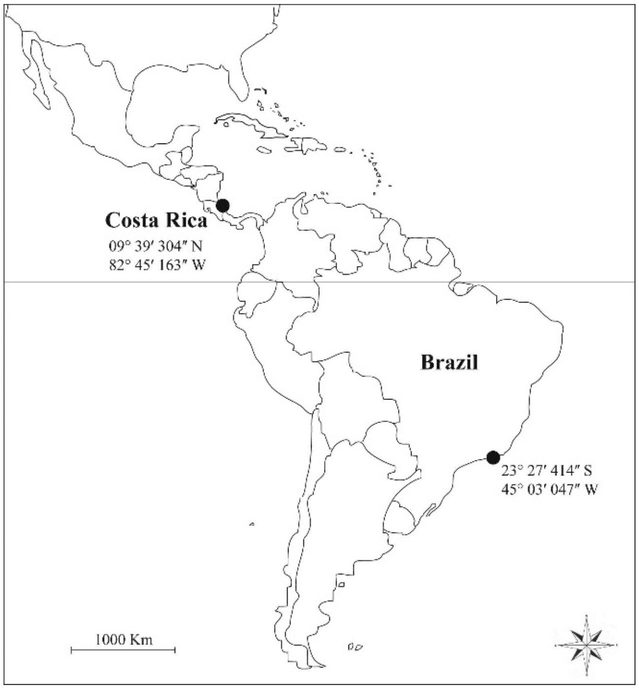

Fig. 1. The locations of the study sites in Costa Rica (Cahuita Beach, Limón) and Brazil (Itaguá Beach, Ubatuba, State of São Paulo).

geographical distribution, and the results will broaden our still-limited knowledge about the life-history traits of this small, but locally abundant, caridean shrimp. In addition, the information about the variability of reproductive traits constitutes an excellent complementary tool that can help to solve some of the existing taxonomic problems among many groups of decapods (Mathews et al., 2002; Mantelatto et al., 2009). Therefore, and considering the two populations of *H. obliquimanus* studied by us (Brazil and Costa Rica), here we test the hypothesis that: 1) ovigerous females attain larger sizes in the southern population, 2) embryo number increases and embryo volume decreases toward lower latitudes (Costa Rica), and 3) reproductive output decreases with increasing latitude.

MATERIALS AND METHODS

Ovigerous females were collected during 2007 (March, May and September) and 2009 (January) at Itaguá Beach (Ubatuba, State of São Paulo, Brazil), and monthly during 2002-2003 at Cahuita Beach (Limón, Costa Rica) (Fig. 1). In Brazil, specimens were obtained in a water depth of approximately one meter, from seaweed (*Sargassum* sp.), which was lifted by hand and stored in plastic bags. In the case of the material from Costa Rica, the females were obtained from seagrass meadows dominated by the turtle grass (*Thalassia testudinum*), using a push net. In both sampling locations, after the collection of the material, ovigerous females were separated and preserved immediately in ethanol (80%). Carapace length (CL) was measured from the posterior margin of the ocular orbit to the posterior margin of the carapace. The developing embryos were classified according to the criteria proposed by Wehrtmann (1990): Stage I – embryos with uniform yolk; Stage II – eye pigment visible; Stage III – eyes clearly visible, free abdomen. All embryos were detached from the females and counted; 15 embryos of each female were separated arbitrarily, and the smallest (a_1) and the largest axes (a_2) were measured to calculate the embryo volume (V) according to the formula $V = (\pi \times (a_1)^2 \times a_2)/6$ (Turner and Lawrence, 1979). These measurements were made under a stereomicroscope equipped with a calibrated ocular micrometer.

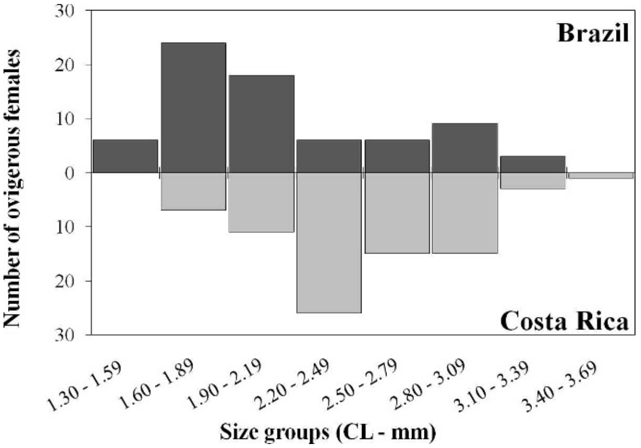

Fig. 2. *Hippolyte obliquimanus*. Size groups (carapace length: CL) of the ovigerous females collected in Costa Rica ($n = 78$) and Brazil ($n = 72$).

Since embryo loss during the incubation period is a well-known phenomenon in decapods (Kuris, 1991), only females with recently extruded embryos (Stage I), and with their pleopods filled with attached embryos were used to estimate fecundity. Data from females carrying embryos in Stage II and III were used only to analyze both the possible embryo volume increase and embryo loss during embryogenesis. We calculated the percentage of embryo volume increase and embryo loss among the stages by comparing the respective mean values per stage.

Females and their entire embryo mass were dried at 60°C for 24 h; they were then weighed on an analytical balance (AT 21 Comparator) with a precision of 1 μg. We calculated the reproductive output (RO, only females with embryos in Stage I) according to the formula proposed by Clarke (1987): RO = total dry weight of embryos/dry weight of female without embryos.

Statistical analyses were carried out using Statistic 8.0. The Kolmogorov-Smirnov test was applied to test for normality of samples. Analysis of variance (ANOVA) was used to compare the size of ovigerous females between populations. Regression analyses were applied to study the relation between carapace length and fecundity. Analysis of covariance (ANCOVA) was used to compare the embryo number and embryo volume between the sampling periods in Brazil (2007 and 2009) and Costa Rica (2002-2003), between the developmental stages of the embryos, and between the populations, always using CL as covariate. ANCOVA also was used to compare the embryo weight between the populations, using female weight as covariate. Voucher specimens were deposited at the Crustacean Collection of the Biology Department of FFCLRP, University of São Paulo, Brazil (CCDB/FFCLRP/USP, accession numbers: 2655 and 2656).

RESULTS

Size of Ovigerous Females

In total, 150 ovigerous females were analyzed, 72 from Brazil and 78 from Costa Rica. Both populations showed non-normal distribution (Brazil: K-S d = 0.20, Costa Rica K-S d = 0.17 - $P < 0.01$). Brazilian individuals ranged in size from 1.40 to 3.30 mm CL, those from Costa Rica varied between 1.70 and 3.00 mm CL. Mean female size was significantly larger in specimens from Costa Rica than in those collected in Brazil (Brazil: 2.09 ± 0.47 mm; Costa Rica: 2.43 ± 0.40 mm; ANCOVA on Ranks: H = 21.650; $P < 0.001$). We analyzed the size-frequency distribution of the ovigerous females from both populations (Fig. 2): in Brazil, most individuals (58%) were found in the size range from 1.60 to 2.10 mm CL, and 33% of the Costa Rican population measured between 2.20 and 2.40 mm CL.

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Table 1. *Hippolyte obliquimanus*. Fecundity and embryo volume of specimens from the Brazilian and Costa Rican populations (x̄ ± SD: mean ± standard deviation; Min and Max: minimum and maximum values).

	Brazil							Costa Rica						
		Fecundity			Embryo volume (mm^3)				Fecundity			Embryo volume (mm^3)		
Stages	*n*	x̄ ± SD	Min	Max	x̄ ± SD	Min	Max	*n*	x̄ ± SD	Min	Max	x̄ ± SD	Min	Max
I	36	141 ± 89	32	366	0.015 ± 0.004	0.009	0.021	43	187 ± 103	49	454	0.012 ± 0.002	0.007	0.017
II	21	94 ± 59	24	232	0.025 ± 0.006	0.018	0.035	14	121 ± 78	24	320	0.018 ± 0.004	0.012	0.024
III	15	70 ± 42	16	154	0.031 ± 0.007	0.021	0.042	21	118 ± 87	16	416	0.026 ± 0.006	0.016	0.041

Embryo Production

There was no significant difference regarding embryo production (number and volume) between the sampling periods in Brazil (ANCOVA, fecundity: slope $F = 0.10$, Y-intercept $F = 0.23$; embryo volume: slope $F = 1.23$, Y-intercept $F = 1.15$; $P > 0.05$) and Costa Rica (ANCOVA, fecundity: slope $F = 2.07$, Y-intercept $F = 1.68$; embryo volume: slope $F = 0.36$, Y-intercept $F = 2.34$; $P > 0.05$). Therefore, we decided to pool the data for further analyses.

Embryo number and volume with respect to the developmental stage of the embryos are shown in Table 1. In Brazil, the fecundity (Stage I) ranged between 32 and 366 embryos, and in Costa Rica between 49 and 454 embryos. In both populations, embryo production (Stage I) increased significantly with female size (Fig. 3a). The slopes of the two regression lines (Brazil – Costa Rica) were not significantly different ($F = 1.91$, $P = 0.17$). However, the Y-intercepts were significantly different ($F = 4.66$, $P = 0.03$), indicating that fecundity (Stage I) was significantly higher in specimens from Costa Rica compared to those collected in Brazil.

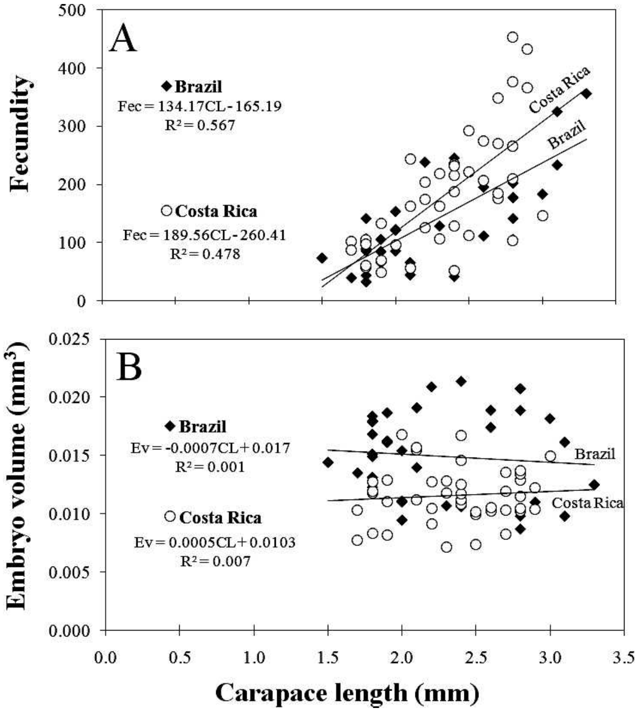

Fig. 3. *Hippolyte obliquimanus*. Linear regression between (A) carapace length (CL) and fecundity, and (B) embryo volume (Ev) for the two populations studied by us (Brazil: $n = 36$; Costa Rica: $n = 43$).

Volume of newly extruded embryos (Stage I) from the Brazilian and the Costa Rican populations ranged between 0.009-0.021 and 0.007-0.017 mm^3, respectively (Table 1). In both populations, embryo volume (Stage I) did not change significantly with female size (Fig. 3b). The slopes of the two regression lines were not significantly different ($F = 0.61$, $P = 0.44$). However, significantly different Y-intercepts ($F = 23.8$, $P < 0.001$) indicate that embryo volume (Stage I) was significantly higher in specimens from Brazil than in those collected in Costa Rica.

Embryo Volume Increase and Embryo Loss

In both populations, embryo volume was significantly different among the stages (see Table 2 for statistic values). Embryo volume increased during embryogenesis by 105.4% and 120.7% in the Brazilian and the Costa Rica populations, respectively. The largest volume increase occurred with 68.5% (Brazil) and 56.0% (Costa Rica) during the early embryo development (Stage I-II). At the end of the incubation period (Stage III), females carried significantly fewer embryos than at the beginning (Stage I) (see Table 2 for statistic values). During embryogenesis, females lost 50.0% (Brazil) and 36.8% (Costa Rica) of the initially produced embryos (Table 2).

Reproductive Output (RO)

The RO varied widely: between 0.03-0.21 and 0.08-0.31 in Brazil and Costa Rica, respectively. Mean RO was higher in Costa Rica (0.17 ± 0.05 SD) than in females from the Brazilian population (0.13 ± 0.06 SD). While the embryo weight in the Costa Rican population increased significantly with female weight (Fig. 4a, $P < 0.05$), we did not detect any significant relation between these variables in specimens from the Brazilian population (Fig. 4a). The slopes of the two regression lines (Brazil vs. Costa Rica) were significantly different ($F = 8.27$, $P < 0.001$). RO decreased with the size of ovigerous females in the Brazilian population (Fig. 4b).

DISCUSSION

The reproductive traits of both populations of *H. obliquimanus* showed some important differences which may reflect adaptations to local environmental conditions, resulting in a high plasticity of reproductive features of the species in Brazilian and Costa Rican waters.

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Table 2. *Hippolyte obliquimanus*. Values of embryo volume increase and embryo loss between stages of development in Brazilian and Costa Rican populations, and values of ANCOVA test.

		Embryo volume increase		Embryo loss	
Stages		Brazil	Costa Rica	Brazil	Costa Rica
I-II	%	68.5*	56.0*	32.8	35.4
	Slope	$F = 0.58$, $P = 0.45$	$F = 1.69$, $P = 0.20$	$F = 0.22$, $P = 0.65$	$F = 0.07$, $P = 0.79$
	Y- intercept	$F = 57.05$, $P < 0.001$	$F = 60.12$, $P < 0.001$	$F = 0.13$, $P = 0.72$	$F = 1.91$, $P = 0.17$
II-III	%	21.9*	41.4*	25.7	2.1
	Slope	$F = 0.02$, $P = 0.88$	$F = 0.01$, $P = 0.94$	$F = 0.13$, $P = 0.70$	$F = 0.33$, $P = 0.57$
	Y- intercept	$F = 6.23$, $P = 0.01$	$F = 13.29$, $P < 0.001$	$F = 1.78$, $P = 0.19$	$F = 2.26$, $P = 0.57$
I-III	%	105.4*	120.7*	50.0*	36.8*
	Slope	$F = 0.62$, $P = 0.44$	$F = 1.25$, $P = 0.27$	$F = 3.35$, $P = 0.07$	$F = 1.45$, $P = 0.36$
	Y- intercept	$F = 93.61$, $P < 0.001$	$F = 154.21$, $P < 0.001$	$F = 11.59$, $P = 0.01$	$F = 14.12$, $P < 0.001$

* Significant % of increase or loss, $P < 0.05$.

Ovigerous Females

There is a trend toward decreasing size of organisms with decreasing latitude (Atkinson and Sibly, 1997; Roy and Martien, 2001; Meiri and Dayan, 2003), which would confirm results on intraspecific latitudinal variation in decapods (Castilho et al., 2007). Nevertheless, our data for *H. obliquimanus* contradict this tendency: the mean size of embryo-bearing females from Costa Rica (09°N) was significantly larger than that from the Brazilian population (23°S). The available data (Table 3), however, cover only part of the known geographical distribution of the species (Udekem d'Acoz, 1997), and especially data regarding the size of ovigerous females from the northern part of its distribution are still lacking. A more complete set of size data over the entire geographical range of *H. obliquimanus* would allow us to study latitudinal trends in the reproductive ecology of this hippolytid shrimp (Bauer, 1992; Castilho et al., 2007).

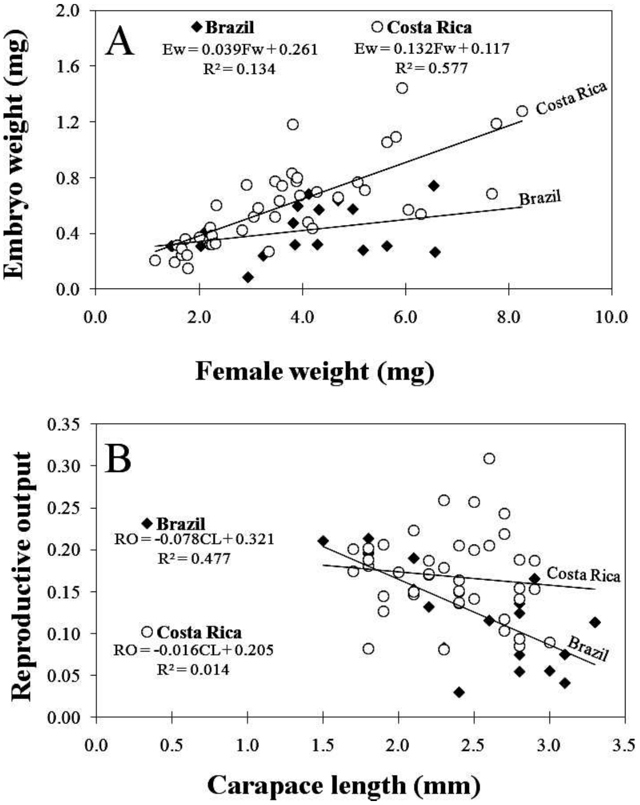

Fig. 4. *Hippolyte obliquimanus*. Linear regression between (A) female weight (Fw) and embryo weight (Ew), and between (B) carapace length (CL) and reproductive output (RO) for the two populations studied by us (Brazil: $n = 20$; Costa Rica: $n = 43$).

Embryo Production

Hippolytid shrimps are known to produce on average between 25 and 431 embryos (Corey and Reid, 1991). A few studies have reported on the fecundity of *H. obliquimanus* (Table 3), and average embryo production ranged between 64 and 187 embryos. Our data fit well into this range, and the 187 embryos of the Costa Rican population is so far the highest fecundity recorded for this species. Interestingly, Mantelatto et al. (1999) studied the embryo production of *H. obliquimanus* in the same area as our sampling location in Brazil, but reported a substantially lower mean fecundity (64 embryos) compared to the data from the Brazilian population studied by us (141 embryos). A possible explanation for such a conspicuous difference might be related to the fact that these authors included all females with embryos, including those which probably were just in the process of extruding their embryos and, thus, carried only one or two embryos (Mantelatto et al., 1999: see Fig. 2). In our study, only females with the pleonal chamber filled with embryos were used to estimate mean fecundity in the species, and this methodological difference probably resulted in a higher mean fecundity than that reported by Mantelatto et al. (1999). However, it is important to note that we found in our set of collected specimens in Brazil two females (CL = 1.8 mm) carrying only six-seven newly extruded embryos, but these were not used in our analyses. Therefore, it is important that future studies use only females with the pleonal chamber filled with embryos to obtain reliable values for comparable fecundity.

The mean embryo number of *H. obliquimanus* seems to increase with decreasing latitude, associated with a concurrent decrease of the mean embryo volume (Table 3). A similar trend of smaller but more numerous embryos toward lower latitudes has been mentioned for a number of decapods (Jones and Simons, 1983; Clarke et al., 1991; Lardies and Castilla, 2001; Lardies and Wehrtmann, 2001). Temperature is considered as an important environmental

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Table 3. Reproductive aspects of different species of the Family Hippolytidae from Americas.

Species	*N*	CL (mm) x ± SD	Fecundity x ± SD	Embryo volume (mm^3) x ± SD	*r*	Embryo volume increase (%)	Embryo loss (%)	Locality	Reference
Hippolyte nicholsoni Chace, 1972	4	0.96	25	0.018	0.97	ns	ns	U.S.A. (27°42′N, 80°34′W)	Corey and Reid 1991
Hippolyte obliquimanus Dana, 1852	43	2.43 ± 0.40	187 ± 103	0.012	0.69	120.7	36.8	Costa Rica (09°39′N, 82°45′W)	Present study
	131	2.4 ± 0.3	153 ± 70	0.005	0.87	–		Puerto Rico (18°29′N, 66°15′W)	Bauer 1991*
	36	2.09 ± 0.47	141 ± 89	0.015	0.73	105.4	50.0	Brazil (23°27′S, 45°03′W)	Present study
	108	4.7 ± 0.6**	64 ± 46	0.020	0.61	–	–	Brazil (23°30′S, 45°06′W)	Mantelatto et al. 1999
Hippolyte zostericola (Smith, 1873)	22	2.77	147	0.037	0.82	ns	50	U.S.A. (27°44′N, 80°24′W)	Corey and Reid 1991
	100	2.4 ± 0.26	104 ± 41	–		–	–	Mexico (18°30′N, 92°00′W)	Negreiros-Fransozo et al. 1996
Latreutes fucorum (Fabricius, 1798)	19	3.16	127	0.030	0.82	23	74	U.S.A. (27°42′N, 80°34′W)	Corey and Reid 1991
	98	2.3 ± 0.3	57 ± 24	0.012	077	–	–	Puerto Rico (18°29′N, 66°15′W)	Bauer 1991
Latreutes parvulus (Stimpson, 1866)	78	2.0 ± 0.2	59 ± 23	0.012	0.72	–	–		
Nauticaris magellanica (A. Milne-Edwards, 1891)	159	–	–	0.031-0.038		74-160	–	Chile (30-42°S, 71-73°W)	Wehrtmann and Kattner 1998
Thor manningi Chace, 1972	7	1.62	37	0.036	0.77	117	ns	U.S.A. (27°42′N, 80°34′W)	Corey and Reid 1991
Tozeuma carolinense Kingsley, 1878	52	1.9 ± 0.2	66 ± 27	0.026	0.55	–	–	Puerto Rico (18°29′N, 66°15′W)	Bauer 1991
	37	6.79	190	0.057	0.80	84	41	U.S.A. (27°44′N, 80°24′W)	Corey and Reid 1991
Trachycaris restricta (A. Milne-Edwards, 1878)	4	6.10	431	0.220	0.88	ns	ns	U.S.A. (18°N, 64°W)	

* As *Hippolyte curacaoensis* Schmitt, 1924.
** Including the rostrum.
ns: embryo increase and embryo loss were not significant; –: data not available.
N: number of ovigerous females with newly extruded embryos; CL: carapace length; x ± SD: mean ± standard deviation; V: embryo volume; r: correlation between carapace length (CL) and embryo number.

factor in shaping life-history traits in marine decapods (Orton, 1920; Wear, 1974; Sastry, 1983), and larger embryo size is generally associated with cooler temperatures (Thorson, 1950; Laptikhovsky, 2006). The observed difference between the embryo volume of *H. obliquimanus* between the Brazilian and the Costa Rican populations may be explained by the marked differences in local water temperatures: mean water-surface temperatures at the Brazilian sampling location are substantially lower (24.7 ± 1.5°C: Terossi and Mantelatto, 2010) than at Cahuita (27-30°C; Nielsen-Muñoz and Cortés, 2008). But again, it should be kept in mind that information concerning embryo size is lacking for the northern regions of the geographical distribution of *H. obliquimanus*, which limits any solid conclusion concerning intraspecific variability in life history traits in this widely distributed hippolytid shrimp.

Hippolytid shrimps produce generally small embryos (Bauer, 1991; Corey and Reid, 1991), and *H. obliquimanus* is no exception: our data on the average embryo volume of recently extruded embryos of *H. obliquimanus* are within the range of values reported in the literature (Table 3). However, the published embryo volume value for a Puerto Rican population (Bauer, 1991) is substantially smaller compared to all other reports for *H. obliquimanus* (Table 3). A simple error can be ruled out, because some embryos collected during Bauer's study (1991) in Puerto Rico were recently measured and their embryo volume calculated (R. Bauer, personal communication): the results coincided with those published by Bauer (1991). Thus, *H. obliquimanus* shows a high plasticity in its embryo volume. The underlying reasons for such intraspecific variability are unknown, but embryo size is often positively correlated with the duration of the embryonic development (Steele and Steele, 1975; Steele, 1977; Bauer, 1991). The available data for this hippolytid shrimp, maintained in the laboratory, confirm this correlation: the incubation period of *H. obliquimanus* in Brazil lasts around 10-12 days (Terossi et al., 2008) versus four days in the Puerto Rican population (Bauer, 1991). Data about the duration of the incubation period of the species in Costa Rica are not available. It might be speculated that the relatively short life span (< one year; Bauer, 1991) together with an intense predation pressure (Bauer, 1991) and relatively stable environmental conditions resulted in a continuous and intense production of extremely small embryos in the Puerto Rican population. However, it cannot be ruled out that the population studied by Bauer (1991) was comprised by a morphologically similar (identical?) but genetically distinct species (R. Bauer, personal communication). Future morphological and molecular work will be required

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Table 4. Reproductive output data available for different caridean families from Americas.

	Species	*N*	CL (mm)	Reproductive output	Locality	Reference
Alpheidae	*Alpheus armillatus* H. Milne Edwards, 1837	31	7.7-14.1	0.048-0.179	Brazil (23°44′S, 45°24′W)	Pavanelli et al. 2008
	Alpheus nuttingi (Schmitt, 1924)	17	8.3-18.6	0.039-0.123		Pavanelli et al. 2010
	Alpheus saxidomus Holthuis, 1981	35	7.8-29.5	0.44*	Costa Rica (5°32′N, 87°04′W)	Wehrtmann unpubl. data
	Betaeus emarginatus (H. Milne Edwards, 1837)	38	9.0-16.3	0.09*	Chile (39°49′S, 73°25′W)	Lardies and Wehrtmann 1997
	Betaeus truncatus (Dana, 1852)	34	8.36	0.07*	Chile (30°07′S, 71°26′W)	Lardies and Wehrtmann 2001
		24	7.11	0.13*	Chile (41°35′S, 72°43′W)	
		68	8.04	0.18*	Chile (42°25′S, 73°44′W)	
Hippolytidae	*Hippolyte obliquimanus* Dana, 1852	20	2.09	0.03-0.93	Brazil (23°27′S, 45°03′W)	Present study
		43	2.43	0.08-0.33	Costa Rica (09°39′N, 82°45′W)	
Pandalidae	*Austropandalus grayi* (Cunningham, 1871)	96	17.6	0.07-0.24	Chile (53°42′S, 70°57′W; 55°09′S, 67°01′W)	Wehrtmann and Lardies 1999
	Heterocarpus reedi Bahamonde, 1955	180	22.1-36.5	0.045-0.056	Chile (31°S, 71°W)	Wehrtmann and Andrade 1998

* No data available about the range value.
N: number of ovigerous females; CL: carapace length.

to solve the intriguing question of why the embryos of *H. obliquimanus* from Puerto Rico are so small compared to other populations of the same species.

The size of hatching larvae is related to embryo size (Strathmann, 1977). Since we detected significant differences in embryo volume between the two populations studied herein, we also expected to find differences in the hatchling size (Boddeke, 1982; Wehrtmann and López, 2003). However, we did not detect any difference in the mean size of the newly hatched zoeae of *H. obliquimanus* from both areas (Terossi et al., in press). Future comparative embryological studies might reveal why considerably larger eggs from *H. obliquimanus* in Brazil did not result in larger hatchlings when compared to those from Costa Rica.

Embryo Volume Increase and Embryo Loss

The embryos of *H. obliquimanus* more than doubled their volume during embryogenesis, which corroborates similar observations with other decapods (Wear, 1974; Lardies and Wehrtmann, 1996, 1997; Wehrtmann and Kattner, 1998; Hernáez and Palma, 2003), including those from hippolytid shrimps from Americas (Table 3): an increase of roughly 100% of the embryo volume has been reported for most of these species, with the exception of *Latreutes fucorum* (Fabricius, 1798) (23%, Bauer, 1991). The increase in embryo volume is typically related to the incorporation of large amounts of water (Pandian, 1970). These swelling embryos occupy more space than the initially produced embryos, and since space is considered as a limiting factor for brood production in decapods (Corey and Reid, 1991; Hines, 1982; Lardies and Wehrtmann, 2001), embryo loss might be expected in *H. obliquimanus*. Thus, it is not surprising that we detected embryo loss of up to 50% (Brazilian population) during the incubation period. Information on embryo loss in hippolytid shrimps is scanty, but the available data indicate values ranging from 41% to 74% (Table 3), which confirms similar findings from decapods with embryo-volume increases similar to that observed in *H. obliquimanus* (Balasundaram and Pandian, 1982; Corey and Reid, 1991; Lardies and Wehrtmann, 2001).

Reproductive Output

In decapods, the energy investment in embryo production constitutes roughly 10% of the female body weight (Hines, 1982, 1988; Hernáez and Palma, 2003; Miranda et al., 2006; Torati and Mantelatto, 2008). The obtained reproductive-output (RO) values for *H. obliquimanus* from the Costa Rican (0.17) and Brazilian populations (0.13) are slightly higher than this value, but similar elevated RO-values have been reported also for other caridean shrimps from Latin America (Table 4).

Clarke (1987) suggested that the RO of some hippolytid shrimps decreases with increasing latitude. Our data for *H. obliquimanus* confirm such a tendency: the mean RO value for the Costa Rican population (09°N) was higher than that from the Brazilian population (23°S) (Table 4). On the other hand, it has been suggested that lower temperatures allow a higher energy investment in embryo production (Woodward and White, 1981) compared to animals living in warmer waters (Díaz, 1980). Such a trend cannot be supported by our data, because both the mean embryo number and RO were significantly higher in the Costa Rican population. However, intraspecific variability in reproductive features cannot be explained by latitude alone; regionally and locally varying environmental conditions may contribute significantly to the observed plasticity in the reproductive biology of decapods (Kyomo, 2000; Bas et al., 2007; Castilho et al., 2007). Moreover, for a more-solid analysis of the reproductive features of *H. obliquimanus*, additional information from other locations along the known geographical distribution of the species is required.

In the Brazilian population of *H. obliquimanus*, the energy allocation for embryo production decreased with increasing female size (Fig. 4b). To the best of our knowledge, this is the first case where such a relationship between increasing female size and decreasing RO has

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been detected in decapods. In general, the energy invested in the production of embryos is independent of the female body size, e.g., in *Heterocarpus reedi* Bahamonde, 1955 (Wehrtmann and Andrade, 1998) and *Austropandalus grayi* (Cunningham, 1871) (Wehrtmann and Lardies, 1999). Thus, further analysis are needed to verify the observed relationship of decreasing RO with increasing female size in the Brazilian population, and to search for the causal factors responsible for this unusual pattern.

In conclusion, our results demonstrated a high plasticity in embryo production of *H. obliquimanus* and confirmed our working hypothesis that embryo number increases and embryo volume decreases toward lower latitudes (Costa Rica), and that the energy allocation for reproduction (RO) decreases with increasing latitude. However, our findings did not support the hypothesis that the size of ovigerous females increases with increasing latitude (Table 3). This aspect needs further attention and confirms that several reproductive features of *H. obliquimanus* (and probably many other hippolytid species) are still unclear. A more complete subset of individuals of the same species from other areas is needed for a comprehensive examination of the reproduction in this species. The outcome of the present study should encourage future analysis of reproductive plasticity in congeners.

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