Embryonic development and duration of incubation period of tropical intertidal hermit crabs (Decapoda, Anomura)

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ABSTRACT. The description of the embryonic development of the hermit crabs *Clibanarius antillensis* Stimpson, 1859, *C. sclopetarius* (Herbst, 1796), *C. vittatus* (Bosc, 1802), and *Pagurus criniticornis* (Dana, 1852) and preliminary observations on the development of *Pagurus brevidactylus* (Stimpson, 1858) and *Paguristes tortugae* Schmitt, 1933 were done. The analysis of the external morphology of the embryos of the studied species allowed the identification of seven stages: Stage 1, Zygote and cleavage; Stage 2, Homogeneous mass (advanced cleavage and gastrulation); Stage 3, Initiation of the germinal disc (yolk-free area); Stage 4, Percentage of yolk-free area from 5% to 50-70%; Stage 5, Eye pigmentation (comma-shape) and heart beating; Stage 6, Percentage of yolk-free area from 70-80% to 95%) and eye development to a darkened irregularly-rounded shape; Stage 7, Zoea visible and hatching. Despite all stages were recorded in all species, interespecific differences were recorded in relation to zygote size and embryo color; cleavage, absolute and relative developmental time, and moment eye pigmentation appeared. Such morphological differences may be associated to variations in the yolk amount and composition and reveal different reproductive strategies at least between *P. criniticornis* and all studied species of *Clibanarius*.
KEY WORDS. *Clibanarius*; life history strategies; *Pagurus*; reproduction.

RESUMO. **Desenvolvimento embrionário e duração do período de incubação de caranguejos ermitões tropicais do entremarés (Decapoda, Anomura).** A descrição do desenvolvimento embrionário dos ermitões *Clibanarius antillensis* Stimpson, 1859, *C. sclopetarius* (Herbst, 1796), *C. vittatus* (Bosc, 1802) e *Pagurus criniticornis* (Dana, 1852) e observações preliminares sobre o desenvolvimento de *Pagurus brevidactylus* (Stimpson, 1858) e *Paguristes tortugae* Schmitt, 1933 foram realizadas. A análise da morfologia externa dos embriões das espécies estudadas permitiu a identificação de sete estágios: Estágio 1, Zigoto e clivagem; Estágio 2, Massa homogênea (clivagem avançada e gastrulação); Estágio 3, início da formação do disco germinal (área livre de vitelo); Estágio 4, Porcentagem da área livre de vitelo de 5% a 50-70%; Estágio 5, Pigmentação do olho (forma de vírgula) e batimentos cardíacos; Estágio 6, Porcentagem da área livre de vitelo de 70-80% to 95%) e desenvolvimento do olho para uma forma escurecida e irregularmente arredondada; Estágio 7, Zoea visível e eclosão. Embora todos os estágios tenham sido registrados em todas as espécies, diferenças interespecíficas foram registradas com relação ao tamanho do zigoto e coloração do embrião, clivagem, tempo de desenvolvimento absoluto e relativo e momento em que a pigmentação do olho apareceu. Estas diferenças morfológicas podem estar associadas variações na quantidade e composição do vitelo e revelam diferenças nas estratégias reprodutivas pelo menos entre *P. criniticornis* e as espécies de *Clibanarius* estudadas.
PALAVRAS-CHAVE. *Clibanarius*; estratégias de vida; *Pagurus*; reprodução.

Hermit crabs are anomuran crustaceans that shelter their soft abdomen in gastropod shells. These shells also protect the eggs hermit crabs incubate in their pleopods. This is a critical period for both females and clutches since egg loss during shell investigation and agonistic encounters may reduce female fitness (*sensu* Childress 1972). This is evidenced by the behavioral modifications undergone by females during egg-brooding (Neil & Elwood 1985). In addition, space limitation due to small shell internal volume may reduce the amount of eggs females can incubate (Fotheringham 1976). Thus, if shell volume is fixed, the larger the eggs the smaller the number of eggs that can be maintained inside the shells. Besides the ecological constraints associated to egg size, its variation may represent adaptations to distinct selective forces (Cody 1966). In fact, relative sizes of

eggs, larvae and juveniles and the duration of the embryonic and larval (post-embryonic) development are important components of the life history strategies of marine invertebrates (Hines 1982, Hadfield & Strathmann 1996).

Although the post-embryonic development is known for some Brazilian species: *Clibanarius antillensis* Stimpson, 1859 (Brossi-Garcia & Hebling 1983, Siddiqui *et al*. 1991), *Clibanarius vittatus* (Bosc, 1802) (Lang & Young 1977), *Clibanarius scloeptarius* (Herbst, 1796) (Brossi-Garcia 1987), *Paguristes tortugae* Schmitt, 1933 (Hebling & Negreiros-Fransozo 1983), *Pagurus criniticornis* (Dana, 1852) (Hebling & Brossi-Garcia 1981), and *Pagurus bravidactylus* (Stimpson, 1858) (Negreiros-Fransozo & Hebling 1987), studies on the embryonic development are inexistent. The first descriptions of embryonic development of hermit crabs were made in very early studies (Rathke 1840, Mayer 1877, Faxon 1882, Jackson 1913, Krainska 1934, 1936, 1938, Scheidegger 1976, see a more review for crustaceans in Anderson 1982). Investigations on the duration and macroscopic characterization of embryonic development are more recent and originating in both laboratory (Kamalaveni 1949, Coffin 1960, Wear 1974, Nyblade 1987, Lancaster 1988) and field studies (Wada *et al*. 1995, 2000, Goshima *et al*. 1996). The study of Scheidegger (1976) furnished the most complete description of the external and internal morphology through the embryonic development of hermit crabs and identified thirteen stages from cleavage to larval hatching. However, the number of stages characterized in studies on the external morphology of embryos is variable (Lancaster 1988). In addition, field studies on the reproductive biology of hermit crabs classify the clutches in less detail but in a still quite variable number of stages (Ameyaw-Akumfi 1975, Fotheringham 1980, Negreiros-Fransozo *et al*. 1992, Wada *et al*. 1995, 2000, Goshima *et al*. 1996, Garcia & Mantelatto 1999, Turra & Leite 1999, 2001, Mantelatto *et al*. 2002).

The aim of this study was to record the external morphology of embryos and the duration of the embryonic development of four intertidal hermit crab species (*Clibanarius antillensis*, *C. sclopetarius* (Herbst, 1796), *C. vittatus* and *Pagurus criniticornis*; preliminary observations were taken for *Pagurus brevidactylus* (Stimpson, 1858) and *Paguristes tortugae*). The developmental sequence was compared among species to propose a framework and a visual key for the morphological identification and classification of embryonic stages for further population or reproductive studies on hermit crabs.

MATERIAL AND METHODS

The hermit crabs species were collected along the São Sebastião Channel during 2001 summer months and maintained separately in plastic swimming pools (1.80 x 1.30m) with circulating seawater. The crabs were then observed during several days and, after successful mating (see Turra 2005 for detailed description of the reproductive behavior of the studied species), the females were removed from their shells by breaking them gently. These females were then supplied with apexless shells and maintained individually in small plastic aquaria (10 cm in diameter for the small-sized species – *C. antillensis*, *P. criniticornis*, *P. brevidactylus*, and *P. tortugae* – and 20 cm in diameter for the large-sized ones – *C. vittatus* and *C. sclopetarius*) at 25°C, 34‰ and 12/12 h photoperiod in an incubation chamber. The water was changed daily and the crabs were fed with commercial fish food after each observation. Observations were taken daily (*Clibanarius* and *Paguristes*) or at 12h intervals (*Pagurus*) until hatching. These differences in observation time were based on pilot observations on total developmental time of the studied species and, as a consequence, allowed roughly equivalent observation periodicity. At each observation, the females were removed from their shells using a flexible rubber-coated wire to force them to leave shells through the aperture.

Ten embryos of each specimen (number and shield length of ovigerous females: *Clibanarius antillensis*, five individuals, 3.0 mm, 3.1 mm, 3.1 mm, 3.6 mm, and 4.7 mm; *C. sclopetarius*, five individuals, 6.6 mm, 7.0 mm, 7.2 mm, 7.4 mm, and 8.3 mm; *C. vittatus*, 3 inds., 6.1 mm, 7.5 mm, and 7.6 mm; *Paguristes tortugae*, two individuals, 4.7 mm and 6.2 mm; *Pagurus criniticornis*, 5 inds., 2.1 mm, 2.3 mm, 2.3 mm, 2.4 mm, and 2.6 mm; *P. brevidactylus*, one individual, 2.1 mm) of each species were removed in each time interval for macroscopic observations of developmental features. These eggs were then fixed in aqueous Bouin solution for 24h, washed in water three times and preserved in 70% alcohol to allow more detailed morphological descriptions. Fresh and preserved zygotes were measured using a micrometer to evaluate, for each species, the reduction in egg maximum diameter after preservation procedure through paired Student t tests (Zar 1999). The mean size of the embryos in newly laid clutches (fresh embryos) was compared among species through ANOVA and Scheffé's post-hoc test to test the null hypothesis that the mean zygote size did not vary among hermit crab species (Underwood 1997). In this analysis, the sizes of the ten eggs sampled in each clutch were averaged to produce a mean value of egg maximum diameter for each specimen that was used as replicate in interespecific comparisons. Homocedasticity was evaluated through the Cochran's test (Underwood 1997).

RESULTS

Egg size and developmental time

Egg laying took place up to one hour after copulation in all species. The size of the eggs (zygote) varied markedly among species (ANOVA, $F = 74.651$, $df = 4$, $p < 0.001$; *Pagurus brevidactylus* was not included in the analyses because egg size measurements were taken for only one individual – 0.373 ± 0.017 mm). *Paguristes tortugae* presented the largest embryos (x ± SD; 0.683 ±0.021 mm, Scheffé's test: $p < 0.05$ for all pairwise comparisons). *Clibanarius sclopetarius* (0.479 ± 0.039 mm) and *C. vittatus* (0.444 ± 0.019 mm) presented eggs of similar sizes (Scheffé's test: $p > 0.05$) as well as the embryos of *C. antillensis* (0.354 ± 0.011 mm) and *P. criniticornis* (0.371 ± 0.003 mm: $p > 0.05$). All other comparisons revealed differences in egg size. The maximum diameter of pre-

served eggs was reduced by a ratio of 3 to 12% in comparison to fresh embryos (Student t test, $p < 0.05$ in all comparisons).

The duration of embryonic development varied markedly among species (ANOVA, $F = 922.275$, $df = 3$, $p < 0.001$). *Pagurus criniticornis* took on average 9.2 ± 0.5 days (mean ± SD) to hatch, a shorter period than recorded for *Clibanarius* species (Scheffé's test: $p < 0.05$ for all comparisons). The embryonic development of *Clibanarius antillensis* (18.2 ± 0.5 days) was also shorter than that of *C. vittatus* and *C. sclopetarius* (24.0 ± 0.2 and 25.3 ± 0.6 days, respectively; $p < 0.05$ for both comparisons), which, in turn, presented similar durations ($p > 0.05$). Preliminary observations were taken for other two common rocky shore hermit crabs, *Paguristes tortugae* and *Pagurus brevidactylus*, and revealed that the duration of the embryonic development of *P. brevidactylus* (nine days) is very similar to that of *P. criniticornis*. The description of the embryonic development of *P. tortugae* was not completed because females lost their few eggs during the experiment. However, the embryonic development of this species, i.e., based on the duration of each stage (Tab. I), was demonstrated to be slower than that of *C. antillensis* but faster than those of *C. sclopetarius* and *C. vittatus*, suggesting that an estimate of the total developmental time for this species would be between 20 and 26 days.

Morphological characteristics

The embryonic development of the studied species was very similar and enabled the identification of seven developmental stages (Tab. I, Figs 1-88).

Stage 1. This stage was composed by the zygote and its subsequent cleavages (Figs 1-3, 20-22, 46-48 and 70-72). The fresh eggs of the studied species differed in color: *C. antillensis*, *P. criniticornis* and *P. brevidactylus* – greenish/dark-yellow; *C. sclopetarius* and *C. vittatus* – dark-red/purple; *Paguristes tortugae* – light-red. In all species, the first, second and third cleavages occurred almost simultaneously forming an 8-cell embryo. After that, subsequent cleavages took 4 hours for species of the genus *Clibanarius* and 2-3 hours for *P. criniticornis*, on average. The observation of cleavage was possible for up to two days (one day for *P. criniticornis*) after copulation.

Stage 2. The embryo was characterized by a homogeneous mass because cell number was very high and cell individualization became difficult (Figs 4-5, 23-24, 49-50 and 73-74).

Stage 3. After some time (five days for *C. antillensis*, *C. sclopetarius*, and *C. vittatus*; four days for *P. tortugae*; two days for *P. criniticornis*; see table I), a concentration of cells was observed in the eggs, evidencing the germinal disc, a grayish/pale yolk-free area (Figs 6-7, 25-26, 51-52 and 75-76). The yolk was broken up into cell-like granules.

Stage 4. The percentage of the yolk-free area increased from 5% to up to 50-70% depending on the species (Figs 8-13, 27-36, 53-61 and 77-84). In this period, some characteristics were recognizable in dorsal and lateral views such as the differentiation into cephalic and abdominal regions and the development of the cephalic lobe, which originates the eyes, first and second (bireme) antenna and mandible. The development of the buds of maxilla and maxilipeds could be observed through transparency in only some embryos.

Stage 5. The dark eye pigmentation became evident (Figs 14, 37, 62 and 85) and heart beats were observed in all species. Eye pigmentation initiated in *Clibanarius* species when the yolk-free area was about 50-60% of the total embryo area in comparison to 70-80% in *P. criniticornis*. In terms of relative developmental time, eye pigmentation appeared later in *P. criniticornis* (75-80% of the total developmental time) than in *Clibanarius* species (60-65% of the total developmental time).

Stage 6. The pigmentation of the eyes increased during development from a comma-shape to an irregularly-rounded darkened area comprising almost 10% of the embryo lateral view. Such alterations in eye pigmentation were followed by variations in the percentage of yolk-free area from 70-80% to 95% (Figs 15-18, 38-43, 63-67 and 86-87) but any evident alteration in embryo color (pigmentation) was recorded.

Stage 7. The zoea became visible when more than 95% of the embryo lateral view was free from yolk. Hatching occurred and a small portion of yolk was still visible in the dorsal region of the zoea (Figs 19, 44-45, 68-69 and 88).

Besides the morphological modifications during embryonic development a tendency of increase in egg size was evident (Figs 1-88). Alterations in egg coloration were recorded in all species, with early stages being characterized by the colour of yolk and the latter ones by the pale/whitish non-pigmented embryo. Such alterations were a direct consequence of yolk consumption during development. The eggs of each female developed synchronously, i.e., all incubated eggs of a given female were in the same developmental stage.

The relative duration of each developmental stage was estimated for each species (Fig. 89). Stages presented different relative durations with stage 4 being the longest in all species. The relative duration of stages was very similar in the three *Clibanarius* species. In *Pagurus criniticornis* stage 4 was proportionally longer and stages 5 and 6 were relatively shorter in comparison to other species.

DISCUSSION

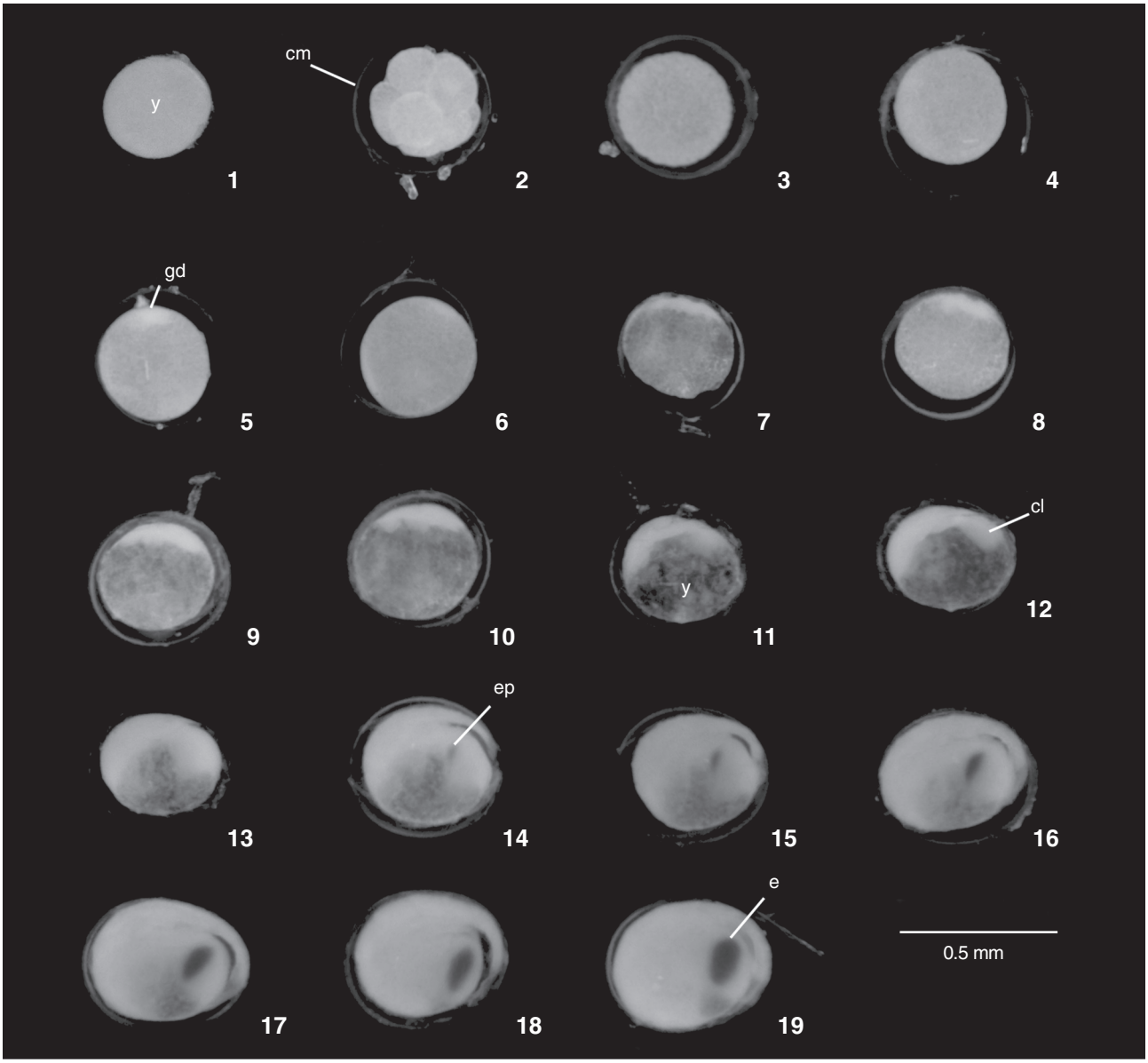
Despite the general sequence (stages) of the embryonic development was very similar in the studied species some specific differences could be recorded in relation to: (1) fresh egg size and color, suggesting that yolk amount and composition varied among species; (2) cleavage (Tab. I), (3) developmental time; (4) appearance of eye pigmentation (Tab. I and Fig. 89). Coffin (1960) and Lancaster (1988) showed that the eye pigmentation occurred almost in the middle of the development of *Pagurus samuelis* and *P. bernhardus*, respectively. On the other hand, the stages preceding eye pigmentation in *Pagurus middendorffii* (Wada *et al*. 1995), *P. nigrofasciata* (Goshima *et al*. 1996) and *P. lanuginosus* (Wada *et al*. 2000) took about 70-80% of the total developmental time, being very similar to *P. criniticornis*. Such differences in duration of embryonic stages

Table I. Comparison of the embryonic development of the four studied hermit crab species (*Clibanarius antillensis*, *C. sclopetarius*, *C. vittatus*, and *Pagurus criniticornis*) including preliminary observations on two other species (*Pagurus brevidactylus* and *Paguristes tortugae*). (C) Cleavage, (HM) homogeneous mass, (GD) initiation of germinal disc (yolk-free area), (%) percentage of yolk-free area, (EP) eye pigmentation, (HB) heart beating, (H) hatching, (?) the observation of the embryonic development stopped due to females lost all embryos.

Time (days)	Species				Time (days)	Species	
	C. antillensis	*C. sclopetarius*	*C. vittatus*	*P. tortugae*		*P. criniticornis*	*P. brevidactylus*
1	C	C	C	C	0,5	C	
2	C	C	C	C	1,0	C	
3	HM	HM	HM	HM	1,5	HM	
4	HM	HM	HM	GD	2,0	GD	
5	GD	GD	GD	GD	2,5	< 5%	
6	< 5%	GD	GD	5%	3,0	5%	
7	5-10%	< 5%	5%	5-10%	3,5	10-15%	20%
8	15-20%	5%	5-10%	10%	4,0	20-30%	
9	20-30%	5-10%	10%	10-20%	4,5	30%	40-50%
10	30%	10%	10-15%	20-30%	5,0	40-50%	
11	40-50%	10-15%	15-20%	30%	5,5	50%	60-70%
12	60-70%/EP	20%	20-30%	40%/EP/HB	6,0	60-70%	
13	70-80%/EP/HB	20-30%	30-40%	40-50%/HB	6,5	70%/EP/HB	70-80%/EP
14	80%/HB	30-40%	40-50%	?	7,0	70-80%/HB	
15	80-85%	40-50%	50-60%/EP	?	7,5	80-90%	90%/HB
16	85-90%	50-60%	50-60%/EP/HB	?	8,0	90-95%	
17	95%	50-60%/EP/HB	60-70%/HB	?	8,5	95%/H	95%
18	> 95%	60-70%/EP/HB	70-75%	?	9,0	95%/H	
19	H	70%	75-80%		9,5	H	H
20	H	70-80%	80%				
21		80%	80-85%				
22		80-90%	90%				
23		90%	95%				
24		90-95%	95%/H				
25		95%	H				
26		95%/H					
27		H					

among species may have a direct relationship with relative egg size (amount of yolk), yolk composition and species-specific reproductive strategies, but further studies are necessary to evaluate these hypothesis.

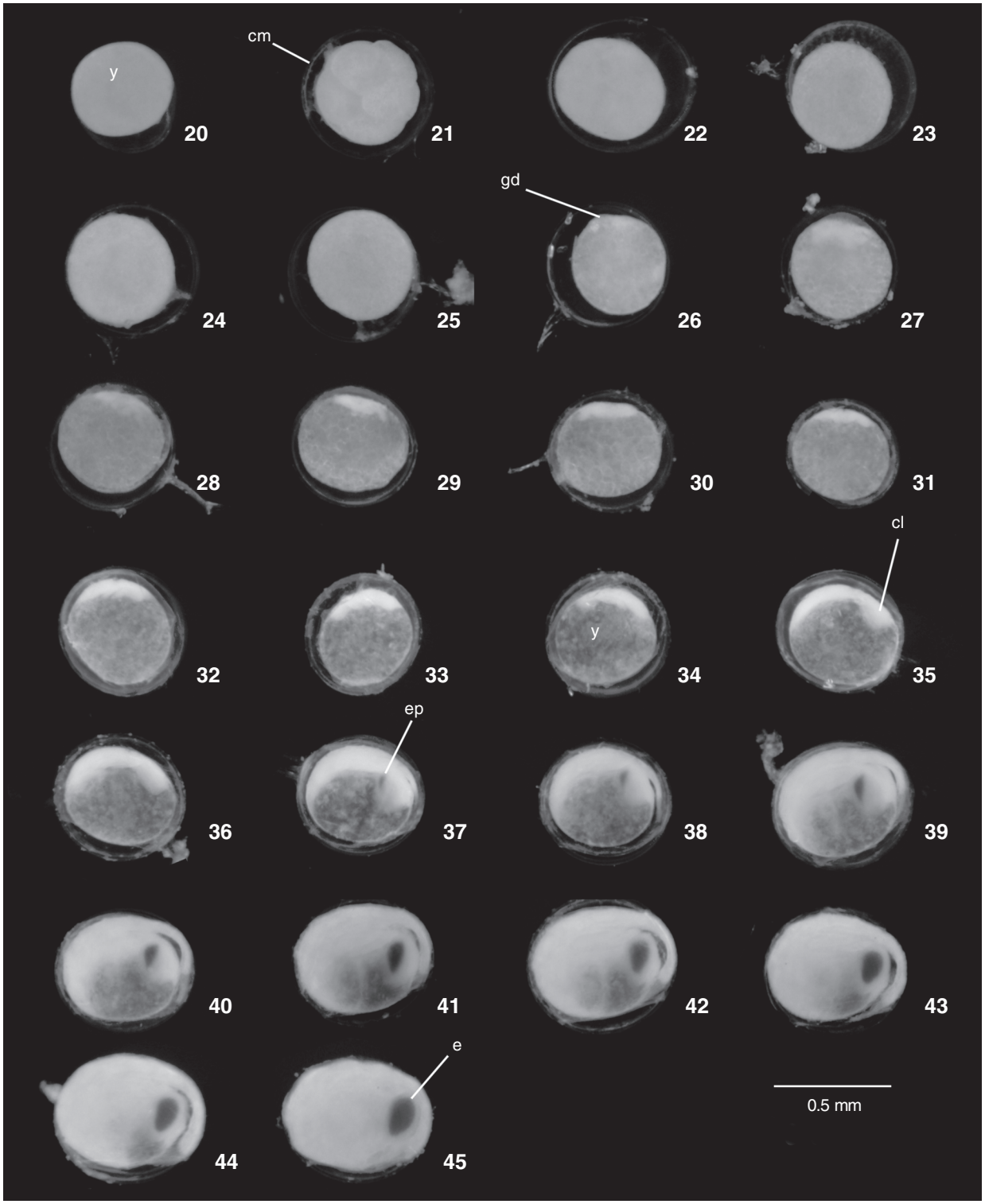
In general, stages of embryonic development are characterized according to embryo external morphology, size and coloration. Based on such characteristics, seven clearly identifiable stages were proposed for the studied species (Figs 1-88). Other field and laboratory studies classified hermit crab embryos in a variable number of stages, which can be compared with the present classification (table II and citations therein). Since classification was highly variable in these studies, there are stages that correspond to one or more stages proposed here. For example, Coffin (1960) did not report the presence of embryos with homogeneous masses prior to the formation of the germinal disc in *Pagurus samuelis* (Stimpson, 1857). In this way, separation of developmental stages may become a less subjective and a more accurate task using the visual hermit crab model presented here as reference. The present study also showed that different egg stages may have different developmental times. Thus, despite being clearly identifiable, they represent quite different periods in relation to total developmental time. This was also reported by Coffin (1960) and Lancaster (1988) in experimental studies and by Wada *et al*. (1995, 2000) and Goshima *et al*. (1996) in field surveys. It becomes clear the necessity to understand the variability in the duration of each developmental



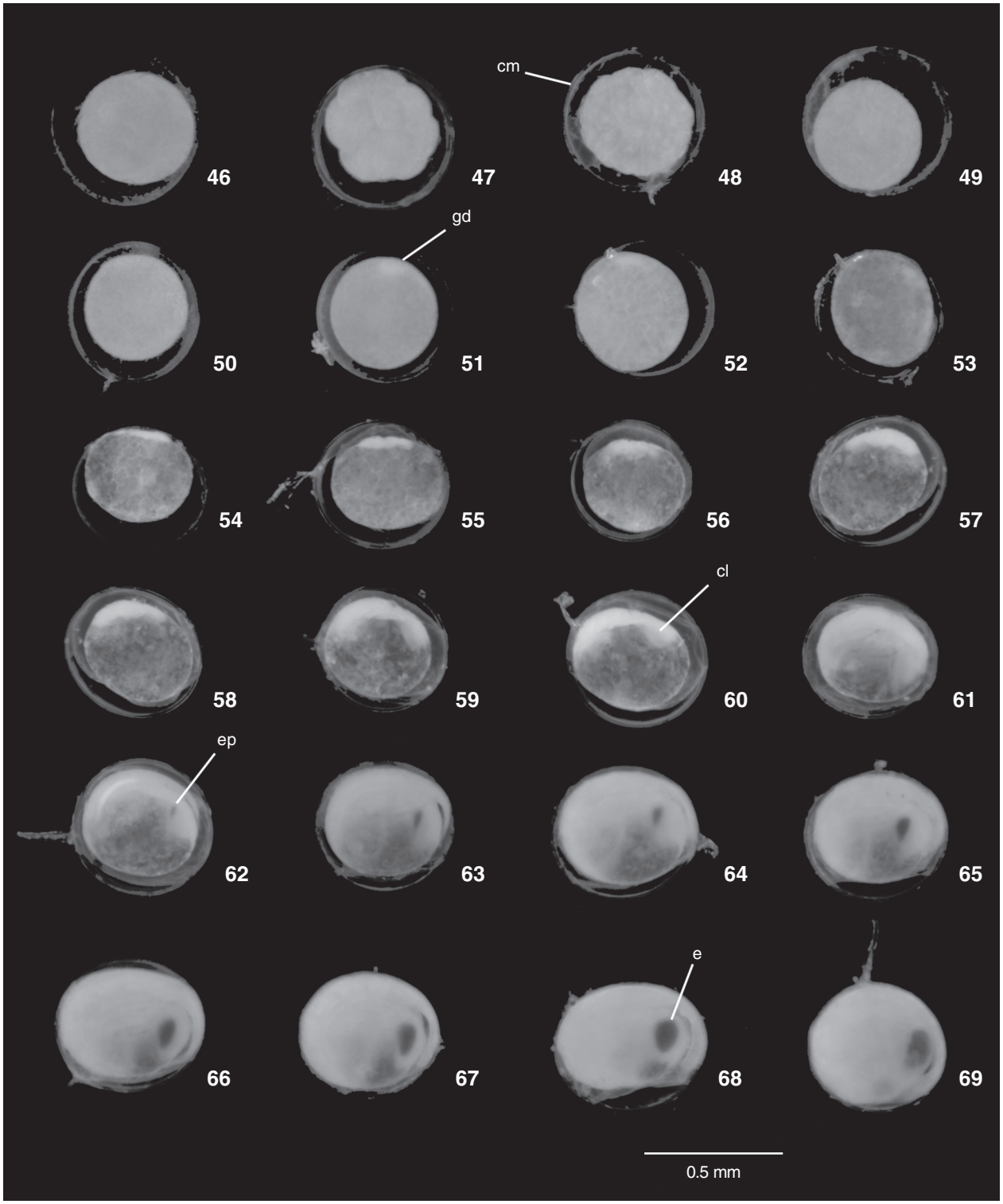
Figures 1-19. Embryonic development of *Clibanarius antillensis*: (1) zygote; (2-19) lateral views of embryos in each subsequent day of observation. (1-3) Stage 1; (4-5) stage 2; (6-7) stage 3; (8-13) stage 4; (14) stage 5; (15-18) stage 6; (19) stage 7. (cl) Cephalic lobe; (cm) chorionic membrane; (e) eye; (ep) eye pigment; (gd) germinal disc (yolk-free area); (y) yolk.

stage to properly select the way into which hermit crab embryos will be grouped for a particular ecological study. For example, embryos without eyes represent 75% of the developmental time in *P. criniticornis* in comparison to 60% in *Clibanarius* (Fig. 89).

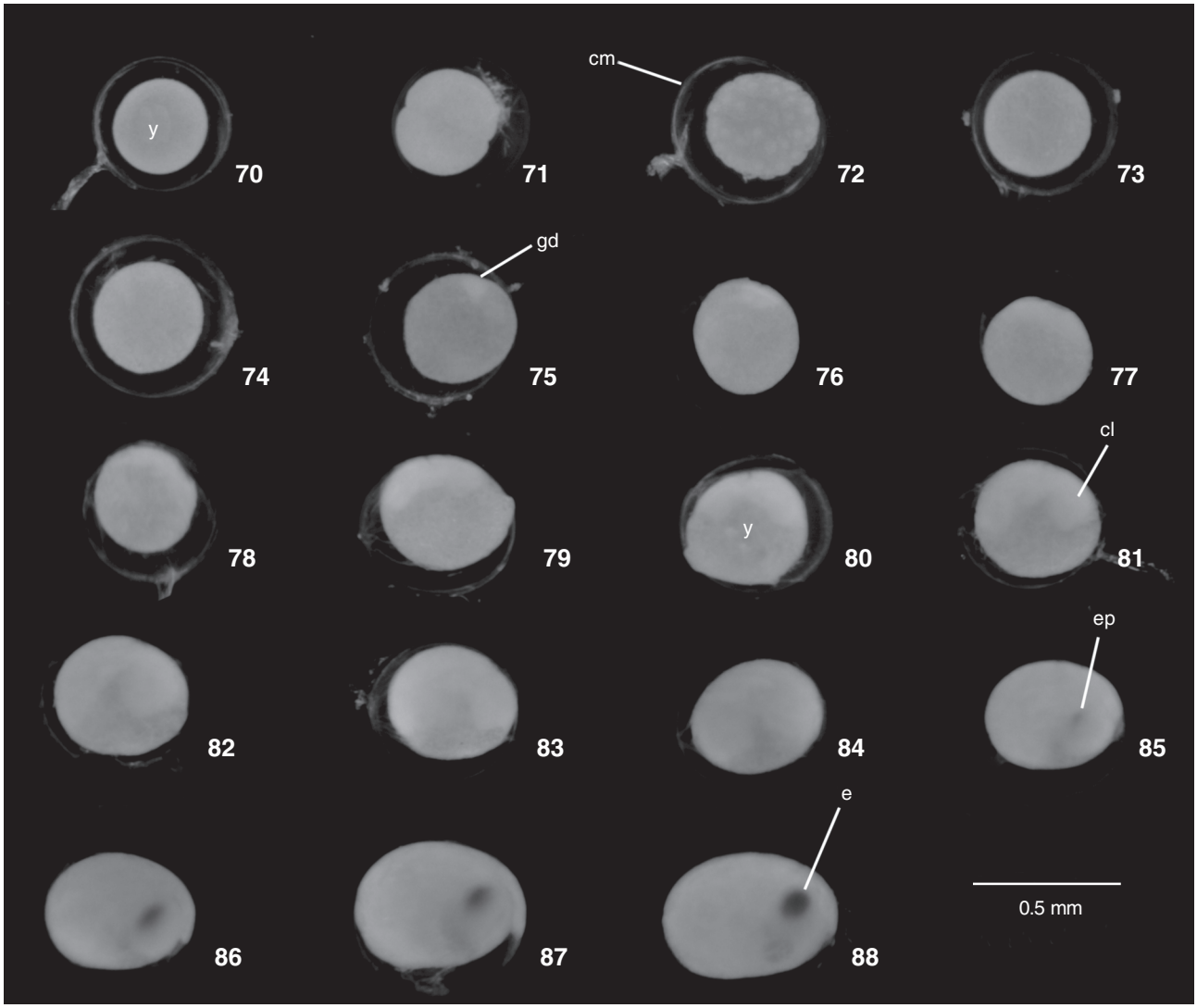
Turra & Leite (2001) studied the fecundity of *C. antillensis*, *C. sclopetarius* and *C. vittatus* and revealed that all the five developmental stages identified (Tab. II) were well represented only in the clutches of *C. antillensis*, while those of the two other species were concentrated in the first one (yolk not consumed). It was hypothesized that such differences could be a consequence of species specific patterns of embryonic development, i.e., the first stage would be shorter in *C. antillensis* than in both *C. sclopetarius* and *C. vittatus*. The results of the present study do not support such a hypothesis once the duration of stage 1 (*sensu* Turra & Leite 2001) is proportionally equivalent in the three species as demonstrated by the present



Figures 20-45. Embryonic development of *Clibanarius sclopetarius*: (20) zygote; (21-45) lateral views of embryos in each subsequent day of observation. (20-22) Stage 1; (23-24) stage 2; (25-26) stage 3; (27-36) stage 4; (37) stage 5; (38-43) stage 6; (44-45) stage 7. (cl) Cephalic lobe, (cm) chorionic membrane, (e) eye, (ep) eye pigment, (gd) germinal disc (yolk-free area), (y) yolk.



Figures 46-69. Embryonic development of *Clibanarius vittatus*: (46) zygote; (47-69) lateral views of embryos in each subsequent day of observation. (46-48) Stage 1; (49-50) stage 2; (51-52) stage 3; (53-61) stage 4; (62) stage 5; (63-67) stage 6; (68-69) stage 7. (cl) Cephalic lobe, (cm) chorionic membrane, (e) eye, (ep) eye pigment, (gd) germinal disc (yolk-free area), (y) yolk.



Figures 70-88. Embryonic development of *Pagurus criniticornis*: (70) zygote; (71-88) lateral views of embryos in each 12 hour observation period. (70-72) Stage 1; (73-74) stage 2; (75-76) stage 3; (77-84) stage 4; (85) stage 5; (86-87) stage 6; (88) stage 7. (cl) Cephalic lobe, (cm) chorionic membrane, (e) eye, (ep) eye pigment, (gd) germinal disc (yolk-free area), (y) yolk.

study. In this way, the differences reported by Turra & Leite (2001) may be associated with differences in reproductive period among species (Turra & Leite 2000), which is an important feature related to differences in the reproductive strategies of marine invertebrates (Hadfield & Strathmann 1996).

As demonstrated by Nyblade (1987) and in the present study, egg size is inversely related to the overall duration of the embryonic development. However, there are only a few adequate data available to allow a general understanding of the ultimate factors governing reproductive strategies in hermit crabs. The fast development of *P. criniticornis*, *P. brevidactylus* and even *C. antillensis* in comparison to *C. sclopetarius* and *C. vittatus* may be also caused by differences in yolk composition, evidenced by differences in egg coloration. Such information is also not available up to date and may elucidate some of the proximate factors related to different reproductive strategies employed by hermit crabs.

Finally, once a reduction in egg diameter was evidenced after preservation procedure, future studies should inform in which condition (fresh or preserved) egg measurements were taken to prevent biased conclusions. Alternatively, in studies focusing the overall investment in reproduction by females, one could use the dry weight of egg masses, which is probably less affected by the fixation procedure than egg diameter.

Table II. Comparison of stages of embryonic development of some species reported in the laboratory and in field studies to those described in the present study.

Stages	Scheidegger (1976)[1]	Lancaster (1988)[2]	Wada *et al.* (1995)[3]	Goshima *et al.* (1996)[4]	Wada *et al.* (2000)[5]	Turra & Leite (2001)[6]	Garcia & Mantelatto (1999)[7]; Mantelatto *et al.* (2002)[8]
1	1		1	1	1	1	1
2	1-3	1	1	1	1	1	1
3	4-5	2	2	2	2	1	1
4	6-10	3	2-3	2-3	2-3	2	1
5	11	3	4	4	4	3	2
6	12	4-5	5	5	5	4	2
7	12-13	6-7	5	5	5	5	3

* Stages: 1) zygote and cleavage; 2) homogeneous mass; 3) initiation of the germinal disc (yolk-free area); 4) percentage of yolk-free area (5 to 50-70%); 5) eye pigmentation (comma-shape) and heart beating; 6) percentage of yolk-free area (70-80 to 95%) and eye development; 7) zoea visible and hatching. References for hermit crab: [1] *Pagurus prideaux* Leach, 1815; [2] *P. bernhardus* (Linnaeus, 1758); [3] *P. middendorffii* Brandt, 1851; [4] *P. nigrofascia* Komai, 1996; [5] *P. lanuginosus* de Haan, 1849; [6] *Clibanarius antillensis* Stimpson, 1859, *C. sclopetarius* Herbst, 1796 and *C. vittatus* (Bosc, 1802); [7] *Calcinus tibicen* (Herbst, 1791); [8] *Paguristes tortugae* Schmitt, 1933.

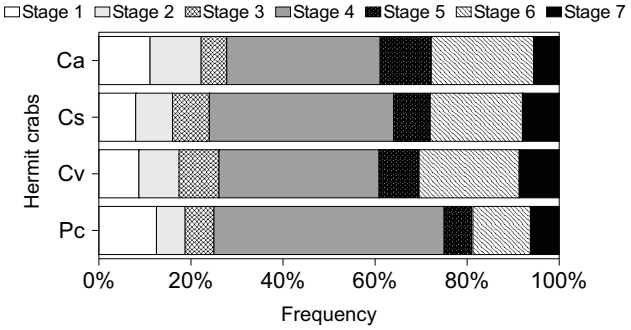


Figure 89. Comparison of the relative duration of the most conspicuous embryonic stages identified for *Clibanarius antillensis* (Ca), *C. sclopetarius* (Cs), *C. vittatus* (Cv) and *Pagurus criniticornis* (Pc) reared in the laboratory at 25°C. Stage 1 – zygote and cleavage; stage 2 – homogeneous mass; stage 3 – initiation of the germinal disc (yolk-free area); stage 4 – percentage of yolk-free area (5 to 50-70%); stage 5 – eye pigmentation (comma-shape) and heart beating; stage 6 – percentage of yolk-free area (70-80% to 95%) and eye development; stage 7 – Zoea visible and hatching.

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REFERENCES

Ameyaw-Akumfi, C. 1975. The breeding biology of two sympatric species of tropical intertidal hermit crabs, *Clibanarius chapini* and *C. senegalensis*. **Marine Biology 29** (1): 15-28.

Anderson, D.T. 1982. Embryology, p. 1-41. *In*: L.G. Abele (Ed.). **Embryology, morphology, and genetics.** *In*: D.E. Bliss (Ed.). **The biology of Crustacea.** New York, Academic Press, XXI+440p.

Brossi-Garcia, A.L. 1987. Morphology of the larval stages of *Clibanarius sclopetarius* (Herbst, 1796) (Decapoda, Diogenidae) reared in the laboratory. **Crustaceana 52** (3): 251-275.

Brossi-Garcia, A.L. & N.J. Hebling. 1983. Desenvolvimento pós-embrionário de *Clibanarius antillensis* Stimpson, 1859 (Crustacea, Diogenidae), em laboratório. **Boletim de Zoologia 6** (1): 89-111.

Childress, J.R. 1972. Behavioral Ecology and Fitness Theory in a Tropical Hermit Crab. **Ecology 53** (5): 960-964.

Cody, M.L. 1966. A general theory of clutch size. **Evolution 20** (1): 174-184.

Coffin, H.G. 1960. The ovulation, embryology and developmental stages of the hermit crab *Pagurus samuelis* (Stimpson). **Walla Walla College Publications of the Department of Biological Sciences and the Biological Station 25** (1): 1-29.

Faxon, E. 1882. Selections from embryological monographs. 1. Crustacea. **Memories of the Museum of Comparative Zoology 9** (1): 1-53.

Fotheringham, N. 1976. Population consequences of shell utilization by hermit crabs. **Ecology 57** (3): 570-578.

Fotheringham, N. 1980. Effects of shell utilization on reproductive patterns in tropical hermit crabs. **Marine Biology 55** (4): 287-293.

Garcia, R.B. & F.L.M. Mantelatto. 1999. Reproductive potential of the hermit crab *Calcinus tibicen* (Crustacea, Anomura) from Ubatuba, São Paulo, Brazil. **Journal of Crustacean Biology 19** (2): 268-275.

Goshima, S.; S. Wada & H. Ohmori. 1996. Reproductive biology of the hermit crab *Pagurus nigrofascia* (Anomura: Paguridea). **Crustacean Research 25** (1): 86-92.

Hadfield, M.G. & M.F. Strathmann. 1996. Variability, flexibility

and plasticity in life histories of marine invertebrates. **Oceanologica Acta 19** (3-4): 323-333.

Hebling, N.J. & A.L. Brossi-Garcia. 1981. Desenvolvimento pós-embrionário de *Pagurus criniticornis* (Dana, 1852) (Crustacea, Paguridae), em laboratório. **Revista Brasileira de Biologia 41** (4): 765-779.

Hebling, N.J. & M.L. Negreiros-Fransozo. 1983. Desenvolvimento pós-embrionário de *Paguristes tortugae* Schmitt, 1933 (Decapoda, Diogenidae), em laboratório. **Boletim de Zoología 6** (1): 157-176.

Hines, A.H. 1982. Allometric constraints and variables of reproductive effort in brachyuran crabs. **Marine Biology 69** (3): 309-320.

Jackson, H.G. 1913. Eupagurus. **Proceedings of the Transaction of the Liverpool Biological Society 27** (1): 495-573.

Kamalaveni, S. 1949. On the ovaries, copulation and egg-formation in the hermit crab, *Clibanarius olivaceous* Henderson (Crustacea, Decapoda). **Journal of the Zoological Society of India 1** (1): 120-128.

Krainska, M.K. 1934. Recherches sur le developpement d'*Eupagurus prideauxi* Leach. 1. Segmentation et gastrulation. **Bulletin International de L'Academie des Sciences Serie B 2** (1): 149-165.

Krainska, M.K. 1936. On the development of *Eupagurus prideauxi* Leach. Proceedings of the XII International Congress of Zoology, Lisboa, 1935, vol. I, Embryologie et Mécanique du Développement. **Arquivos do Museu Bocage 6** (A): 554-566.

Krainska, M.K. 1938. Etudes sur l'oogenese chez *Eupagurus prideauxi* Leach (Decapoda). **Pubblicazione della Stazione Zoologica di Napoli 17** (1): 92-129.

Lancaster, I. 1988. *Pagurus bernhardus* (L.). An introduction to the natural history of hermit crabs. **Field Studies 7** (1): 189-238.

Lang, W.H. & A.M. Young. 1977. The larval development of *Clibanarius vittatus* (Bosc) (Crustacea: Decapoda: Diogenidae) reared in the laboratory. **Biological Bulletin 152** (1): 84-104.

Mantelatto, F.L.M.; V.F. Alarcon & R.B. Garcia. 2002. Egg production strategies of the tropical hermit crab *Paguristes tortugae* from Brazil. **Journal of Crustacean Biology 22** (2): 390-397.

Mayer, P. 1877. Zur Entwicklungsgeschichte der Dekapoden. **Jenaische Zeitschrift für Naturwissenschaft 11** (1): 188-229.

Negreiros-Fransozo, M.L. & N.J. Hebling. 1987. Desenvolvimento pós-embrionário de *Pagurus brevidactylus* (Stimpson, 1858) (Decapoda, Paguridae), em laboratório. **Revista Brasileira de Zoologia 4** (3): 181-193.

Negreiros-Fransozo, M.L.; A. Fransozo; F.L.M. Mantelatto; J.M. Nakagaki & M.C.F. Spilborghs. 1992. Fecundity of *Paguristes tortugae* Schmitt, 1933 (Crustacea, Decapoda, Anomura) in Ubatuba (SP) Brazil. **Revista Brasileira de Biologia 52** (4): 547-553.

Neil, S.J. & R.W. Elwood. 1985. Behavioral modifications during egg brooding in the hermit crab, *Pagurus bernhardus* L.. **Journal of Experimental Marine Biology and Ecology 94** (1-3): 99-114.

Nyblade, C.F. 1987. Phylum or subphylum Crustacea, class Malacostraca, order Decapoda, Anomura, p. 441-450. *In*: M.F. Strathmann (Ed.). **Reproduction and development of marine invertebrates of the northern Pacific coast. Data and methods for the study of eggs, embryos, and larvae.** Seattle, University of Washington Press, 670p.

Rathke, H. 1840. Zur Entwicklungsgeschichte der Dekapode. **Archiv für Naturgeschichte 6** (1): 241-249.

Scheidegger, G. 1976. Stadien der Embryonalentwicklung von *Eupagurus prideauxi* Leach Crustacea, Decapoda, Anomura) unter besonderer Berücksichtigung der Darmentwicklung und der am Dotterabbau beteiligten Zelltypen. **Zoologische Jahrbücher, Abteilung für Anatomie und Ontogenie der Tiere 95** (1): 297-353.

Siddiqui, F.A.; P.A. McLaughlin & J.A. Crain. 1991. Larval development of *Clibanarius antillensis* Stimpson, 1859 (Crustacea: Anomura: Diogenidae) reared under laboratory conditions: a comparison between Panamanian and Brazilian populations. **Journal of Natural History 25** (5): 917-932.

Turra, A. 2005. Reproductive behavior of intertidal hermit crabs (Decapoda: Anomura) in southeastern Brazil. **Revista Brasileira de Zoologia 22** (2): 313-319.

Turra, A. & F.P.P. Leite. 1999. Population structure and fecundity of the hermit crab *Clibanarius antillensis* Stimpson, 1862 (Anomura, Diogenidae) in southeastern Brazil. **Bulletin of Marine Science 64** (2): 281-289.

Turra, A. & F.P.P. Leite. 2000. Population biology and growth of three sympatric species of intertidal hermit crabs in southeastern Brazil. **Journal of the Marine Biological Association of the United Kingdom 80** (6): 1061-1069.

Turra, A. & F.P.P. Leite. 2001. Fecundity of three sympatric populations of hermit crabs. **Crustaceana 74** (10): 1019-1027.

Underwood, A.J. 1997. **Experiments in ecology. Their logical design and interpretation using analysis of variance.** Cambridge, Cambridge University Press, 504p.

Wada, S.; H. Kitaoka & S. Goshima. 2000. Reproduction of the hermit crab *Pagurus lanuginosus* and comparison of reproductive traits among sympatric species. **Journal of Crustacean Biology 20** (3): 474-478.

Wada, S.; S. Goshima & S. Nakao. 1995. Reproductive biology of the hermit crab *Pagurus middendorffii* Brandt (Decapoda: Anomura: Paguridae). **Crustacean Research 24** (1): 23-32.

Wear, R.G. 1974. Incubation in British Decapod Crustacea, and the effects of temperature on the rate and success of embryonic development. **Journal of the Marine Biological Association of the United Kingdom 54** (4): 745-762.

Zar, J.H. 1999. **Biostatistical analysis.** New Jersey, Prentice Hall, 663p.

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