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MORPHOMETRIC AND REPRODUCTIVE TRAITS OF TROPICAL CARIDEAN SHRIMPS

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ABSTRACT

Life-history traits were studied in one marine and four fresh-water shrimps from tropical regions of western South America: *Palaemon northropi, P. pandaliformis, Macrobrachium acanthurus,* and *M. olfersii* (Palaemonidae). Occasional data are given for *Macrobrachium carcinus* and an atyid shrimp, *Potimirim potimirim.* Size was measured as total body length (TBL), carapace length (CL), and telson length (TL), weight as dry weight (W), and realized fecundity as number of eggs per female. Size and W of eggs were determined in an early stage of development. Relationships between measurements of size, weight, and fecundity are described with regression equations. Significant species- and sex-specific variation was found in the slopes of the allometric TBL–W relationship. In the 2 species of *Palaemon,* females grew to a larger size than males; they showed also a steeper W increase with increasing TBL. Opposite patterns were observed in *M. acanthurus* and *M. olfersii,* suggesting different traits on the generic level. The minimum sexable size (minimum size of males with appendix masculina) was unrelated to the species-specific maximum size. Size at the onset of female maturity (minimum size with eggs) was larger in *M. acanthurus* than in the other species (29 versus 20–22 mm); W at the onset of female maturity increased with the maximum size of a species. Regressions of egg number on TBL indicated the highest overall level as well as the strongest size-dependence of fecundity in *M. olfersii;* these parameters were lowest in *P. pandaliformis.* The reproductive output (RO:W of egg mass in relation to female body W) was lowest in the only marine species studied here, *P. northropi* (14.4 versus 18.6–21.7%). With the possible exception of the RO, the life-history traits of these tropical shrimps appear unrelated to the climatic origin or habitat of a species.

Growth and reproduction are important aspects of the ecology and life history of a species. In crustaceans, they have been quantified with several measurements of body size, weight, and fecundity, and relationships between these characteristic data have been described with linear or nonlinear regression models. While growth may be quantified as an increase in total body length (TBL), carapace length (CL), telson length (TL), fresh weight (FW), or dry weight (W), reproduction is frequently measured in terms of fecundity. We distinguish the concepts of potential fecundity (i.e., the number of oocytes in the ovary), realized fecundity (number of eggs attached under the abdomen), and actual fecundity (number of larvae hatched; Corey, 1991). Depending on the purpose of a particular study and the kind of materials available, some of these measures of growth and reproduction are more convenient than others. In cultivation experiments with a limited number of living individuals available, for instance, nondestructive sampling techniques, such as size measurements in cast exuviae, may be required. Since TBL is, in this case, often difficult or impossible to measure, CL

or TL may yield more reliable growth data. Furthermore, W measurements are not possible without sacrificing valuable live material. Hence, it is important to know quantitative relationships between measurements of size, weight, and reproduction, which can then be used to predict one from another.

The parameters of regression equations are useful not only for conversions, but also as indices for intra- and interspecific comparisons of morphometric or reproductive traits. As further key life-history parameters, the absolute or relative "size at the onset of maturity" (SOM, Wenner, 1985; RSOM, Charnov, 1990) have been used to compare the reproductive performance of different species or populations. The RSOM compares the minimum size of sexually mature individuals with the theoretical maximum, represented by the asymptotic parameter L_∞ of the von Bertalanffy growth equation. As another comparative index of the investment by a species in offspring production, the "reproductive output" (RO) is frequently given in the literature (Hines, 1982, 1988, 1991; Clarke *et al.,* 1991; Lardies and Wehrtmann, 1996). This is usually measured as a weight ratio between

the egg mass (i.e., realized fecundity) and female body weight (on an FW or W basis). In caridean shrimps, quantitative relationships among measures of growth and reproduction have been described for several taxa (e.g., Clarke et al., 1991; Corey and Reid, 1991; Reid and Corey, 1991; Lardies and Wehrtmann, 1996). Most of the existing data, however, originate from boreal and subtropical rather than tropical species.

In the present investigation, we measured body size (as TBL, CL, and TL), dry weight (W), female reproduction (realized fecundity; as number of eggs), and the size and W of eggs in four species of tropical palaemonid shrimps from the coastal region of the state of São Paulo, Brazil: Palaemon (Palaeander) northropi Rankin, 1898; P. (Palaemon) pandaliformis Stimpson, 1871; Macrobrachium acanthurus Wiegmann, 1836; and M. olfersii Wiegmann, 1836. For all of these species, morphometric relationships between different measurements of size as well as those between size, weight, and fecundity are described with regression equations. From these data, we estimate female SOM, RSOM, and RO, and the minimum size of males with a developed appendix masculina (i.e., with an identifiable sex) is given. In addition, a few occasional data on size and fecundity are presented for two further species, Macrobrachium carcinus Linnaeus, 1758, and Potimirim potimirim Müller, 1881 (Atyidae).

Thus, our data allow for intra- and interspecific comparisons of life-history traits in four shrimp taxa belonging to the same family, the Palaemonidae (including two subgenera of the genus Palaemon), and preliminary comparisons with another palaemonid and an atyid shrimp. All these species are widely distributed in tropical regions of eastern South America, some also in Central America, the Caribbean, and the southeastern United States. They are characterized by different specific body size (small Palaemon versus large Macrobrachium) and different life styles (fresh-water versus marine).

Species Studied: Brief Summary of Life History and Distribution.—*Palaemon northropi* is a marine shrimp that is commonly found in intertidal rock pools (Moreira and McNamara, 1984) and on sandy mud flats near mangrove areas (Chace, 1972). All four other species studied (*P. pandaliformis, Mac-*

robrachium acanthurus, M. olfersii, M. carcinus, Potimirim potimirim) live as adults in fresh water (Holthuis, 1952, 1959; Chace and Hobbs, 1969). However, experimental evidence suggests that their life history follows an "export strategy," i.e., their larvae leave the adult habitat with outflowing currents and develop subsequently in adjacent brackish estuaries or coastal marine waters. As a consequence of their limited adaptation to the limnic parental environment, the larvae can survive in fresh water for a maximum of about one week, but they are not able to develop there beyond the first zoeal stage. Brackish and sea-water conditions, in contrast, allow for successful development from hatching to metamorphosis (Choudhury, 1971a, b; Dobkin, 1971; Dugger and Dobkin, 1975; Moreira et al., 1979; McNamara et al., 1980; Moreira and McNamara, 1984; Bakker, 1989). The larvae of the fully marine species *P. northropi*, in contrast, are stenohaline, surviving for only a few hours in fresh water (Moreira et al., 1982; Moreira and McNamara, 1984).

All species studied occur in coastal waters or adjacent fluvial systems, respectively, in the tropical zones of eastern South America, with Brazil as their southern limit of distribution. The geographic ranges of *P. northropi, M. olfersii, M. carcinus,* and *P. potimirim* extend north to Florida (not including the Caribbean islands for *M. olfersii* and *P. potimirim*), for *P. pandaliformis* to Guatemala, and for *M. acanthurus* to North Carolina and Bermuda (Holthuis, 1952, 1959; Smalley, 1963; Chace and Hobbs, 1969; Holthuis and Provenzano, 1970; Chace, 1972; Dugger and Dobkin, 1975; Gore et al., 1978; López and Pereira, 1994). Some fresh-water shrimps, in particular species of *Macrobrachium*, have been extensively studied with respect to larval metabolism and salinity tolerance, osmoregulation, and the function of neuroendocrine regulation systems (e.g., Souza and Moreira, 1987; McNamara et al., 1990; Santos and McNamara, 1996). In contrast, surprisingly little is known about the basic morphometric and reproductive traits of these species.

MATERIALS AND METHODS

This investigation was carried out in April 1995 and February 1996 at the marine biological center (CEBIMar) of the University of São Paulo (USP), near the town of São

Sebastião, Brazil. Fresh-water shrimps (*Palaemon pandaliformis, Macrobrachium acanthurus, M. olfersii, M. carcinus,* and *P. potimirim*) were caught with hand nets (approximately 3-mm mesh size) from the lower reaches of creeks that are located near the CEBIMar (Pitangueira; Guaecá) and on the island of Ilhabela (approximately 23°49′S, 45°27′W). The salinity at these sampling sites was usually close to 0‰, but, sometimes, when sea water intruded into the mouths of the creeks with high tide or landward winds, up to 6‰ were measured (by means of a hand refractometer). The temperature varied with weather conditions, tide, and time of day between 22° and 30°C. Marine shrimps (*P. northropi*) were caught in intertidal rock pools on the beach in front of the CEBIMar. The salinity in this habitat was approximately 35‰, and the temperature about 25°C.

Shrimps were transported live to the laboratory and maintained for up to 2 days in aquaria with either tap water or sea water. Immediately before measurements, they were taken out of the water and killed by exposure to –10°C for a few minutes. Total body (TBL), carapace length (CL), and telson length (TL) were measured under a dissecting microscope (Wild M3B) with a calibrated eye-piece micrometer to the nearest 0.01 mm; in large individuals, TBL was measured with vernier calipers to the nearest 0.1 mm. In our material, CL is defined as the shortest distance from the rear margin of the eye orbit to the median posterior edge of the carapace. TBL was measured from the rear margin of the eye orbit to the base of the median distal telson spine, and TL was taken from the midanterior margin of the telson to the base of the median distal telson spine.

To determine the presence of an appendix masculina, the second pleopod was dissected free and inspected under a dissecting microscope (in small individuals under a compound microscope, Nikon Labophot 2). This allowed for an identification of the minimum body size at which individuals of a given species may be sexed (in the following termed "minimum sexable size," MSS). Since smaller (not sexable) individuals were morphologically similar to young females, we counted these as females. Theoretically, juvenile males below the MSS that were erroneously "sexed" as females may have introduced a statistical error into our morphometric data of female shrimps. However, we assume that this bias did not significantly change the morphometric or other regressions given in this paper, because (1) juveniles smaller than the MSS show probably no significant sexual dimorphism, and (2) this size group constituted in general only a minor fraction of our material (5 individuals in both *P. northropi* and *P. pandaliformis*, 14 in *M. olfersii,* and none in the other species). This problem must be considered in population studies, when the sex ratio is given; in that case, a "juvenile" category must be distinguished from safely identified males and females.

In ovigerous females, the eggs were carefully removed from the pleopods and counted under a dissecting microscope. Large egg masses (>1,000 eggs; for example, in large females of *Macrobrachium*) were transferred to preweighed and numbered pieces of aluminum foil, dried at 105°C to constant weight (for at least 15 h), and total dry weight (W) of the egg mass determined to the nearest 0.1 mg on a Mettler laboratory balance. The egg number was in these cases estimated from the average W of one egg (determined in subsamples; see below).

A small sample of eggs was inspected under a compound microscope in order to identify the stage of embryonic development and to measure egg size (longest and shortest diameter, to the nearest 5 µm; N = 10 eggs per female). Embryonic development was classified in three categories: (I) more than two-thirds of the egg volume occupied by yolk, no eye pigments visible, embryo showing little or no differentiation, (II) phase of eye formation and embryonic differentiation (segmentation, development of appendices), heart beat visible but often irregular, yolk occupying more than one-third of egg volume, and (III) eye fully developed, heart beat regular, differentiation of appendages in final phase, yolk occupying less than one-third of egg volume.

During a short preliminary study in 1995, body size and fecundity were measured in a total of 23 ovigerous *P. pandaliformis*. Egg size was determined in different stages of embryonic development in 17 individuals of *P. pandaliformis*, 15 *M. acanthurus*, 10 *M. olfersii*, and 1 *P. potimirim*. In the 1996 study, the total body W of shrimps and the average W and elemental composition of eggs were also measured. After the measurements of body size (TBL, CL, TL), determination of sex, and removal of eggs (where applicable), the shrimps were transferred to aluminum foil, and W was measured as described above for egg masses. Samples of eggs (N = 5 replicates, with 10 eggs each) in different stages of embryonic development were transferred to preweighed tin cartridges and frozen at –20°C for later determinations of W and elemental composition (Anger and Harms, 1990).

In total, the material of the present paper comprises morphometric and weight measurements from N = 93 individuals of *P. northropi*, 123 *P. pandaliformis* (W data for only N = 100), 155 *M. acanthurus,* and 119 *M. olfersii*; fecundity data were available from N = 25, 74, 29, and 49 ovigerous females, respectively. Additional data of size, weight, and fecundity were obtained from 12 females of *P. potimirim* (8 of these were ovigerous) and 3 of *M. carcinus.*

Statistical analyses followed standard methods as described by Sokal and Rohlf (1995). The data were first tested for normality and homoscedasticity (goodness-of-fit *G* test; Durbin-Watson Statistic; no significant deviations found) before parametric tests were applied. Quantitative relationships between different measurements of body size (TBL, CL, TL), dry weight (W), and fecundity (egg number) were described by means of least-square regressions (with or without logarithmic transformation of data). Correlation and regression coefficients were tested for significant deviations from zero (ANOVA). Slopes of different regression equations were compared with each other employing multiple ANCOVA, intercepts with the *Y*-axis with an ANOVA (i.e., after removal of the interaction term). Percentage figures (reproductive output, RO) were arcsin-transformed before pairwise interspecific comparisons were made (Student's *t*-test) or tested with ANCOVA for size dependence. The following levels of statistical significance are distinguished in the paper: $P < 0.05$, $P < 0.01$, $P < 0.001$.

Since the morphometric relationships between TBL, CL, and TL are usually described with a linear regression model (Lovett and Felder, 1989; Dall *et al.,* 1990; Gabche and Hockey, 1995), but sometimes as a power function (i.e., as a linear function after logarithmic transformation of both the dependent and the independent variables; Wickins, 1972; Rodríguez, 1987), we give both types of regression to allow for intra- and interspecific comparisons with all literature data. In relationships between fecundity and size or W, we applied exclusively the generally accepted allometric model (see, e.g., Hartnoll, 1985).

Table 1. Range of total body length (TBL, mm) and dry weight (W, mg) of males and females (M, F); size at onset of maturity (SOM, minimum TBL and W of ovigerous females); average size and W of eggs in an early stage of development (largest × smallest diameter, mm; W, μg); range of fecundity (egg number) and reproductive output (RO, total egg mass in % of female W, range and $\bar{x} \pm$ SD).

| | Species | | | | | | | |
| | Palaemon northropi | | Palaemon pandaliformis | | Macrobrachium acanthurus | | Macrobrachium olfersii | |
	M	F	M	F	M	F	M	F
TBL (mm)	9.3–21.6	7.2–26.7	12.6–26.2	9.8–32.0	10.5–89.5	10.7–53.5	15.2–53.8	8.0–50.5
W (mg)	2.7–54.0	0.9–126	6.9–62.0	3.0–110	4.0–5,772	4.1–808	15.2–1,659	1.9–1,093
SOM (TBL, mm)		21.1		20.0		29.7		22.1
(W, mg)		57.4		27.3		138.4		67.0
Egg size (mm)		0.65 × 0.48		0.77 × 0.63		0.73 × 0.57		0.63 × 0.51
Egg W (μg)		42		54		50		27
Fecundity		172–418		102–375		440–3,042		170–8,960
RO (range, %W)		8.9–19.3		12.6–24.5		13.5–30.0		6.9–38.4
($\bar{x} \pm$ SD)		14.4 ± 2.7		18.6 ± 3.0		19.1 ± 4.5		21.7 ± 6.6

RESULTS

Body Size: Identification of Males and Onset of Female Reproduction

Biometric data summarized for the four species of which we had the most material (*Palaemon northropi, P. pandaliformis, Macrobrachium acanthurus, M. olfersii*; Table 1) include: observed range in total body length (TBL) and dry weight (W) of males and females (the latter including a few juveniles below the minimum sexable size, MSS), size at

Table 2. *Palaemon northropi*. Parameters of linear regressions (with or without preceding ln-transformation of dependent and independent variable, Y, X) describing relationships between measurements of body size (mm), weight (mg), and fecundity (egg number). TBL = total body length; CL = carapace length; TL = telson length; W = dry weight; Fec = fecundity; N = number of observations (data pairs); r^2 = coefficient of determination (ANOVA: all regression coefficients significantly different from zero, $P < 0.001$, except for ln Fec regressed onto ln W, $P < 0.01$; ln Fec onto ln TL not significant, n.s.). Morphometric and size-weight regressions computed separately for males (M) and females (F), Fec onto size or weight separately for early and late embryonic stages (St. I versus II and III combined); slopes statistically compared between sexes or embryonic stages (multiple ANCOVA); intercepts compared (after removal of the interaction term) when slopes were not significantly different from each other; levels of significance indicated with asterisks: *, **, *** ($P < 0.05$, $P < 0.01$, $P < 0.001$); regressions for pooled data (Σ) given when neither the slope nor the intercept parameter differed significantly between sexes or stages, respectively.

Y	X	Sex/stage	Intercept	Slope	N	r^2
TBL	CL	M	4.2260***	3.2542	48	0.8569
		F	2.8325***	3.3880	45	0.9788
ln TBL	ln CL	M	1.7729***	0.7752	48	0.8970
		F	1.6862***	0.8144	45	0.9915
TBL	TL	Σ	1.1442	6.4380	93	0.8853
ln TBL	ln TL	Σ	1.9241	0.9965	93	0.9265
CL	TL	M	0.8063	1.3029*	48	0.4976
		F	−0.3318	1.8636*	45	0.8698
ln CL	lnTL	M	0.5387	0.9289*	48	0.6009
		F	0.2837	1.2350*	45	0.9368
ln W	ln TBL	Σ	−6.9903	3.5950	93	0.9663
ln W	ln CL	M	−0.1300	2.4295*	48	0.6946
		F	−0.9159	2.9394*	45	0.9716
ln W	ln TL	M	−0.5321	2.9205*	48	0.9386
		F	−0.1551	3.6969*	45	0.9443
ln Fec	ln TBL	Σ I–III	−2.9303	2.6958	25	0.5141
ln Fec	ln CL	Σ I–III	2.1158	1.9163	25	0.3794
ln Fec	ln TL	Σ I–III	4.6750	0.7639	25	0.1439[n.s.]
ln Fec	ln W	Σ I–III	2.5643	0.6880	25	0.3501

Table 3. *Palaemon pandaliformis.* Parameters of linear regressions (with or without preceding ln-transformation of dependent and independent variable, Y, X) describing relationships between measurements of body size (mm), weight (mg), and fecundity (egg number). TBL = total body length; CL = carapace length; TL = telson length; W = dry weight; Fec = fecundity; N = number of observations (data pairs); r^2 = coefficient of determination (ANOVA: all regression coefficients significantly different from zero, $P < 0.001$). For further explanation see Table 2.

Y	X	Sex/stage	Intercept	Slope	N	r^2
TBL	CL	M	0.6198	4.4921*	35	0.9137
		F	1.9924	3.8652*	88	0.9444
ln TBL	ln CL	M	1.5552***	0.9839	35	0.9447
		F	1.5751***	0.9222	88	0.9620
TBL	TL	Σ	2.6316	5.5340	123	0.9509
ln TBL	ln TL	Σ	1.9505	0.9104	123	0.9670
CL	TL	M	0.7047***	1.1618	35	0.8673
		F	0.4335***	1.3619	88	0.9154
ln CL	ln TL	M	0.4631***	0.8786	35	0.9163
		F	0.4426***	0.9591	88	0.9441
ln W	ln TBL	M	−5.7334***	3.0158	35	0.9796
		F	−5.7628***	3.0615	65	0.9754
ln W	ln CL	M	−1.1223***	3.0191	35	0.9580
		F	−0.9828***	2.8213	65	0.9711
ln W	ln TL	M	−0.1659**	2.7429	35	0.9386
		F	−0.0742**	2.9057	65	0.9516
ln Fec	ln TBL	Σ I–III	−2.8787	2.5292	74	0.8695
ln Fec	ln CL	Σ I–III	1.1543	2.3124	74	0.8489
ln Fec	ln TL	Σ I–III	2.4406	2.0387	74	0.8214
ln Fec	ln W	Stage I	2.2531**	0.7511	23	0.7801
		Stages II and III	1.3392**	0.9426	26	0.7632

the onset of maturity (SOM, given as TBL and W) in females, average size and W of early eggs, fecundity, and reproductive output (RO).

The minimum TBL or W in males represents the MSS of a species (with the possible exception of *M. acanthurus*, where no individuals smaller than the smallest identifiable males occurred). The MSS varied in these species between 9 and 15 mm TBL, without showing a correlation with the maximum size of the species. In *Palaemon*, the females grow to larger size than males, while the opposite is true for *Macrobrachium*. These differential patterns are reflected also in the maximum TBL and W measured in our material (Table 1).

The SOM of females may be related to the maximum size of a species. The greatest SOM (in terms of TBL) was found in the largest shrimp (*M. acanthurus*), the minimum occurred in the smallest species (*P. northropi*). However, the difference between the SOM in *M. olfersii* and in the much smaller species of *Palaemonetes* is almost negligible. SOM, expressed as W, increases in the same order, but with clearer interspecific differences: *P. pandaliformis* < *P. northropi* < *M. olfersii* < *M. acanthurus* (Table 1).

Morphometrics: Relationships between Size Dimensions

In all four species for which we had sufficient material, we found significant correlations among different measurements of body size (TBL, CL, TL; Tables 2–5). Similar relationships were found in *Potimirim potimirim* (Table 6). Allometric functions consistently provided a better fit for morphometric relationships than did linear functions. This is indicated by higher coefficients of determination, r^2, after logarithmic transformation of both the X and Y values (only exception: TBL versus CL in male *M. acanthurus*). Thus, these relationships indicate allometric growth in different parts of the body. We give here, however, the parameters of both the linear and power functions to allow comparisons with other data from the literature, which include various models. All morphometric regressions were calculated separately for males and females; pooled regressions are given only where differences between the slopes or intercepts of separate regressions were statistically not significant. Significant differences indicate sex-specific differences in al-

Table 4. *Macrobrachium acanthurus*. Parameters of linear regressions (with or without preceding ln-transformation of dependent and independent variable, Y, X) describing relationships between measurements of body size (mm), weight (mg), and fecundity (egg number). TBL = total body length; CL = carapace length; TL = telson length; W = dry weight; Fec = fecundity; N = number of observations (data pairs); r^2 = coefficient of determination (ANOVA: all regression coefficients significantly different from zero, P < 0.001). For further explanation see Table 2.

Y	X	Sex/stage	Intercept	Slope	N	r^2
TBL	CL	M	7.3949	2.6711***	66	0.9843
		F	4.3201	2.9428***	89	0.9649
ln TBL	ln CL	M	1.7923	0.7659**	66	0.9673
		F	1.6147	0.8304**	89	0.9786
TBL	TL	Σ	−0.0120	6.2506	155	0.9222
ln TBL	ln TL	M	1.9421	0.9132**	66	0.9437
		F	1.8202	1.0117**	89	0.9493
CL	TL	M	−2.5244**	2.2440	66	0.8986
		F	−1.3131**	2.1166	89	0.9183
ln CL	ln TL	M	0.2287***	1.1690	66	0.9377
		F	0.2720***	1.2019	89	0.9442
ln W	ln TBL	M	−6.7847	3.4202**	66	0.9806
		F	−5.8806	3.1678**	89	0.9742
ln W	ln CL	M	−0.7102*	2.6489	66	0.9700
		F	−0.8258*	2.6596	89	0.9744
ln W	ln TL	M	−0.1596*	3.1357	66	0.9326
		F	−0.1198*	3.2084	89	0.9268
ln Fec	ln TBL	Σ I–III	−3.6715	2.8994	29	0.7603
ln Fec	ln CL	Σ I–III	0.4367	2.6555	29	0.7188
ln Fec	ln TL	Σ I–III	2.1739	2.6210	29	0.6249
ln Fec	ln W	Stage I	0.9830*	1.0636	17	0.7942
		Stages II and III	0.5706*	1.1012	12	0.8461

lometric growth and, thus, reflect sexual dimorphism. Since we consider differences between slopes as biologically more meaningful than those between intercepts alone (see below, Discussion), we describe only the former cases.

In *P. northropi*, different slopes were observed only in the relationship between CL and TL, indicating that the CL increases in females proportionally faster in relation to TL than in males. In *P. pandaliformis*, significantly different slopes in the linear relationship between TBL and CL suggest that male TBL increases during growth in relation to CL at a faster rate than in females. An opposite tendency was observed in species of *Macrobrachium*. The size data showed here a significantly higher slope in the regressions of TBL on CL in females.

Size-Weight Relationships

When size-weight relationships are compared among different species or sexes, inter- and intraspecific differences in the size-dependence of weight can be detected. In a comparison of male and female *P. northropi*,

statistically significant differences were found between the slopes of the regressions W on CL or TL. In both species of *Palaemon*, the increase in W with increasing TBL was steeper in females than in males (Fig. 1a; but not significant statistically in *P. northropi*; Table 2). Likewise, the dependence of W on TBL differed significantly between sexes in both species of *Macrobrachium*, but with an opposite pattern (Fig. 1b). These differential sex-specific patterns appear to reflect generic differences in sexual dimorphism.

Among the species studied, *P. northropi* showed on the average the steepest slope in the regression W on TBL, *P. pandaliformis* the smallest, and the two species of *Macrobrachium* as well as *Potimirim potimirim* were intermediate (Tables 2–6). The few measurements obtained from *M. carcinus* suggest that this species shows a size-weight relationship similar to that of *M. acanthurus*.

Size-Specific Fecundity

In all species for which we had sufficient data, realized fecundity showed significant relationships with all measurements of body

Table 5. *Macrobrachium olfersii*. Parameters of linear regressions (with or without preceding ln-transformation of dependent and independent variable, *Y*, *X*) describing relationships between measurements of body size (mm), weight (mg), and fecundity (egg number). TBL = total body length; CL = carapace length; TL = telson length; W = dry weight; Fec = fecundity; *N* = number of observations (data pairs); r^2 = coefficient of determination (ANOVA: all regression coefficients significantly different from zero, *P* < 0.001). For further explanation see Table 2.

Y	X	Sex/stage	Intercept	Slope	N	r^2
TBL	CL	M	6.7152	2.3601***	42	0.9808
		F	3.0066	2.7877***	77	0.9912
ln TBL	ln CL	M	1.5892	0.7947*	42	0.9832
		F	1.5131	0.8378*	77	0.9946
TBL	TL	M	−0.3077***	6.5690	42	0.9602
		F	−1.3013***	7.1252	77	0.9599
ln TBL	ln TL	M	1.8331***	1.0230	42	0.9697
		F	1.8020***	1.0752	77	0.9828
CL	TL	Σ	−1.6790	2.5703	119	0.9531
ln CL	ln TL	Σ	0.3584	1.2670	119	0.9780
ln W	ln TBL	M	−7.1200	3.5971*	42	0.9293
		F	−6.1783	3.3230*	77	0.9877
ln W	ln CL	Σ	−1.1646	2.7794	119	0.9724
ln W	ln TL	M	−0.5086**	3.6694	42	0.8960
		F	−0.1840**	3.5683	77	0.9682
ln Fec	ln TBL	Stage I	−7.1847**	4.1710	23	0.8721
		Stages II and III	−4.1974**	3.2367	26	0.6250
ln Fec	ln CL	Stage I	−1.2541*	3.6294	23	0.7143
		Stages II and III	0.4705*	2.8167	26	0.5887
ln Fec	ln TL	Stage I	0.6595**	4.3252	23	0.7388
		Stages II and III	1.8959**	3.3493	26	0.6126
ln Fec	ln W	Stage I	0.1670***	1.3382	23	0.8592
		Stages II and III	1.8206***	0.9655	26	0.6280

size (Tables 2–5). As an exception, the regression of egg number on telson length (TL) was in *P. northropi* not significant statistically. In this species, the size range of ovigerous females was very small. Consequently, fecundity showed only weak correlations with size or W. Moreover, TL showed in general the lowest correlations with other biometric data. Fecundity in terms of total egg mass can easily be obtained by multiplication of the initial egg weight in a given species (Table 1) with the regressions for egg number on female body size.

In comparison with all other species, *M.*

Table 6. *Potimirim potimirim*. Parameters of linear regressions (with or without preceding ln-transformation of dependent and independent variable, *Y*, *X*) describing relationships between measurements of body size (mm), and weight (mg). TBL = total body length; CL = carapace length; TL = telson length; W = dry weight; *N* = number of observations (data pairs); r^2 = coefficient of determination (ANOVA: all regression coefficients significantly different from zero, *P* < 0.001). For further explanation see Table 2.

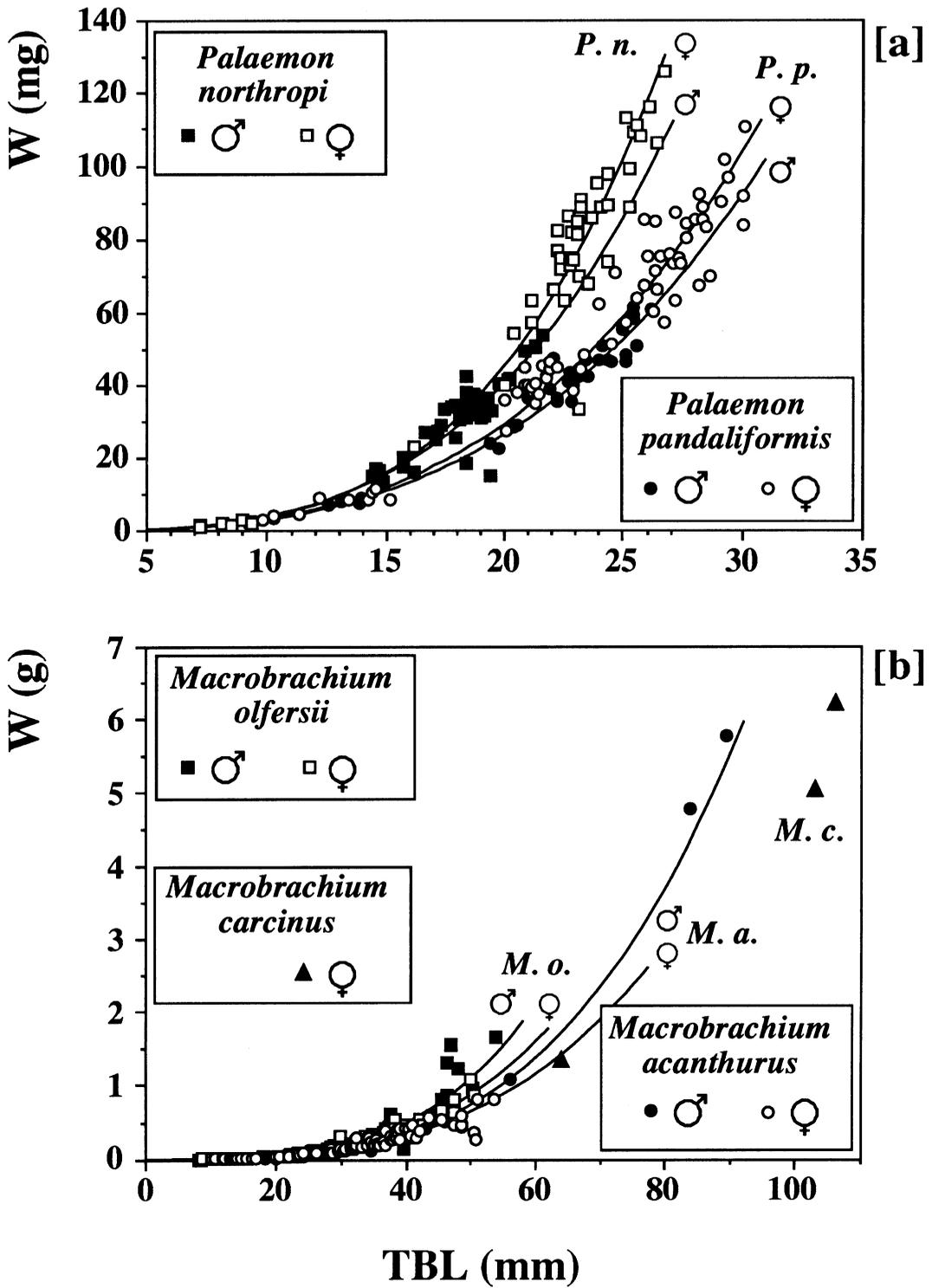| Y	X	Intercept	Slope	r^2
TBL	CL	1.3952	3.1252	0.9416
ln TBL	ln CL	1.3301	0.9380	0.9735
TBL	TL	0.3871	7.5257	0.9518
ln TBL	ln TL	2.0442	0.9993	0.9776
CL	TL	−0.0215	2.2532	0.8850
ln CL	ln TL	0.7806	1.0347	0.9471
ln W	ln TBL	−5.9250	3.2357	0.9798
ln W	ln CL	−1.6524	3.0568	0.9675
ln W	ln TL	0.7106	3.1999	0.9380

Fig. 1.   Allometric relationship between total body length (TBL, mm) and dry weight (W, mg or g) in males and females of (a) *Palaemon northropi* (*P.n.*), *P. pandaliformis* (*P.p.*), (b) *Macrobrachium acanthurus* (*M.a.*), *M. olfersii* (*M.o.*); three occasional measurements from *M. carcinus* (*M.c.*) included; for fitted parameters of regression equations see Tables 2–5.
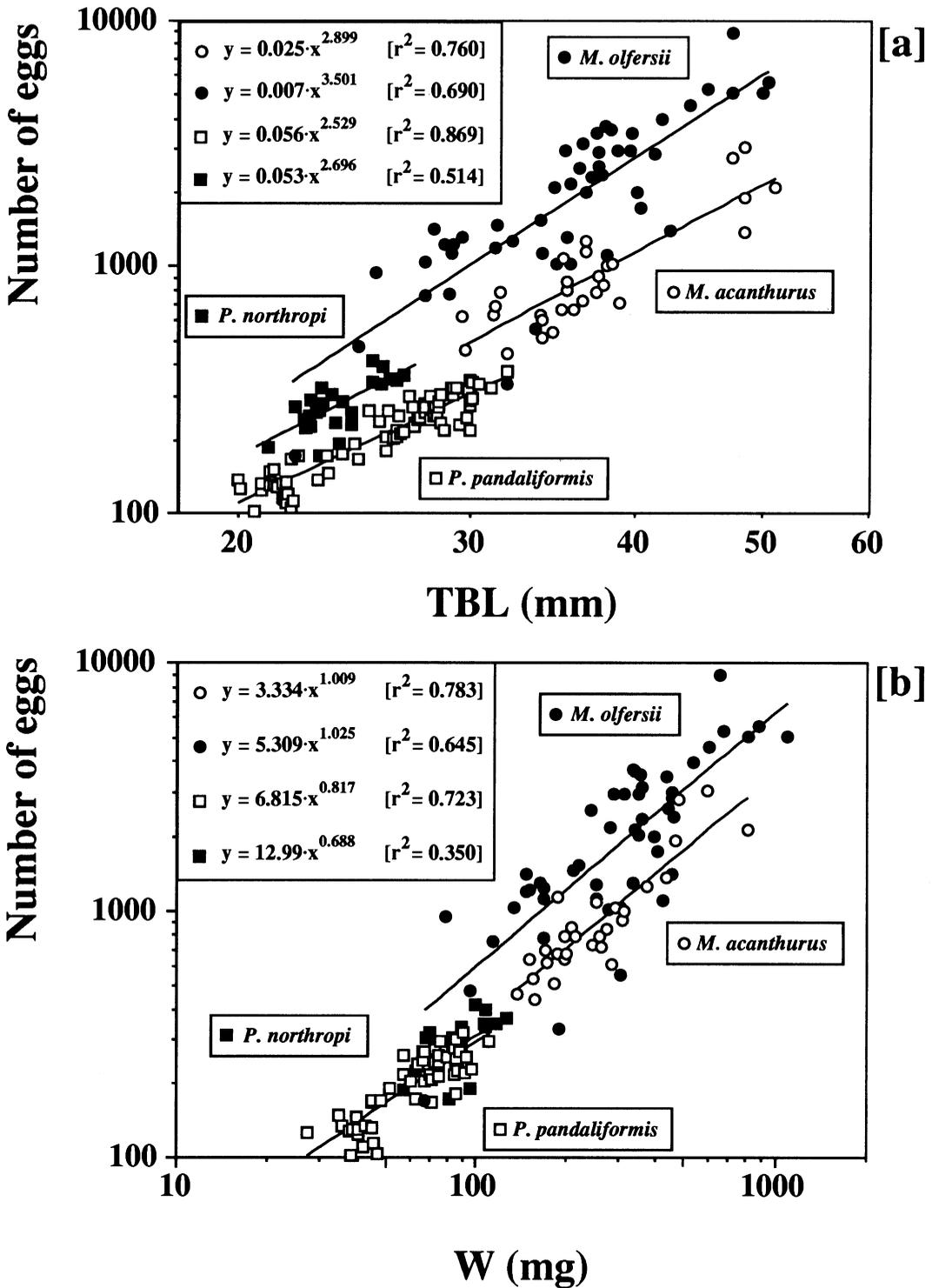
Fig. 2. Relationship between fecundity (number of eggs, pooled data of all developmental stages) and (a) total body length (TBL, mm), (b) female dry weight (W, mg), in: *Palaemon northropi, P. pandaliformis; Macrobrachium acanthurus, M. olfersii*; allometric regression equations and coefficients of determination, r^2, given in graphs; for fitted parameters of regression equations calculated separately for eggs in early and late stages of development see Tables 2–5; graphic presentation of regressions linearized by ln-ln-transformation.

olfersii showed a stronger dependence of fecundity on size (TBL), as indicated by a significantly steeper slope parameter ($P < 0.05$). In addition, our regressions showed species-specific differences in the overall level of egg production. A comparison of pooled data of fecundity in *M. acanthurus* and *P. northropi* (these regressions were not significantly different) with those in *P. pandaliformis* showed a highly significant difference between the intercepts. This indicates an almost parallel shift of regression lines, i.e., differential fecundity at equal female size (Fig. 2a; $P < 0.001$). Among the species studied, *M. olfersii* showed the highest level of size-specific fecundity, *P. pandaliformis* the lowest.

These patterns change when fecundity is considered in relation to body W rather than TBL (Fig. 2b), reflecting species-specific differences in the size-weight relationships. The slopes of the regressions of egg number on W were similar in all species, without statistically significant differences. As in the relationship between egg number and TBL (cf. Fig. 2a), the overall level of fecundity in relation to female W was significantly higher in *M. olfersii* than in all other species (pooled data; differences between intercepts, $P < 0.001$). No significant interspecific differences between slopes or intercepts occurred among the other species.

Only three ovigerous females of *M. carcinus* were caught (64, 103, and 106-mm TBL; 1.352, 5.057, and 6.2214 g W), carrying 16,100, 34,500, and 50,300 eggs, respectively. These data fit well into the relationships between fecundity and female size or W in *M. acanthurus*. In our material of the atyid shrimp *Potimirim potimirim,* a small number of observations ($N = 8$) and a narrow size range of ovigerous females (16.1–18.1-mm TBL) did not allow for calculating regressions of fecundity on other biometric data. The number of eggs per female varied in this species between 103 and 410 ($\bar{x} \pm$ SD = 247 ± 91).

Egg Size and Reproductive Output (RO)

Initial values of egg size and W were lowest in *M. olfersii,* highest in *P. pandaliformis* (Table 1). These life-history parameters did not show a relationship with the genus, the maximum size, or the ecology of the species.

When egg production (expressed as W of the entire egg mass) is considered in relation to the W of ovigerous females, the reproductive output (RO) is obtained (Table 1). On the average, this was significantly lower in the only marine shrimp studied here, *P. northropi,* than in the three fresh-water species ($P < 0.01$). The highest values were observed in species of *Macrobrachium.* The mean RO in *M. olfersii* was also significantly higher than in *P. pandaliformis* ($P < 0.05$). In *M. olfersii,* the RO was significantly influenced by female body size (TBL), tending to increase in larger females (ANCOVA; $P < 0.01$). By contrast, no significant dependence on female size or weight could be detected in the other species.

DISCUSSION

Size at the Onset of Maturity (SOM) and Minimum Sexable Size (MSS)

Size at the onset of maturity (SOM) is considered as a key life-history parameter that should reflect also the longevity and life-time investment in reproduction of a species. In all species studied here, the minimum size of ovigerous females (Table 1) was considerably below that reported in the literature (Holthuis, 1952; Gomes Corrêa, 1977; Lobão, 1977), suggesting that our data represent a fair approximation of their actual SOM. In both species of *Palaemon,* these values were surprisingly similar to those in a much larger shrimp, *M. olfersii,* suggesting a poor correlation with the maximum size of the species. However, size at the onset of egg production may vary among conspecific populations (Wenner *et al.,* 1985).

The comparability of SOM in different species is increased when it is given as a relative number, the RSOM. This is calculated as the quotient of SOM in relation to maximum body size in a species; this is estimated as parameter L_∞ of the von Bertalanffy equation of growth (Charnov, 1990). In decapod taxa with a terminal molt (e.g., majid crabs; Hartnoll, 1985), the RSOM is identical with the maximum size (RSOM = 100%). Other taxa continue to molt after reaching sexual maturity, but often with little additional growth. In the shrimp family Pandalidae, Charnov (1990) observed a rather constant RSOM of approximately 55%, regardless of the species or latitude, and suggested that this might be a more generally applicable number in the Crustacea. When female SOM values from the present study are related to max-

imum body size of females in the species studied, an estimate of their RSOM is obtained. Since our material was not representative of overall size range, we may use data from the literature. According to Sawaya (1946), Holthuis (1952), and Gomes Corrêa (1977), maximum female size of about 44 mm TBL may be assumed for *P. northropi*, 43 mm for *P. pandaliformis*, 65 mm for *M. olfersii*, and 110 mm for *M. acanthurus*. From these data, RSOM values of 48, 46, 34, and 27%, respectively, are calculated for these species of shrimps.

These figures indicate a greater interspecific variability than assumed by Charnov (1990), and all are well below the 55% suggested as a possible biological rule. This indicates that the onset of female maturity may occur early within the life cycle of caridean shrimps. In fact, their actual RSOM might be even smaller, because the maximum size reported in the literature is only an approximation of the theoretical maximum, L_∞, and the possible minimum size of ovigerous females may still be smaller than in our material. On the other hand, our estimates may be biased due to geographic variation in both SOM and maximum size. If our estimates are correct, the RSOM is, in the species studied, inversely correlated with maximum body size.

As another life-history parameter, the minimum sexable size (MSS) has practical value. We defined it here as the minimum body size of males with a developed appendix masculina. This is not necessarily identical with male SOM, but it allows for sex separation in studies of population structure. The MSS was surprisingly similar in the species studied (Table 1). As a percentage of the maximum TBL reported for males (Sawaya, 1946; Holthuis, 1952; Gomes Corrêa, 1977), the MSS was reached with 28, 33, 6, and 17% in *P. northropi*, *P. pandaliformis*, *M. acanthurus*, and *M. olfersii*, respectively. Since no unsexable juveniles occurred in our material of *M. acanthurus*, the actual MSS of this species might be even smaller than 6% of maximum male size.

Morphometric Relationships among Size Dimensions

In all species studied, statistically significant sex-specific differences were observed in the morphometric relationships among different dimensions of body size. However, different intercepts are difficult to interpret, because this parameter may represent an extrapolation below the range measured, and its comparison may have little biological meaning. By contrast, the slope should be a more useful growth parameter, indicating a different degree of dependence among size dimensions. For intra- and interspecific comparisons, however, the same regression model must be used. In our study, the model with the best fit (highest r^2) was almost consistently an allometric function (linear after log-log transformation). On the other hand, a linear model has also been used in the literature, and to facilitate comparisons, we give linear regressions.

In agreement with the literature, our data show that carapace length is a reliable measurement of the total body size of shrimps. When the relationships between TBL and CL in the species studied are described with the allometric model, the slope parameter is similar to that in other palaemonid shrimps (Wickins, 1972), while higher values were reported for penaeids (Kutkuhn, 1966; Rodríguez, 1987). This may indicate a difference in growth characteristics of caridean and penaeid shrimps. However, when the linear model is applied, the slope of this relationship varied in our study within the same range as reported for several species of both caridean (Shafi et al., 1977; Shumway et al., 1985; Rodrigues Capitulo and Freyre, 1989; Gabche and Hockey, 1995) and penaeid shrimps (Farmer, 1986; Dall et al., 1990). Not enough data are available to allow for generalizations of morphometric patterns in shrimps, in particular with regard to sexual dimorphism in the proportions of CL and TBL. The available data do not show a relationship of these traits with geographic origin, climate, or ecology of the species.

Since telson length (TL) has been used very little as a measure of body size, no interspecific comparisons with literature data from other palaemonid shrimps are possible. Our data show that TL is a fairly good predictor of TBL or CL, although its relatively small size, individual variability, and difficulties in its measurement (e.g., including versus excluding terminal spines) cause high residual errors in regressions on other size dimensions, weight, or fecundity. We suggest that TL should be measured in cases where restricted quantities of live material are available, re-

Table 7. Slope parameters of the allometric size-weight relationship (linear after ln–ln transformation of size and weight data) in several palaemonid and one atyid shrimp species; given separately for males and females, where data are available; otherwise for pooled data, Σ; size measured as total body length (mm; except for Hartnoll and Salama, 1992: carapace length, mm); weight as fresh or dry weight (FW, W, mg); * = *M. olfersii* (Holthuis, personal communication).

| Species | Slope | | | Size | Weight | Reference |
	Males	Σ	Females			
Palaemon northropi Rankin	3.29		3.61	TBL	W	present study
P. pandaliformis Stimpson	3.02		3.06	TBL	W	present study
P. xiphias Risso	2.97		3.14	TBL	FW	Guerao *et al.* (1994)
P. paucidens de Haan	3.07		3.20	TBL	FW	Ogawa and Kakuda (1988)
P. elegans Rathke		2.82		CL	W	Hartnoll and Salama (1992)
P. serratus Pennant		3.76		TBL	W	Reeve (1969)
Palaemonetes argentinus Nobili	3.04		3.34	TBL	FW	Donatti (1986)
Macrobrachium acanthurus Wiegmann	3.42		3.17	TBL	W	present study
M. olfersii Wiegmann	3.60		3.32	TBL	W	present study
M. holthuisi Genofre and Lobão*	3.38		2.58	TBL	FW	Lobão (1977)
M. völlenhovenii Herklots	2.88		2.92	TBL	FW	Gabche and Hockey (1995)
M. völlenhovenii Herklots		3.32		TBL	FW	Willführ-Nast *et al.* (1993)
M. rosenbergii de Man		3.23		TBL	FW	Wickins (1972)
M. rosenbergii de Man		3.36		TBL	FW	Kuris *et al.* (1987)
M. lamarrei Edwards		3.53		TBL	FW	Shafi *et al.* (1977)
M. mirabilis Kemp		2.68		TBL	FW	Shafi *et al.* (1977)
Potimirim potimirim Müller			3.24	TBL	W	present study

quiring nondestructive sampling procedures, e.g., size measurements in cast exuviae. In such materials, it is usually impossible to measure TBL, and that of CL may be difficult, because the carapace tends to be deformed in shrimp exuviae.

Size-Weight Relationships

The allometric relationship between size and weight is consistently described in the literature with a power function (Kurata, 1962; Hartnoll, 1985). The logarithmic transformation of size and weight data "is necessary in order to conform more closely to the assumptions of linear regression analysis regarding homogeneity of error variance over the range of the equation" (Bird and Prairie, 1985). While the intercept depends strongly on the dimension of size measured in a particular study, the slope should be more independent of this and other methodological details. An interspecific comparison of slope parameters of size-W relationships in shrimps is given in Table 7. Among these species, variation in the slope appears to be unrelated to the generic or family position, and to the specific ecology or geographic origin.

Sex-specific differences in this relationship were observed in the species studied (only in *P. northropi* not significant statistically), and in numerous other caridean and penaeid shrimps (Lobão, 1977; Donatti, 1986; Rodríguez, 1987; Ogawa and Kakuda, 1988; Dall

et al., 1990). In species of *Palaemon* and *Palaemonetes*, a higher slope was consistently observed in females, while species of *Macrobrachium* show the opposite tendency (with the possible exception of *M. völlenhovenii* Herklots; Table 7). The faster weight gain in relation to TBL in female *Palaemon* and species of *Palaemonetes* may be caused by proportionally greater tissue production in the ovaries compared with that in the testes. This effect should occur also in species of *Macrobrachium*, but here it may be overcompensated for by stronger sexual dimorphism in other organs, namely, by disproportionate growth of chelae in large males.

Size-Specific Fecundity

The relationship between female size and egg number is usually described as an allometric function equivalent to that between size and weight (Hartnoll, 1985; Somers, 1991), although linear regressions have also been used (e.g., Shumway *et al.*, 1985; Corey, 1991; Corey and Reid, 1991). Furthermore, fecundity has been described as a function of female carapace volume (Corey and Reid, 1991; Reid and Corey, 1991) or body weight (Clarke, 1993; present study). Since an allometric function is the most commonly used model of size-specific fecundity, the slope parameter of the linearized regression equation (ln egg number regressed on ln TBL or CL) may be compared among species or popula-

Table 8. Slope parameters of the allometric size-fecundity relationship (after ln–ln transformation of size and egg numbers) in several palaemonid shrimp species; size measured as total body length (mm; except for Yan, 1987; Bauer, 1991: carapace length).

Species	Slope	Habitat	Reference
Palaemon northropi Rankin	2.70	marine	present study
P. pacificus Stimpson	2.60	marine	Emmerson (1985)
P. xiphias Risso	3.59	marine	Guerao *et al.* (1994)
P. elegans Rathke	2.57	marine-estuarine	Hoglund (1943); Somers (1991)
P. pandaliformis Stimpson	2.53	freshwater-estuarine	present study
P. paucidens de Haan	2.26–2.78	freshwater	Mashiko (1982); Ogawa and Kakuda (1988)
Palaemonetes pugio Holthuis	2.62	estuarine	Yan (1987)
P. vulgaris Say	2.37	estuarine	Yan (1987)
Leander tenuicornis Say	3.17	marine	Bauer (1991)
Periclimenes americanus Kingsley	3.28	marine	Bauer (1991)
Macrobrachium acanthurus Wiegmann	2.90	freshwater	present study
M. olfersii Wiegmann	4.17	freshwater	present study
M. nippoense de Haan	2.68–4.02	estuarine-freshwater	Mashiko (1983, 1990)
M. amazonicum Heller	0.93	freshwater	Collart (1991)

tions (Table 8). In our study, this index varied between 2.6 and 2.7 in species of *Palaemon*, and from 2.9 to 4.2 in species of *Macrobrachium*. Among other palaemonid species, the size-dependence of fecundity varies without showing a relationship with the habitat of the adult population (fresh water, brackish water, or marine; cf. Corey and Reid, 1991; Reid and Corey, 1991); it appears to be particularly strong in *M. olfersii*.

Significantly different intercepts (i.e., parallel shifts) in fecundity-size regressions, by contrast, seem to be related to different habitats. In palaemonid shrimps from Japan, both intra- and interspecific variation were shown in the overall level of fecundity (Mashiko, 1982, 1983, 1990). Fresh-water populations tend to produce a smaller number of larger eggs, whereas those living in estuaries produce more but smaller eggs. In the present study, the fresh-water species *P. pandaliformis* showed a significantly lower level of size-specific fecundity than the marine congener *P. northropi*. However, when fecundity was regressed on W rather than TBL, similar relations were obtained in these ecologically different species of *Palaemon*. The two species of *Macrobrachium*, which live together in the same habitat, differed greatly in this respect (Fig. 2). This demonstrates that these life-history traits may be affected by methodological details, and that they may be more related to taxonomic position than to climatic variables.

To make intercept parameters universally comparable among literature data, and thus, to identify possible relationships between size-specific fecundity and habitat conditions,

a standardization of size and weight measurements is necessary. Since the length of spines on the rostrum and telson may vary considerably among species, even among individuals, we suggest that measurements of CL and TBL be taken from the rear margin of the eye orbit rather than from the tip of the rostral spine. The rear margin of the telson (without terminal spines) should define the posterior mark for measurements of body size. Moreover, we suggest the general use of the allometric model for regressions of fecundity on size or weight, since this is analytically simple and independent of the relative scale (for discussion of various models, see Somers, 1991).

Egg Loss

While the number of freshly laid eggs per female represents its "realized reproduction," the number of eggs in late stages of development is closer to the "actual reproduction," i.e., the number of larvae produced (Corey, 1991). The latter is lower, due to various causes of brood mortality (Kuris, 1991; Lardies and Wehrtmann, 1996; Ohtomi, 1997). Egg loss is thus another life-history parameter that can be compared among species, populations, size groups, or habitats. Quantitative estimates are possible when size- or weight-specific fecundity is compared between egg clutches in early and late stages of embryonic development, and a significant decrease occurs between the intercept parameters. When egg loss varies significantly with female size, the slope of this relationship should change.

In our material, significantly reduced intercept parameters in regressions of fecundity versus female W indicate substantial egg losses in *P. pandaliformis* and *M. acanthurus*. Calculation of theoretical egg numbers in early and late stages of development suggests that the percentage of egg loss in these species may amount to maximally about 23%.

Egg Size

In decapods that reproduce in fresh water, egg size is frequently enlarged compared with that of marine relatives (Mashiko, 1982, 1983; Anger, 1995). Among the species studied here, we should thus expect the smallest eggs in the marine species *P. northropi*. In fact, they are smaller than in the limnic congener *P. pandaliformis*. However, they are larger than in *M. olfersii*, which is frequently encountered several kilometers upstream in rivers and mountain streams (McNamara and Moreira, 1987; López and Pereira, 1994). The difference in egg size between the two species of *Macrobrachium* is difficult to explain in this context, since these shrimps have a similar ecology. Thus, egg size is in these species apparently not related to ecological traits.

Within a group of related taxa, large eggs frequently indicate an enhanced endotrophic potential (lecithotrophy) of early larvae (Anger, 1995). In *P. northropi*, no experimental evidence of lecithotrophy has been shown, in spite of relatively large eggs. In contrast, all fresh-water palaemonids investigated here are known to develop through the first larval stage in the absence of food: *P. pandaliformis* (see Bakker, 1989), *M. olfersii* (see Moreira *et al.*, 1979; McNamara *et al.*, 1980), *M. carcinus* (see Choudhury, 1971a), *M. acanthurus* (see Choudhury, 1971b). This gives the larvae sufficient time to leave fresh-water streams or rivers, where strong water currents may prevail and plankton production is low. In conclusion, egg size alone seems to be a poor predictor of the nutritional independence of early larvae, suggesting that the chemical composition of the eggs must also be considered (Anger, 1995).

Reproductive Output

The "mass-specific brood mass" (Clarke, 1987) or reproductive output, RO, is another frequently used parameter in life-history studies, quantifying the energetic investment of

a species into egg production (Hines, 1982, 1988, 1991; Hartnoll, 1985; Clarke *et al.*, 1991). For several species of pandalid, hippolytid, and crangonid shrimps, average RO values ranging from 12–24% (on a wet-weight basis) were reported, increasing with rising environmental temperature (Clarke, 1987; Clarke *et al.*, 1991). On a dry-weight basis, these values would probably be slightly higher, due to differential water content of the eggs and the female body (for recent discussion, see Luppi *et al.*, 1997). Thus, the average RO values measured in the present investigation (ranging from 15–22%) compare well with those in temperate shrimps. In contrast, considerably lower ROs have been reported in most brachyuran and anomuran crabs (Hines, 1982, 1988, 1991; Lardies and Wehrtmann, 1996; Luppi *et al.*, 1997). The marine species *P. northropi* had a significantly lower RO than all fresh-water shrimps in our study. Future comparative investigations should show whether this was a coincidence or a rule of reproductive ecology.

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