Journal of
Crustacean Biology
A quarterly of The Crustacean Society for publication of research on the biology of Crustacea & marine arthropods

EGG PRODUCTION OF THE COMMERCIALLY EXPLOITED DEEPWATER SHRIMP, *HETEROCARPUS VICARIUS* (DECAPODA: PANDALIDAE), PACIFIC COSTA RICA

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ABSTRACT

The pandalid *Heterocarpus vicarius* is a deepwater shrimp, commercially exploited along the Pacific coast of Costa Rica and neighboring countries. The constant decrease of commercial landings in recent years has provoked an increasing concern about the sustainability of this deepwater resource. To facilitate an adequate management of *H. vicarius*, we examined 240 ovigerous females collected between 2004 and 2007. Females ranged in size between 29.4 and 45.4 mm carapace length and carried on average 15,008 newly-extruded eggs. To our best knowledge, the maximum of 33,549 eggs for *H. vicarius* is the highest number so far reported for any pandalid species. During embryogenesis, the average number of eggs decreased by 46.9%, while the average egg volume increased by 53.3%. Average egg volumes were statistically different between early (Stage I: 0.045 mm^3) and late (Stage III: 0.069 mm^3) development. The egg mass volume comprised on average 17.8% of the dry weight of ovigerous females (Stage I). Although fecundity increased significantly with female size, the relation between reproductive output (Stage I) and female size was not significant. We compare our results with those from other pandalids, especially with the closely-related *H. reedi* from Chilean waters.

KEY WORDS: Costa Rica, deepwater fishery, egg loss, fecundity, *Heterocarpus*, reproductive output

DOI: 10.1651/10-3400.1

INTRODUCTION

During the last decades, and along with the global decline of the resources in shallow coastal waters, fishing efforts have been expanded to offshore areas and into deeper water (Pauly et al., 2005; Morato et al., 2006). The fact that the mean depth of bottom fish catches increased from around 103 m in the early 1950s to 145 m in 2001 can be interpreted as a consequence of this trend (Morato et al., 2006), as well as searching for new resources to exploit. Deepwater species, however, are considered to have high longevity, slow growth, late maturity, and low fecundity (Young and Eckelbarger, 1994; Koslow et al., 2000). All these life history features make them especially vulnerable to exploitation. Therefore, solid knowledge about their ecology is of special importance for the development of adequate management measures toward a sustainable fishery of these resources (Polidoro et al., 2008).

Several decapod species from deepwater habitats are the target of commercial fisheries along the Pacific coast of Latin America (see Arana et al., 2003; Wehrtmann and Echeverría-Sáenz, 2007; Arana et al., 2009; Wehrtmann and Nielsen-Muñoz, 2009). Among carideans, there is an important body of literature on the biology and fishery of the nylon shrimp, *Heterocarpus reedi* Bahamonde, 1955 from Chilean waters (Arana-Espina and Nakanishi-Campos, 1971; Pérez and Defeo, 2003; Pérez, 2005). More recently, several authors (Arana et al., 2003; Arana and

Ahumada, 2006; Barriga et al., 2009) have provided information on the ecology of the red royal shrimp, *Haliporoides diomedeae* (Faxon, 1893), and the razor shrimp, *Campylonotus semistriatus* Bate, 1888. In addition, Hendrickx (1996, 2001, 2003) and Hendrickx et al. (1998) reported on the presence, abundance, and distribution of deepwater decapod shrimp in the Gulf of California. However, and despite the fact that there is an ongoing and important fishery on deepwater shrimp along the Pacific coast of Central America, there is almost no published information concerning neither the fisheries (exceptions: Wehrtmann and Echeverría-Sáenz, 2007; Wehrtmann and Nielsen-Muñoz, 2009), nor the ecology of these species.

Heterocarpus vicarius Faxon, 1893 is a pandalid known to occur from the Gulf of California to the coast of Peru (Hendrickx et al., 1998). As far as we know, the species is commercially exploited only along the Pacific coast of Costa Rica and neighboring countries (see also Holthuis, 1980). The shrimp inhabits mainly waters ranging between 200 and 400 m depth, which is the depth range where in Costa Rica the commercially exploitation takes place (Wehrtmann and Nielsen-Muñoz, 2009). However, this species has been reported also from substantially deeper (up to 1454 m, caught in traps; Hendrickx, 1995) and shallower waters (73 m; Holthuis, 1980). According to the results of Wehrtmann and Echeverría-Sáenz (2007) who studied the decapod fauna associated with the fishery for *H.*

vicarius in Costa Rica, this species co-occurs, among others, along with decapods such as *Solenocera agassizi* Faxon, 1893 (Solenoceridae), *Plesionika trispinus* Squires & Barragán, 1976 (Pandalidae), *Pleuroncodes* sp. (Galatheidae), and *Cancer johngarthi* Carvacho, 1989 (Cancridae). Considering the period between 1995 and 2006, reported landings of *H. vicarius* in Costa Rica peaked in 1996 with 539,101 kg; however, during the recent years landings decreased constantly (Wehrtmann and Nielsen-Muñoz, 2009), which has provoked an increasing concern about the sustainability of this commercially exploited deepwater resource.

Since accurate information regarding fecundity is a primary consideration for the adequate management of any crustacean fishery (Caddy, 1989), the aim of this study is to provide basic information concerning the reproductive biology of *H. vicarius* from the Pacific coast of Costa Rica, and to compare the obtained fecundity data with those reported for other pandalid shrimp species.

MATERIALS AND METHODS

For the collection of the material, monthly scientific fieldtrips on board of commercial shrimp trawlers (for technical details: Wehrtmann et al., 2010) were conducted between January 2004 and December 2007. Depth varied between 192 and 350 m. Samples of egg bearing females of *H. vicarius* were separated on board from the catches (three to five 20-min hauls per month) and transported frozen to the laboratory of the Universidad de Costa Rica in San José.

Carapace length of the females (CL; from the posterior edge of the orbital arch to the posterior midpoint of the carapace) was measured using a caliper with a precision of 0.1 mm. All eggs were removed, counted, and categorized according to criteria proposed by Wehrtmann (1990).

> Stage I: eggs recently produced; uniform yolk, and no eye pigments visible
>
> Stage II: eye pigments barely visible
>
> Stage III: eyes clearly visible and fully developed, pleon free.

The length and width of a minimum of 10 and a maximum of 30 eggs per female was measured with a Leica CME microscope, equipped with a calibrated ocular micrometer. Individual egg volume (EV) was calculated using the formula for oblate spheroids (Turner and Lawrence, 1979). To estimate the egg mass volume (EMV), the mean egg volume was multiplied by the total number of eggs carried by the female. The reproductive output (RO) was determined for females carrying recently-extruded eggs (Stage I), according to the formula RO = weight of the total dry egg mass of the female/weight of the dry female without eggs *100 (Clarke, 1987).

Total number of eggs was estimated by separating three sub-samples of the egg mass of each female. These sub-samples were photographed, and the eggs were counted directly from the photo (one photo/sub-sample) using the software UTHSCSA Image-tool (University of Texas Health Science Center of San Antonio, Texas; http://ddsdx.uthscsa.edu/dig/itdesc.html). A fourth sample contained the remaining eggs. All the eggs were weighed with an analytical balance (using pre-weighed aluminum foil containers); subsequently, they were dried (60°C for 24 h) and weighed again. Dry weight of each sub-sample was divided by the number of eggs previously counted to calculate the weight of an individual egg; an average of the individual egg weight from the three sub-samples was calculated. This average was used to estimate the number of eggs of the fourth sub-sample with the remaining eggs. The total number of the entire egg mass per female is comprised by the three counted sub-samples plus the number of eggs estimated for the fourth sub-sample. Percent egg water content was calculated by the following formula: (egg wet weight – egg dry weight) *100/egg wet weight.

Analyses of variance (ANOVA) were applied to detect possible differences in egg volume and fecundity with respect to stages of embryonic development. Simple regressions were used to analyze the relation of egg production and egg mass volume to female size. We also constructed 1 mm size intervals to relate egg loss during embryogenesis to female size, using simple regressions.

RESULTS

Females

The size of ovigerous females of *H. vicarius* (N = 17,273) ranged from 20 to 49 mm CL (I.S. Wehrtmann, unpublished data). Females analyzed in the present study for egg production (N = 240) varied in size between 29.4 and 45.4 mm CL; the majority (80%) of them ranged from 33 to 39 mm CL.

Egg Production

The average number of eggs in Stage I was 15,008 ± 6,350, with minimum and maximum counts of 5,147 and 33,549, respectively (Table 1). Mean egg number was significantly different between the three embryonic stages, being highest in Stage I and lowest in Stage III ($F = 27.85$; $d.f. = 236$; $P = 0.0000$). The number of produced eggs increased significantly ($F = 84.47$; $d.f. = 95$; $P = 0.0000$; $r^2 = 47.33$) with female size (Fig. 1).

During embryogenesis, the average number of eggs decreased by 46.9% between stages I and III. Egg loss was similar between Stage I-II (27.4%) and Stage II-III (26.8%), and was more pronounced in larger females ($F = 10.39$; $d.f. = 7$; $P = 0.02$; $r^2 = 57.3$; Fig. 2).

Egg volume was significantly different between the stages of embryonic development. Recently-produced eggs (Stage I) had a mean volume of 0.045 ± 0.014 mm^3, while eggs close to hatching (Stage III) measured on average 0.069 ± 0.023 mm^3 ($F = 1781$; $d.f. = 11,809$; $P = 0.0000$), which corresponds to an egg volume increase during the incubation period of 53.3%. The volume increase was more pronounced during the first part of egg development (Stage I-II: 30.6%) than during later embryogenesis (Stage II-III: 17.6%).

Average egg mass volumes (EMV) were statistically different between developmental stages ($F = 5.17$; $d.f. = 232$; $P < 0.05$). Average EMV was statistically not different between Stage I (655 ± 347 mm^3) and Stage II (576 ± 295 mm^3), or Stage II-III, but we detected significant differences between Stage I-III. At the end of the embryogenesis (Stage III: 495 ± 286 mm^3), average EMV was 24.4% lower than directly after egg extrusion (Stage I). The maximum egg mass volume (2722 mm^3) was found for a female (CL = 39 mm) carrying eggs in Stage II.

Water content of the eggs increased significantly ($F = 80.38$; $d.f. = 244$; $P = 0.0000$) during embryogenesis, from $60 \pm 12\%$ (Stage I) to $79 \pm 8\%$ (Stage III; Table 2).

Reproductive Output

The egg mass volume comprised on average 17.8% of the dry weight of females with eggs in Stage I. Based upon dry weight, the RO of *H. vicarius* was 0.178 ± 0.06, varying between 0.06 and 0.34. Although the number of produced eggs increased significantly with female size, we did not detect a statistically significant relation between RO (in

Table 1. Comparison of reproductive parameters of *Heterocarpus vicarius* from Pacific Costa Rica during the three stages of embryogenesis. N = number of observations; SD = standard deviation; Min = minimum; Max = maximum.

|	Stage I					Stage II					Stage III				
	N	Mean	SD	Min	Max	N	Mean	SD	Min	Max	N	Mean	SD	Min	Max
CL (mm)	100	36.3	2.7	30.1	45.4	70	35.7	2.8	29.4	44.4	70	36.2	2.5	30.7	41.6
Number of eggs	96	15,008	6462	5147	33,549	70	10,899	6811.9	3127	32,629	70	7976	4617	1061	25,412
Egg volume (mm³)	184	0.045	0.014	0.003	0.158	129	0.059	0.018	0.010	0.226	115	0.069	0.023	0.002	0.258
Egg mass volume (mm³)	96	654.8	346.7	208.0	1611.5	70	576.2	294.8	143.6	1336.3	70	495.2	285.9	99.1	1281.3
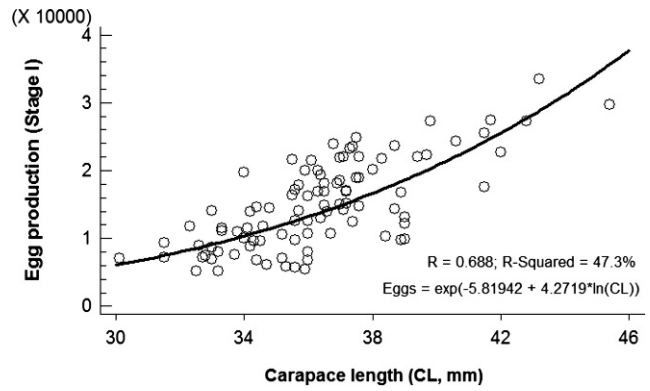
Fig. 1. *Heterocarpus vicarius* from Pacific Costa Rica: relation between egg production and female carapace length; $N = 96$.

Stage I) and female size (CL) ($F = 2.58$; $d.f. = 98$; $P > 0.05$; Fig. 3).

DISCUSSION

Egg Number

The deepwater shrimp *H. vicarius* can be considered as a decapod producing a high number of eggs. In fact, to the best of our knowledge, the maximum of 33,549 eggs for *H. vicarius* is the highest number so far reported for any pandalid species (Table 3). Fecundity data of *H. vicarius* are only comparable to those of *H. reedi* from Chile. However, even this similar-sized species produces in Stage I on average just 10,836 eggs (Wehrtmann and Andrade, 1998), which is substantially less (38.5%) than *H. vicarius* (average: 15,008 eggs). On the other hand, Wehrtmann and Andrade (1998) reported a maximum fecundity of 27,237 eggs for *H. reedi*, which is relatively close to the value we found for *H. vicarius* (Table 1). It is assumed that the smaller size of the females analyzed by Wehrtmann and Andrade (1998) for their study on *H. reedi* (from 22.1 to 36.5 mm CL) may have contributed to the differences
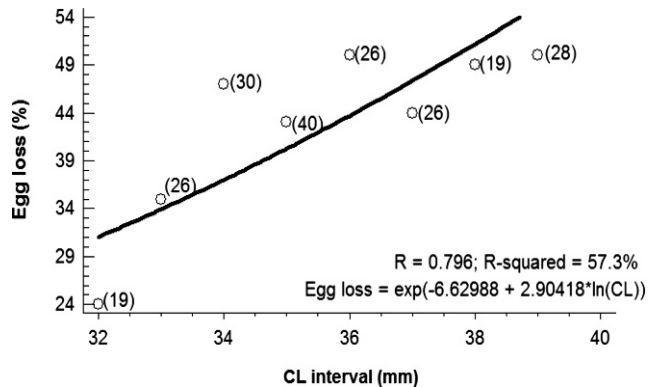

Fig. 2. *Heterocarpus vicarius* from Pacific Costa Rica: relation between egg loss during embryogenesis and female size (average values per 1 mm carapace length – intervals; 32 represents females smaller than 32 mm CL, 40 represents females with CL > 40. Values indicated by each data point refer to the number of individuals examined per size interval. $N = 233$.

Table 2. *Heterocarpus vicarius* from Pacific Costa Rica: mean (with standard deviation, ± SD) dry weight and water content of females and egg mass; N = number of observations.

	Stage I; N = 100		Stage II; N = 70		Stage III; N = 70	
	Mean	SD	Mean	SD	Mean	SD
Females						
Dry weight (g)	1.611	0.527	1.598	0.506	1.718	0.465
Water content (%)	79.1	3.2	80.3	2.5	80.8	2.3
Egg mass						
Dry weight (g)	0.284	0.123	0.1705	0.089	0.1178	0.1168
Water content (%)	59.9	12.5	73.1	8.4	78.9	7.8

observed in the fecundity of these two pandalid shrimp from Pacific Latin America.

Egg Volume

Average egg volume of *H. vicarius* is four times smaller than that of *H. reedi* (Wehrtmann and Andrade, 1998) from Chile (0.045 ± 0.014 mm^3 versus 0.179 ± 0.0189 mm^3, respectively). Since the size of the eggs is related to the size of the hatching larvae (Strathmann, 1977; Boddeke, 1982; Wehrtmann and López, 2003), it is speculated that the Zoea I of *H. reedi* is substantially larger than the hatchlings from *H. vicarius*. Such data, however, are still not available for these species.

It is generally assumed that larger eggs imply longer incubation periods (Mashiko, 1987; Bauer, 1991). Thus, it seems reasonable to presume that embryogenesis in *H. reedi* lasts longer that in *H. vicarius*. The strategy to produce a large amount of relatively small eggs may be interpreted as an adaptation of *H. vicarius* to increase lifetime egg production by decreasing the duration of the incubation period. However, additional information about growth patterns, longevity, and reproductive periodicity are needed to substantiate the above-mentioned speculation.

During embryogenesis, eggs of *H. vicarius* increased its volume by 53.3%, while egg number decreased by 46.9% during the incubation period. These data seems to indicate a certain balance between egg volume increase and egg loss, which can be corroborated by the fact that the EMV was statistically not different between Stage I and Stage II, or between Stage II and III. The lower EMV in Stage III suggests that brood mortality was more pronounced at the end of the incubation period, when eggs incorporate substantial amounts of water to facilitate the hatching process (Nagao et al., 1999; Pinheiro and Hattori, 2003; García-Guerrero and Hendrickx, 2006). The observed value for egg volume increase in *H. vicarius* is similar to that reported for *H. reedi* (57.4% and 48.8% in living and iced females, respectively: Wehrtmann and Andrade, 1998), but considerably lower than in *Austropandalus grayi* (Cunningham, 1871) from South America (88.4%; Wehrtmann and Lardies, 1999). The underlying reasons for these interspecific differences remain to be explored.

Egg loss during the incubation period is a well-known phenomenon in decapods (Balasundaram and Pandian, 1982). The swelling egg mass temporarily outgrows the attachment area, which facilitates the mechanical abrasion of the outer embryos (Kuris, 1991; Wehrtmann and Lardies, 1999). Reported values for brood mortality in decapods vary between 4 and 75% (Kuris, 1991; Brillon et al., 2005), and our values for *H. vicarius* are in the upper half of this range. Interestingly, the calculated percentage of egg loss during the incubation period was practically identical when comparing the data for *H. reedi* (47%: Wehrtmann and Andrade, 1998) and *H. vicarius* (46.9%: present study).

Considering that both species of *Heterocarpus* occur in similar habitats and have been reported from similar depths (Andrade and Báez, 1980), the striking differences in both egg numbers and egg volume seem to indicate different strategies concerning egg production: while the species inhabiting southern latitudes (*H. reedi*) produces fewer but larger eggs, *H. vicarius* from lower latitudes produces small but numerous eggs. Such a trend in egg production corroborates the hypothesis of increasing egg size and decreasing egg numbers toward higher latitudes (Thorson, 1950; Clarke, 1992; Lardies and Castilla, 2001), and this tendency has been also documented for other carideans (Clarke et al., 1991; Gorny et al., 1992; Wehrtmann and Kattner, 1998; Lardies et al., 2008; Terossi et al., 2010)

Egg Mass Volume

Despite the fact that *H. vicarius* produces considerably more eggs than *H. reedi*, the mean EMV of the latter species (Stage I: 1480.1 mm^3; Wehrtmann and Andrade, 1998) was substantially higher compared to that of *H. vicarius* (Stage I: 655 mm^3). We assume that this conspicuous difference is related to the four-time smaller egg size produced by females from *H. vicarius*.

Reproductive Output

Since the EMV of *H. reedi* is substantially higher than that of *H. vicarius*, it might be expected that the RO is also higher in the former species. However, this is not the case: the average RO of *H. vicarius* (0.18) is three times as high as that of *H. reedi* (Wehrtmann and Andrade, 1998: 0.06). The explanation for this surprising result is probably related
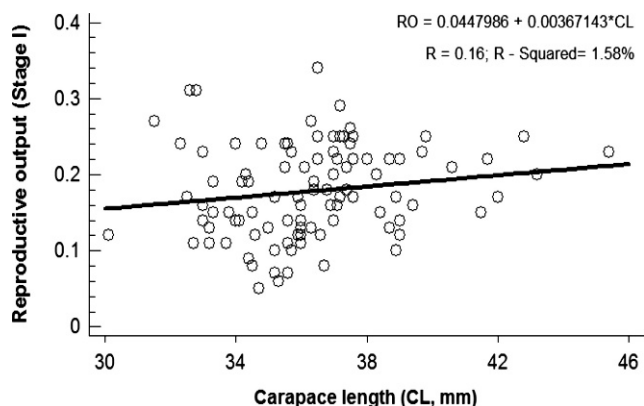

Fig. 3. *Heterocarpus vicarius* from Pacific Costa Rica. Relation between reproductive output and female size, including exclusively females carrying recently-produced eggs (Stage I). N = 99.

Table 3. Range of fecundity and size (carapace length, CL) of ovigerous females in different pandalid shrimp species. [1] These numbers refer to a study that used living instead of frozen females. [2] Values estimated from Allen (1965; Fig. 4). [3] Mean absolute individual fecundity. n.a. Information not available from abstract.

Species	Range of spawned eggs per species	Size range (CL, mm)	Study area	Reference
Austropandalus grayi (Cunningham, 1871)	50–1858	10.7–24.6	Magellan Region, South America	Wehrtmann and Lardies (1999)
Dichelopandalus bonnieri Caullery, 1896	162–2639	11–21.8	Isle of Man, Irish Sea	Al Adhub and Bowers (1977)
Heterocarpus reedi Bahamonde, 1955	1044–27,237[1]	22.1–36.5	Northern Chile	Wehrtmann and Andrade (1998)
Heterocarpus vicarius Faxon, 1893	1617–33,549	29.4–45.4	Pacific Costa Rica	Present study
Pandalus borealis Krøyer, 1838	600–4900	20–30.9	Synopsis of FAO	Shumway et al. (1985)
Pandalus borealis Krøyer, 1838	958–2554	n.a.	Western Bering Sea	Andronov (2003)
Pandalina brevirostris (Rathke, 1843)	200–1000	5.5–9.2[2]	Northumberland coast, England	Allen (1965)
Pandalus goniurus Stimpson, 1860	1377–2220[3]	N/A	Western Bering Sea	Andronov (2004)
Pandalus gracilis Stimpson, 1860	44–168	7.9–14.9	Southeastern Korea	Oh et al. (2008)
Pandalus montagui Leach, 1814	200–3000	9.5–19.0	Northumberland coast, England	Allen (1966)
Pandalus kessleri Czerniavski, 1878	192–918	28–45	Southern Kuril Islands	Dautov et al. (2004)
Pandalus platyceros Brandt, 1851	1393–3162	33.5–41.4	Synopsis of FAO	Butler (1967)
Parapandalus narval (Fabricius, 1787)	200–7500	7.9–18.7	Rhodos Island, Greece	Thessalou-Legaki (1992)
Plesionika edwardsii (Brandt, 1851)	920–19,792	15–29	Western Mediterranean	Possenti et al. (2007)
Plesionika martia (A. Milne-Edwards, 1883)	618–6244	9.3–29.1	Eastern Ionian Sea	Chilari et al. (2005)

to the egg size, which is substantially larger in the South American species of *Heterocarpus*. Decapod eggs contain large amounts of water, which is considered as the major constituent of developing eggs (Pandian, 1970; Valdés et al., 1991; Wehrtmann and Lardies, 1999). However, the RO-values in both *H. reedi* (Wehrtmann and Andrade, 1998) and *H. vicarius* (present study) are based on dry weight, thus eliminating differences regarding the water content of the eggs. Therefore, the results seems to indicate that *H. vicarius* invest more energy in the production of eggs than *H. reedi*, but the latter species produces larger eggs containing more water compared to those extruded by *H. vicarius*.

Our knowledge about the ecology of deepwater decapods is still rather limited, while the commercial fleets continue exploiting these highly profitable deepwater resources (Latin America: Arana et al., 2009; Central America: Wehrtmann and Nielsen-Muñoz, 2009). The present study provides valuable information regarding fecundity and other aspects of the reproductive biology of *H. vicarius*, which can be used for management purposes and fishery regulations. On the other hand, it is noteworthy that even two closely related species such as *H. vicarius* and *H. reedi* show considerable differences in their reproductive strategies, and such differences must be taken into account when aiming for an adequate management of these resources.

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