



Somatic and gametic resources in male rock shrimp, *Rhynchocinetes typus*: effect of mating potential and ontogenetic male stage

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Investment in somatic and gametic resources may vary during the ontogeny of an organism. In the rock shrimp, *Rhynchocinetes typus*, males pass through several stages during ontogeny, and a dominance order reflects this developmental order (typus < intermedius < robustus). During mating in a competitive environment, subordinate males use a sneaking tactic characterized by rapid placement of many spermatophores, but dominant males transfer few spermatophores during matings. We therefore hypothesized that males in the different ontogenetic stages (1) invest differently in somatic and gametic growth and (2) differ in their ability to engage in multiple matings. The relative weight of the hepatopancreas (adjusted for total body weight), an organ related to somatic growth, was significantly lower in robustus males than in all other ontogenetic stages examined. The relative weight of the vas deferens (Vd), a measure of sperm reserves, was significantly higher in robustus males than in males in the other stages. In typus males that had mated once, the total weight of Vd was significantly lower than in unmated typus males, but no such difference was found in robustus males. All robustus males mated successfully with five females during 5 consecutive days, but many typus males failed to mate after the second or third day. Typus males that mated successfully with females placed significantly more spermatophores than did robustus males during the first mating but not in subsequent matings. The results suggest that robustus males, in contrast to typus males, can invest more in sperm production and due to their ability to defend a female, can use spermatophores economically allowing them to mate with subsequent females. We conclude that, during ontogeny, *R. typus* males invest simultaneously in somatic and gametic growth in accordance with their mating behaviour and chance to mate. In this and other crustacean species, male resource investment during ontogeny thus may depend on their probabilities at different ontogenetic stages for obtaining mating opportunities.

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Production of gametes requires energy, and ultimately it is the availability of energy that determines how much an organism can invest in reproduction. Adult organisms must allocate available energy to different requirements, namely, maintenance of body functions, production of new body tissue and production of gametic resources. When energy is limited, organisms reduce their reproductive efforts (Parker 1992) or even stop reproducing altogether (Baba et al. 1999). Metabolic costs may be so high that limited energy remains available for production of gametic resources (Honkoop et al. 1998). Depending on the species, developmental stage or physiological state, the proportional allocation of resources to distinct requirements is variable. For example, most insects do

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not grow after reaching sexual maturity, so they do not need to invest energy for somatic growth while being sexually active. In contrast, many fish and most marine invertebrate species continue to grow after reaching sexual maturity, and available energy must be divided between maintenance, production of gametes (gametic growth) and new body tissue (somatic growth). In these species with indeterminate growth, all energy not necessary for maintenance (surplus energy, Heino & Kaitala 1999), is available for gametic and somatic growth.

Partitioning of surplus energy between somatic and gametic growth usually shows an inverse relationship. Individuals that invest in reproduction may have substantially lower growth rates than individuals that delay reproduction (fish: Taborsky 1994; crustaceans: Berglund & Rosenqvist 1986). Abstaining from reproduction during a given breeding cycle may allow individuals to

allocate all available energy directly to somatic growth. These individuals may attain large sizes and have high reproductive success during subsequent reproductive periods (Taborsky 1994; Peterson & Warner 1998). Similarly, individuals that have reached a terminal stage do not need to invest in somatic growth and can invest all surplus energy in gametic growth. These considerations, lead to the prediction that, for species that continue to grow during adulthood, allocation of surplus energy to either somatic or gametic growth may largely depend on their respective ontogenetic stage. Although a wealth of models and hypotheses on energy allocation in reproductive males has been generated during the past three decades (starting with Parker 1970), resulting in many experimental and empirical studies, there are few data on ontogenetic changes in resource investment. This information is of particular importance in crustaceans and fish, where both males and females may reach sexual maturity at an early age (and small size) and continue to grow throughout part or most of their remaining lives. These animals must allocate a proportion of surplus energy to somatic growth, possibly imposing constraints on their gametic resources and consequently offspring production.

Although energy allocation to reproductive products (eggs) is well studied in female crustaceans (e.g. Sastry 1983; Hines 1992), production of sperm by male crustaceans is not. Studies on sperm competition in decapods (Koga et al. 1993; Urbani et al. 1998) have directed increasing attention towards production of gametic resources in male crustaceans (e.g. Kendall et al. 2001). Like males of other species (Dewsbury 1982), males of decapod species cannot participate in an unlimited number of matings (Powell et al. 1974) and may require at least several days to replenish their sperm reservoir (e.g. Kendall & Wolcott 1999). Small males of some decapod species do not have sufficient spermatid resources to fully fertilize female clutches (MacDiarmid & Butler 1999), which further indicates that sperm production in decapod crustaceans requires substantial energy. Male decapods should therefore administer their spermatid resources carefully and attempt to maximize their fertilization success. In species with intense male–male competition for access to mating opportunities and the risk of sperm competition, males use sperm plugs or mate guarding to improve chances of paternity (Diesel 1990; Bauer & Lin 1993; Jivoff 1997).

In the rock shrimp, *Rhynchocinetes typus*, oocytes are fertilized externally by spermatozoa released from spermatophores, which are attached by the male to the ventral side of the female's abdomen. The transfer of oocytes from the female oviduct to the abdomen usually lasts at least 60 min (Correa et al. 2000), and females may frequently change mates during this process (C. Correa, personal communication) – consequently, there exists ample opportunity for sperm competition in *R. typus*. Furthermore, because females become receptive asynchronously, the operational sex ratio is highly male biased and competition between males for access to receptive females is high (Correa et al. 2003). Males reach sexual maturity at the female-like typus stage, then grow

through several intermedium moult stages to the robustus stage, the terminal moult stage, in which males are characterized by their powerful first pereopods and strongly developed third maxillipeds (C. Correa & W. Stotz, personal communication). Competitive interactions between males are won by males in the most developed ontogenetic stage, robustus, which easily displace males in intermedium and typus stages from receptive females (Correa et al. 2003). Consequently, the probability of mating with multiple females in nature is high for robustus males but low for typus males. Because robustus males represent the terminal moult stage of male *R. typus*, they may also allocate all surplus energy to sperm production rather than to growth, possibly allowing them to mate multiply.

Based on these considerations, we hypothesized that robustus males have (1) larger sperm reservoirs and (2) a higher capability to engage in multiple matings than typus males. We tested these hypotheses using laboratory experiments.

METHODS

Collection and Maintenance of Rock Shrimp

Rock shrimp were collected in Bahia La Herradura near Coquimbo (29°58'30"S, 71°22'30"W), Chile, using two methods. Most subjects were sampled with a diver-operated airlift suction sampler (Wahle & Steneck 1991), and a small proportion of shrimp was caught with baited traps that were checked every morning. Immediately following capture, the shrimp were transferred to the flowing sea water laboratory on the university campus. In the sea water laboratory, male and female shrimp were maintained separately to avoid uncontrolled matings. All male subjects were maintained in sexual isolation for a minimum of 7 days. The shrimp were fed ad libitum with dead fish, molluscs, epifauna and the soft bodies of solitary ascidians. Male subjects were in the intermoult phase.

Ontogenetic stages

Four categories of ontogenetic male stages were distinguished: typus, early intermedium, advanced intermedium and robustus, as follows.

Typus stage. Males are female-like in appearance (Correa et al. 2000). Their third maxilliped is small with seven small teeth at the terminal end, the ratio of maxilliped length to cephalothorax length (ML/CL) is less than 1, their first pereopod is without hairs but has four small teeth on the dactylus.

Early intermedium stage. These males were similar to typus males, but on their first pereopod the first tufts of hair have developed.

Advanced intermedium stage. ML/CL is between 1 and 2.1, and their first pereopod bears patches of

hair, substantially denser than on early intermedium males.

Robustus stage. In this terminal ontogenetic stage, ML/CL is greater than 2.1, the propodus of the first cheliped bears a dense cover of hair, and the tip of the third maxilliped bears only one tooth (see also [Correa et al. 2000](#)).

Because males continue to grow during ontogeny, males in the early ontogenetic stages used in our study were smaller than those in the subsequent ontogenetic stages ($\bar{X} \pm SD$ cephalothorax length: typus: 13.77 ± 1.52 mm, range 11.1–18.0; early intermedium: 17.90 ± 1.60 mm, range 15.1–20.5; advanced intermedium: 18.88 ± 1.90 mm, range 14.9–21.7; robustus: 18.50 ± 2.17 mm, range 15.0–24.0). All males used herein had reached sizes at which they are sexually mature ([Correa et al. 2000](#); [Hinojosa, unpublished data](#)).

Ovigerous females were maintained in 15 small trays ($60 \times 40 \times 25$ cm deep) in groups of up to 40 females. Trays were checked every day for the presence of recently shed exoskeleton, whereupon the still-soft female was identified. These females were isolated until the next day when they were used for mating experiments following the protocol described in [Correa et al. \(2000\)](#). Female subjects varied between 11.6 mm and 16.2 mm CL.

Biometric Analysis

In crustaceans, the hepatopancreas (Hp) is an organ of great importance in digestive processes ([Dall & Moriarty 1983](#)), and it is important in the assimilation of energy, storage and mobilization of resources during the moulting process ([Travis 1955, 1957](#); [Sagi & Ra'anan 1988](#); [Vega-Villasante et al. 1999](#)). Thus, the size and weight of the Hp provides a good indication of somatic resources ([Sagi & Ra'anan 1988](#)). In male decapods, developing and mature sperm are stored in the vas deferens (Vd; [Sainte-Marie & Sainte-Marie 1999](#)); its weight provides a good indication of the gametic resources of male decapods ([Sagi & Ra'anan 1988](#); see also [Kendall et al. 2001](#)). Thus, we used the weights of Hp and Vd as proxies of the energy investment of the different ontogenetic male stages of *R. typus* in somatic and gametic growth, respectively.

Following 7 days of sexual abstinence, 20 males from each of the four categories of ontogenetic stages were selected randomly for the analysis of biometric data. The males were killed by a short incision through the central nervous system and their bodies were individually weighed. Males were then dissected to extract the Hp and Vd to determine their wet weight. All weight measurements were done with an analytical balance (± 0.1 mg), and length measurements were made with a regular caliper (± 0.05 mm).

For statistical analysis, all weight data were log transformed. The relationship between total body weight and organ weight was examined, and we tested for significant differences between the different ontogenetic male stages with analysis of covariance (ANCOVA) using total body weight as the covariable.

Mating History and Sperm Reservoirs

Randomly selected male rock shrimp of the typus and robustus stages were used to examine the effect of mating history on sperm reservoirs (Vd). Half of the males ($N=20$) were allowed to mate with a receptive female, and the other half (controls, $N=20$) were not given the opportunity to mate. Individual mating pairs were maintained separately in small trays ($20 \times 20 \times 15$ cm), where they were surveyed periodically to ensure that males had successfully mated with the female. If no mating attempt was observed over 2 h or if the female had no eggs under her abdomen at the end of the experiment we disregarded the replicate. If a successful mating was observed, we left the mating pair together until the male and female had separated again. Following a successful mating, the males were subjected to the analysis of their body measures as described above. Control males were analysed in the same way. Because the data were not normally distributed, we used nonparametric statistics (Mann–Whitney *U* test) to test for the effect of mating history on the weight of Vd for each ontogenetic male stage.

Mating History and Mating Behaviour

Male rock shrimp of the typus and robustus stages were allowed to mate successively with five receptive females. We exposed 36 typus and 11 robustus males to one receptive female on the first day, and thereafter only males that had mated successfully were offered subsequent mating opportunities during the days after a successful mating. Males that did not mate during a first opportunity ($N=25$ typus males) were not considered in the statistical analysis.

Following their introduction into a glass aquarium (20×30 cm bottom area, 12-litre volume), males and females were maintained separated from each other by an acrylic plate for an acclimatization period of 15 min. The separating plate was then removed, and each pair was observed for 30 min. If mating was initiated during this period, the pair was monitored throughout the entire mating process; otherwise the mating was considered unsuccessful. We counted the number of spermatophores transferred during each mating and determined the total mating time.

We counted the maximum number of successive matings that a male could realize successfully. A mating was considered successful if the male transferred spermatophores and the female thereafter carried developing embryos. Following a mating during which spermatophores were transferred, females were maintained for 5 additional days to examine whether their eggs had been fertilized. Females with unfertilized eggs lost these within 5 days after the reproductive moult. We tested for differences between typus and robustus males in the total number of successful successive matings (Mann–Whitney *U* test). Furthermore, we used a two-way ANOVA to examine whether the number of successive matings had an effect on the number of spermatophores that males placed during a mating. Because many typus males failed to mate during the experiment, some treatments (second

Table 1. Results of ANCOVA for common slope of regression and adjusted means examining differences in wet weight of hepatopancreas of male rock shrimp at different ontogenetic stages (typus, early intermedium, advanced intermedium, robustus; $N=20$ males of each stage)

	Sum of squares	df	F	P
Common slope				
Ontogenetic stage	0.035	3	1.364	0.261
Total body weight	1.293	1	150.423	<0.001
Ontogenetic stage*total body weight	0.047	3	1.823	0.151
Error	0.661	72		
Adjusted means				
Ontogenetic stage	0.684	3	25.885	<0.001
Covariable (total body weight)	1.293	1	146.832	<0.001
Error	0.661	75		

Data were log transformed for analysis.

Table 2. Results of ANCOVA for common slope of regression and adjusted means examining differences in wet weight of vas deferens of male rock shrimp at different ontogenetic stages (typus, early intermedium, advanced intermedium, robustus; $N=20$ males of each stage)

	Sum of squares	df	F	P
Common slope				
Ontogenetic stage	0.105	3	1.420	0.244
Total body weight	0.274	1	11.107	0.001
Ontogenetic stage*total body weight	0.123	3	1.660	0.183
Error	1.779	72		
Adjusted means				
Ontogenetic stage	2.178	3	28.623	<0.001
Covariable (total body weight)	0.346	1	13.653	<0.001
Error	1.902	75		

Data were log transformed for analysis.

through fifth mating opportunities) were not replicated to the same degree as others, and we used ANOVA with unequal replication (Zar 1999). Sample variances were homogeneous so we conducted the analysis with the untransformed data.

The number of eggs produced by female rock shrimp corresponds closely to their body length (Vásquez & Castilla 1982). Thus, the quantity of sperm transferred to a given female may also correspond to the body size of the female. We tested for a relation between the body length of a female and the number of spermatophores that she received from one male during a complete mating. All results from typus and robustus males that had mated successfully in the multiple mating experiment were pooled for this analysis. The size of spermatophores may also vary (MacDiarmid & Butler 1999), but we quantified only the number of spermatophores transferred by males.

RESULTS

Biometric Comparisons Between Ontogenetic Male Stages

The total body weight of males ranged from 1.4 to 14.8 g (typus: 1.4–4.9 g; early intermedium: 3.3–8.3 g;

advanced intermedium: 3.3–9.6 g; robustus: 3.3–14.8 g). The total weight of Hp ranged from 51.6 to 525.5 mg and the weight of Vd from 8.0 to 122.7 mg in individual males. The slopes of the regressions were homogeneous between males (Tables 1, 2), and after adjusting for the effects of total body weight, the ANCOVA revealed significant differences among male stages with respect to both Hp and Vd (Tables 1, 2). The Hp of robustus males was significantly smaller than that of the other ontogenetic male stages (Fig. 1a), but their Vd was significantly larger than that of the other male stages (Fig. 1b). Between the other ontogenetic male stages, these relationships did not differ significantly, with the sole exception that Vd differed significantly between early and advanced intermedium stages (Fig. 1b).

Mating History and Sperm Reservoirs

Because the weight of the Vd differed significantly between typus and robustus males, we conducted the analysis on the effect of mating history separately for each male stage. In typus males, the weight of the Vd decreased significantly after a successful mating event (Mann–Whitney U test: $U=53.5$, $N_1=20$, $N_2=20$, $P<0.05$; Fig. 2a). In robustus males, one successful mating did not

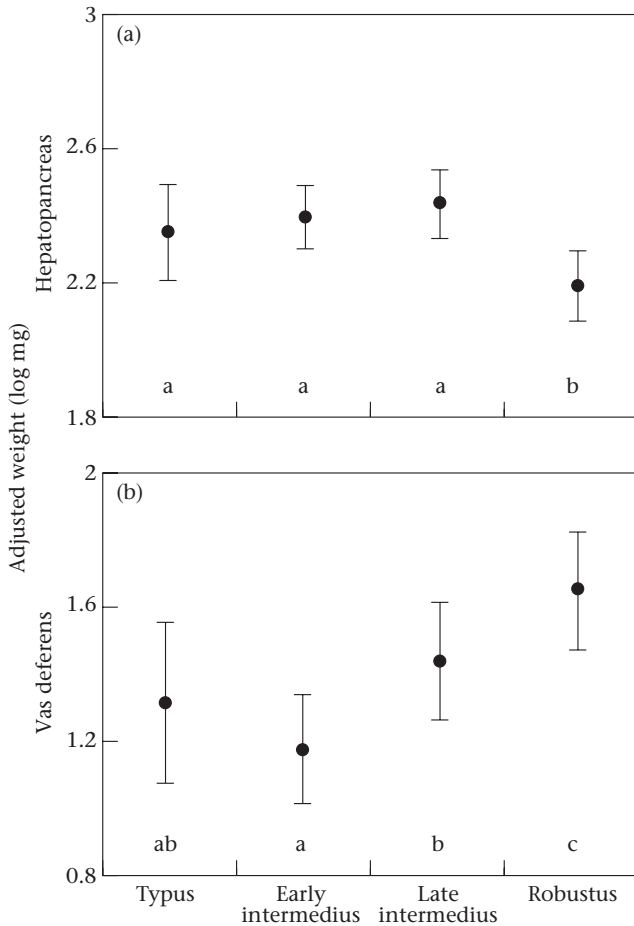


Figure 1. Mean±SD weight of (a) hepatopancreas and of (b) vas deferens of *R. typus* males at different ontogenetic stages after adjusting for effects of total body weight. Ontogenetic stages with the same letters did not differ significantly (ANCOVA on adjusted weights of respective organs, followed by Tukey test: $\alpha=0.05$; $N=20$ males at each stage).

significantly affect the weight of the Vd (U test, $U=189.0$, $N_1=20$, $N_2=20$, $P=0.766$; Fig. 2b).

Mating History and Mating Behaviour

Of 36 typus males that were offered a first mating opportunity, 11 successfully mated with a female, but when offered the chance to mate with multiple females on subsequent days, only three of these 11 typus males conducted the maximum possible number of multiple matings ($N=5$; Fig. 3a). In some of the later mating opportunities, typus males placed spermatophores, but females aborted the entire clutch; this never happened in robustus males, where all females developed viable embryos. In contrast to the typus males, all 11 robustus males mated successfully with a female during the first mating opportunity. Ten of these robustus males realized the maximum number of multiple matings over the 5 days of the experiment (Fig. 3b). Only one robustus male did not mate during the final opportunity, but the female

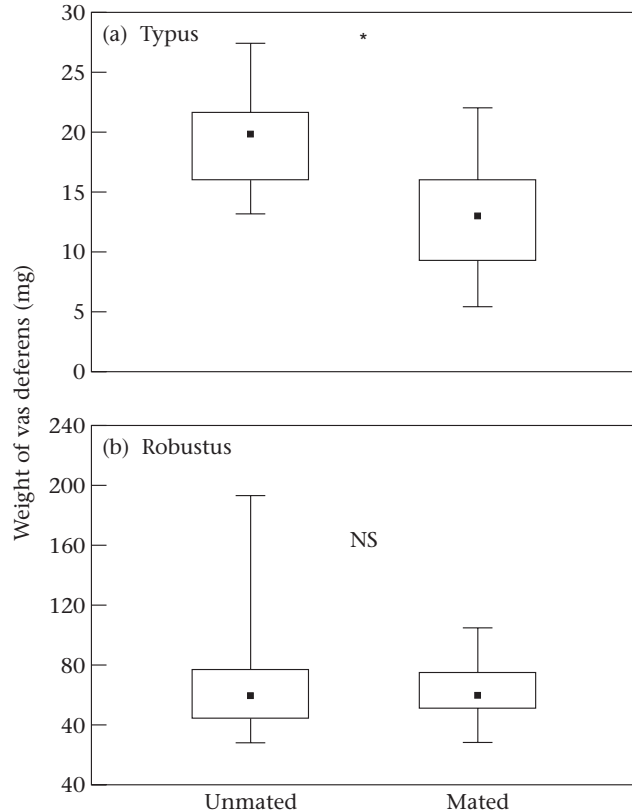


Figure 2. Weight of vas deferens of (a) typus and (b) robustus males that had not mated for at least 7 days and that had mated with a female within the past 5 h. Box plot shows range (whiskers), 25% and 75% quartiles (lower and upper edge of box) and median (dot); $N=20$ males of each treatment and ontogenetic stage. Note different scales for typus and robustus males. * $P=0.05$ (Mann–Whitney U test).

used during that day was nonreceptive (as we later confirmed by presenting her to an additional robustus male) and no additional receptive female was available. The average number of successful multiple matings obtained by typus males that engaged in a first mating was significantly lower than that obtained by robustus males (Mann–Whitney U test, $U=103.0$, $N_1=11$, $N_2=11$, $P<0.05$; Fig. 3a).

The two-way ANOVA revealed that the number of multiple matings had a significant effect on the number of spermatophores placed by a male during a mating opportunity (Table 3). Ontogenetic stage had no significant effect, but the interactive term did, because typus males transferred more spermatophores than robustus males during a first mating, but they did not differ during subsequent matings (Fig. 3c). During a first mating, typus males transferred a mean ± SE of 9.73 ± 0.68 spermatophores, which differed significantly from all other combinations (Fig. 3c). All typus males that participated in five subsequent matings placed, at most, half as many spermatophores in their last mating as in their first mating (number of spermatophores placed by three typus male in matings 1–5: typus a: 8, 8, 5, 4, 4; typus b: 8, 6, 4, 5, 2; typus c: 10, 7, 4, 3, 4). The number

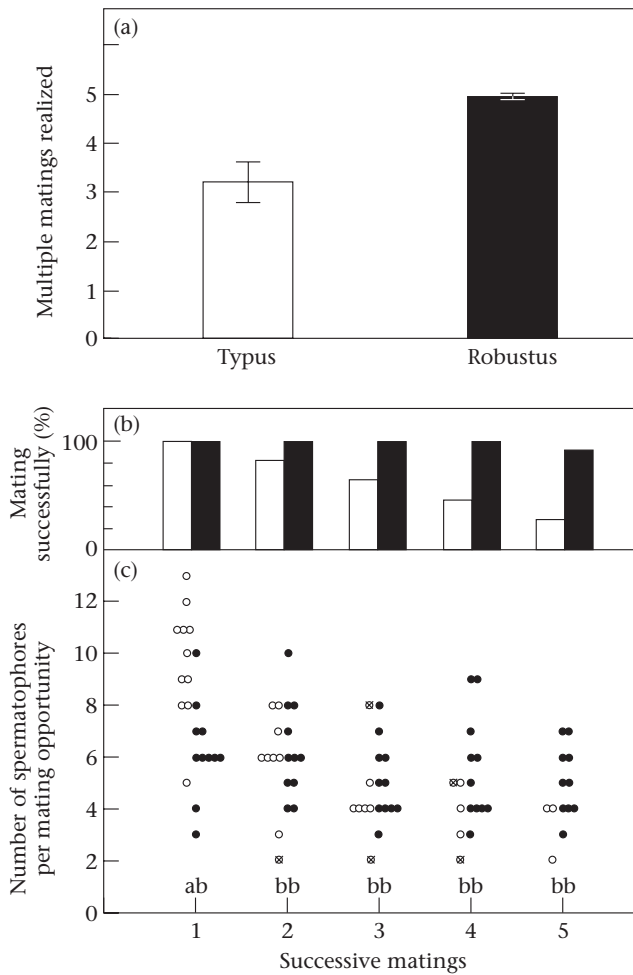


Figure 3. (a) Mean±SE number of multiple matings realized by typus and robustus *R. typus* males that were offered the opportunity to mate five times consecutively. (b) Percentage of typus and robustus males that mated successfully during five consecutive mating opportunities. (c) Number of spermatophores transferred by typus (○) and robustus (●) males during five consecutive mating opportunities. Data points marked with a cross were not included in statistical analysis, because females did not produce viable offspring; two-way ANOVA with unequal replication, followed by post hoc Tukey, $\alpha=0.05$; treatments that did not differ significantly are marked by the same letters.

of spermatophores transferred by robustus males during a first mating did not differ from that transferred during subsequent matings. Similarly, the number of spermatophores

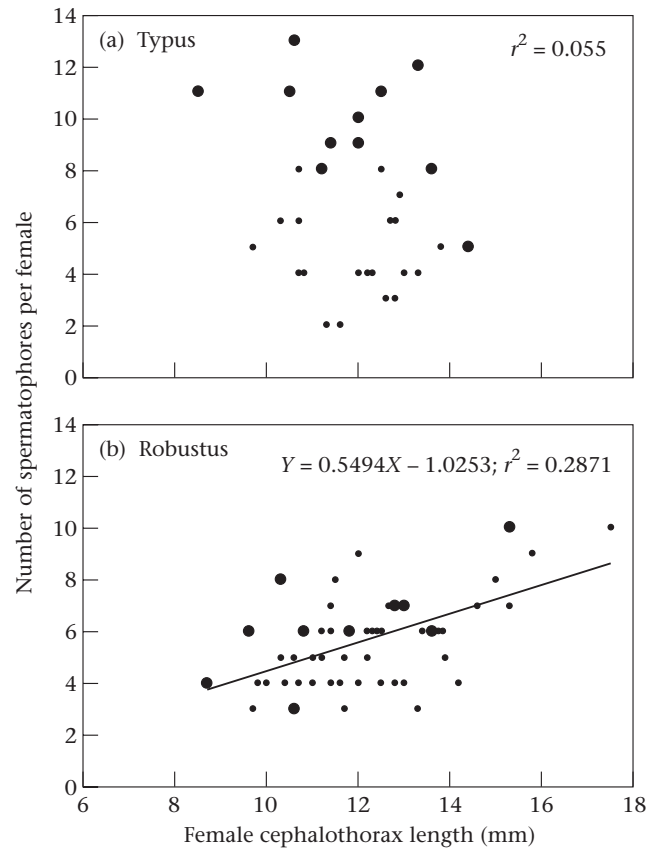


Figure 4. Relation between female cephalothorax length (mm) and number of spermatophores that each female *R. typus* received during a mating from (a) typus and (b) robustus males ($N=11$ each). All multiple matings of each type of male were pooled. Large dots indicate first mating and small dots indicate subsequent (2nd–5th) matings.

phores transferred by typus males during successive matings 2–5 did not differ between themselves, nor did it differ from the number transferred by robustus males during a given mating (Fig. 3c).

We found a significant relationship between the number of spermatophores transferred to a female and the body size of the female for robustus males ($F_{1,52}=20.95$, $P<0.001$), but not for typus males ($F_{1,28}=1.63$, $P=0.212$; Fig. 4). Robustus males transferred more spermatophores to large females than to small females (Fig. 4b).

Table 3. Results of two-way ANOVA for the number of spermatophores placed by male rock shrimp at different ontogenetic stages during five multiple matings with unequal replication and factors ontogenetic stages (typus, robustus) and multiple matings (1, 2, 3, 4, 5; $N=11$ males of each stage)

	Mean squares	df	F	P
Ontogenetic stage	0.385	1	0.127	0.723
Multiple mating	39.497	4	13.045	<0.0001
Ontogenetic stage*multiple mating	19.398	4	6.407	0.0002
Residual	3.028	74		

DISCUSSION

We found distinct differences between different ontogenetic male stages of *R. typus* in the weight of organs that are indicative of somatic (hepatopancreas) and gametic resources (vas deferens), respectively. Mating history had a significant effect on the availability of sperm reserves in the Vd of males in the first ontogenetic stage (typus), but not of males in the terminal ontogenetic male stage (robustus). This result is confirmed by the observations that robustus males mated with multiple females without showing signs of diminished mating capability, but many typus males failed during multiple matings. Because there is a strong dominance hierarchy in *R. typus*, in the chronological order of typus < intermedius < robustus, dominant (robustus) males have a higher probability of obtaining subsequent mating opportunities. In contrast, early ontogenetic male stages are at a strong competitive disadvantage, which suggests that (1) while participating in a mating, they administer sperm differently than do dominant males, and (2) whenever possible, they allocate resources to somatic growth to overcome their disfavoured position within the dominance hierarchy.

Sperm Investment of Ontogenetic Male Stages During a First Mating Opportunity

In species with strong male sexual competition, males may counteract the risk of sperm competition by different means, such as by sperm plugs (Diesel 1990; Bauer & Lin 1993), prolonged guarding (Jivoff & Hines 1998; Rondeau & Sainte-Marie 2001) or increasing their sperm investment (e.g. Svärd & Wiklund 1989; Birkhead & Møller 1992; Gage 1994; Hosken 1998). Dominance status and the imminent risk of sperm competition have strong effects on the sperm investment of a given male during a single mating (Parker 1998). Subordinate males that face a high risk of sperm competition are hypothesized to invest substantial amounts of sperm in a single mating to dilute sperm investments of potential competitors (Parker 1998). Our results confirm this for the rock shrimp: subordinate typus males placed significantly more spermatophores during a first mating opportunity than did dominant robustus males, even in a competition-free situation (see also Correa et al. 2000). This high sperm investment of typus males can be interpreted as a response to the imminent risk of sperm competition (see also Gage 1991). In nature, where *R. typus* occurs in high densities (personal observations), the probability of losing a receptive female to a dominant male is very high for a typus male (see also Correa et al. 2003). After a typus male loses a female, subsequent males may place spermatophores onto the female's abdomen, and, as a consequence, sperm enter in direct competition for fertilizations. Similar observations have also been made in free-spawning fish where subordinate males, which face a high risk of sperm competition, place large quantities of sperm whenever they gain access to a batch of fertilizable eggs (Taborsky 1994).

The high resource-holding power of dominant robustus males allows them to displace most competitors and thus

ensure 'private' fertilizations (sensu Peterson & Warner 1998). Consequently, robustus males face a reduced risk of sperm competition, because take-over of a female by other males is unlikely to occur. The low risk of sperm competition in robustus males may be reflected in the small number of spermatophores (compared with subordinate typus males) that they place during the first mating opportunity.

Sperm Investment of Ontogenetic Male Stages During Multiple Matings

Participation in a limited number of matings is common for subordinate males: for example, in several fish species, subordinate males participate in substantially fewer matings than do dominant males (Taborsky 1994). In *R. typus*, subordinate typus males, as a consequence of their high sperm investment during the first mating opportunity and of their small Vd, participate only in a few matings. We hypothesize that this limited capacity to engage in multiple matings in a laboratory setting reflects the low probability that subordinate males will obtain mating opportunities in nature.

In contrast to subordinate typus males, dominant robustus males showed high endurance, engaging in multiple matings without apparent mating fatigue. This result probably reflects their high potential to monopolize receptive females and thus to mate successively with different females in nature. Shapiro et al. (1994) made similar observations in a small coral reef fish, *Thalassoma bifasciatum*, in which pair-spawning 'terminal-phase' (TP) males that engage in such 'private' pair-spawnings invest fewer sperm than do males that participate in group spawnings. Shapiro et al. suggested that TP males invest only limited quantities of sperm in such a private spawning (sufficient to achieve fertilization of most eggs) in order to maintain sufficient sperm reserves to permit a high rate of subsequent spawning events (sperm economy). In our study, robustus males apparently responded to the need of large females (which in *R. typus* produce more eggs; e.g. Vásquez & Castilla 1982) for more sperm (Fig. 4). Our results thus suggest that robustus males of *R. typus* also use their sperm in an economic manner that allows them to fertilize several subsequent females interrupted only by short intermating intervals.

In other crustacean species, large or terminal-phase males also show a high capacity to mate multiply (Paul & Paul 1990; Sainte-Marie & Lovrich 1994). However, in most of these studies, multiple matings were not conducted daily, but rather were spread over irregular periods. Intervals between subsequent matings were usually at least 3 days and often on the order of tens of days (Paul & Paul 1990; Sainte-Marie & Lovrich 1994). These long mating intervals may also be responsible for the fact that small as well as large males mated successfully with multiple females (Table 4). Replenishment of sperm reservoirs in several male crustaceans has been reported to occur on the order of several days (Leung-Trujillo & Lawrence 1987; Jivoff 1997; Kendall & Wolcott 1999). Matings in decapod crustaceans often involve lengthy periods of precopulatory (and postcopulatory) mate

Table 4. Crustacean species in which males were exposed to multiple matings

	Size or stage	Matings	Mating interval (days)	Fatigue*	Mate guarding	Risk of sperm competition	Female sperm storage	Seasonal reproduction
<i>Chionoecetes opilio</i> ^{1,2,3,4}	Morphom, immature	5	3-10	No	Yes (days, weeks)	High	Yes	Yes
	Morphom, mature (T)	5	3-10	No	Yes (days, weeks)	Medium		
<i>Chionoecetes bairdii</i> ^{5,6,7}	Small (<100 mm CW)	2-6	6-25	No	Yes	High	Yes	Yes
	Large (>100 mm CW)	2-5	0-14	No	Yes (days, weeks)	Medium		
<i>Paralithodes camtschaticus</i> ^{8,9}	Small (<120 mm CL)	4	1-71	Yes	Yes (days, weeks)	?	No?	Yes
	Large (>120 mm CL)	4	1-71	No	Yes (days, weeks)	Low?	No	No
<i>Lithodes aequispinus</i> ¹⁰	Small (<100 mm CL)	3	1-2	Incapable of mating successfully	Yes	Low?	No	No
	Large (>100 mm CL)	3	1	No	No	High	No	No
<i>Rhynchocinetes typus</i> ¹¹	Small (typus)	5	1	Yes	No	High	No	No
	Large (robustus T)	5	1	No	Yes (hours)	Low		

T: Terminal stage; CW: carapace width; CL: carapace length.

*Mating fatigue was inferred when males either did not continue to mate, or could not fertilize all eggs of a female.

¹Sainte-Marie & Lovrich 1994; ²Sainte-Marie et al. 1997; ³Sainte-Marie et al. 1999; ⁴Sainte-Marie et al. 2000; ⁵Adams & Paul 1983; ⁶Paul & Paul 1992; ⁷Paul & Paul 1984; ⁸Powell et al. 1974; ⁹Paul & Paul 1990; ¹⁰Paul & Paul 2001; ¹¹This study.

guarding (Table 4). These guarding periods may allow males to replenish their sperm reservoirs (Jivoff 1997) and consequently to engage successfully in multiple matings as they become available in nature. In contrast to most of these species, in *R. typus* guarding time is relatively short; a single mating usually does not last more than 3 h (Correa et al. 2000). Given the proportion of robustus males in the field and the dominance hierarchy in *R. typus*, robustus males may obtain frequent mating opportunities, on the order of one every day (C. Correa, personal communication). Our results demonstrate that robustus males are capable of maintaining this high level of mating for some time. This result suggests that the capability of dominant male crustaceans to mate multiply apparently corresponds closely to their probability of obtaining matings in nature.

Investing in Somatic or Gametic Growth or Both?

Upon reaching sexual maturity, many organisms have the option of investing all available energy into reproduction or of continuing to invest a certain proportion into growth. In many crustacean species, growth continues throughout their lifetime (Hartnoll 1969; Sastry 1983). Male *R. typus* start to produce sperm early on during their ontogeny when they are morphometrically very different from the more advanced male stages (Correa et al. 2000), as has been reported in other crustaceans (Sagi & Ra'anan 1988; Elner & Beninger 1995). In the snow crab, *Chionoecetes opilio*, small (morphologically immature) males are capable of transferring spermatophores to females (Elner & Beninger 1995), yet the largest males (morphologically mature; Elner & Beninger 1995) usually obtain access to the most valuable females (Sainte-Marie et al. 1999). In snow crabs, adolescent males that engage in reproduction apparently compromise their somatic growth because they have slower growth rates than similar-sized non-reproductive males (Sainte-Marie et al. 1995). In the freshwater shrimp *Macrobrachium rosenbergii*, very small males with female-like appearance produce sperm at the total expense of somatic growth, which stagnates while they are reproductively active (Sagi & Ra'anan 1988). Similarly, for several fish species, males, regardless of their dominance status, do not get larger while participating in reproduction (Taborsky 1994). Some males that refrain from reproduction during a given reproductive season achieve very high growth rates compared with reproductive males (Taborsky 1994). Males of these species apparently pursue an either-or strategy, either investing in reproduction at the total expense of growth or allocating all surplus energy into growth, temporarily abstaining from reproduction. The results of the present study indicate that subordinate rock shrimp males pursue a double strategy: after achieving sexual maturity, they invest simultaneously in gametic and somatic growth. This opportunistic 'double strategy' may allow small (morphologically immature) males to take advantage of mating opportunities and to slowly overcome their disfavoured position in the dominance hierarchy.

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