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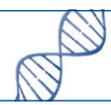
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Testing the role of male–male competition in the evolution of sexual dimorphism: a comparison between two species of porcelain crabs

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Theory predicts marked sexual dimorphism in terms of body size and body structures used as weapons (e.g. chelipeds) in gonochoric species with intense male sexual competition for receptive females and reduced or no sexual dimorphism in species where competition among males is trivial. We tested this hypothesis using a pair of closely-related species of symbiotic porcelain crabs as a model. In one species that inhabits sea anemones solitarily, competition among males for receptive females is unimportant. In a second species that dwells as dense aggregations on sea urchins, male–male competition for sexual partners is recurrent. We expected considerable sexual dimorphism in body size and weaponry in the urchin-dwelling crab and reduced sexual dimorphism in the anemone-dwelling crab. In agreement with expectations, in the urchin-dwelling crab, male body size was, on average, larger than that of females and males invested considerably more to cheliped length than females. Also supporting theoretical considerations, in the anemone-dwelling crab, sexual dimorphism in terms of body size was not detected and differences between the sexes in investment to cheliped length were minor. Interestingly, chelipeds were more developed both in males and females of the anemone-dwelling crab than in the urchin-dwelling crab as a result of the importance of these structures for monopolization of their naturally scarce anemone hosts. Another difference between the studied species was the existence of two clearly distinguishable ontogenetic phases in males of the urchin-dwelling crab but not in males of the anemone-dwelling crab. Whether the two different male morphs display different male reproductive strategies in the urchin-dwelling crab remains to be addressed. Other conditions that might additionally explain the observed differences in sexual dimorphism (e.g. female mate choice) between the studied species remain to be explored. © 2011 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2012, 105, 548–558.

ADDITIONAL KEYWORDS: mating system – ontogenetic phase – Porcellanidae – selection – symbiosis.

INTRODUCTION

Sexual dimorphism in terms of body size and body structures used as weapons (e.g. chelipeds) varies considerably in organisms with separate sexes. In some species, males attain body sizes considerably larger than that of females and/or invest heavily in structures that might be used as armament (e.g. in Phocidae seals, males are 3.56 times larger than females in the southern elephant seal *Mirounga*

leonina: Lindenfors, Tullberg & Biuw, 2002; in Charadrii birds, males are 1.5 times larger than females in *Chalidris melanotos*: Szekely, Reynolds & Figuerola, 2000). Other species display no (e.g. Phocidae seals: males are the same size than females in *Phoca caspica*: Weckerly, 1998) or reduced sexual dimorphism (*Homo sapiens*; Richmond & Jungers, 1995). Even in other species sexual dimorphism is reverse (e.g. in Phocidae seals, males are 0.68 times smaller than females in the Hawaiian monk seal *Monachus schauinslandi*: Weckerly, 1998; in Charadrii birds, males are 0.85 times smaller than

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females in *Chalidris canutus*: Szekely *et al.*, 2000). Furthermore, one of the most extreme cases of reverse sexual dimorphism is that of the banana spider *Nephila pilipes*, in which the body length of adult females is more 12 times greater than that of the adult males (Robinson & Robinson, 1973). Explaining the direction and extent of sexual dimorphism both in terms of body size and weapons is one of the most relevant yet still not completely understood problems in evolutionary ecology (Clutton-Brock, 2007).

Conditions assumed to drive sexual dimorphism both in terms of body size and weapons include fecundity selection in females (Andersson, 1994; Huber, 2005) and sexual selection in males (Emlen & Oring, 1977; Shuster & Wade, 2003). Among the latter, male–male competition is considered most relevant in driving differences between the sexes. All else being equal, when male sexual competition for sexual partners is intense and when monopolization of receptive females occurs via overt aggression, males are expected to attain larger body sizes than females and invest considerably in body structures use as weapons (Darwin, 1871; Andersson, 1994; Shuster & Wade, 2003; Baeza & Thiel, 2007). In males of these species, increasing investments to body size and weaponry augments their resource holding potential (*sensu* Parker, 1974a) and, thus, their opportunities to access and defend receptive females from other male competitors (Shuster & Wade, 2003; Baeza & Thiel, 2007). In turn, reverse sexual dimorphism in body size and no or reduced weaponry in males are expected in species in which males compete for females using exploitation tactics; males do not interact agonistically with other males but continuously search for females in an attempt to inseminate as many as possible in the shortest time period (Shuster & Wade, 2003; Bauer, 2004; Baeza & Thiel, 2007; although, for exceptions, see Lawrence 1992; Andrade, 1996). In this scenario, intrasexual selection favours a small body size and no weaponry because this leads to an increase in agility and in the encounter rate of males with potential mating partners (Shuster & Wade, 2003; Bauer, 2004; Baeza & Thiel, 2007). Lastly, no or reduced sexual dimorphism in body size and weaponry is expected in species in which the environment restricts any form of competition (e.g. interference and exploitation) among males for receptive females (Baeza & Thiel, 2007).

Although male sexual competition is considered an important evolutionary force driving sexual dimorphism in body size and weaponry, comparative studies on this topic are relatively rare (e.g. in various mammalian orders: Clutton-Brock, Harvey & Rudder, 1977; Weckerly, 1998; in various bird families: Szekely *et al.*, 2000; in *Anolis* lizards: Carothers, 1984; Butler & Losos, 2002; Lailvaux &

Irschick, 2007; in spiders: Huber, 2005). Furthermore, most of these studies have been conducted in terrestrial and marine vertebrates but only rarely in marine invertebrates. The scarcity of these studies in marine organisms holds true even for crustaceans, a species-rich group of invertebrates in which the diversity (but not the causes) of sexual dimorphism is well documented (e.g. isopods: Shuster, 1986; Shuster & Wade, 1991; crabs: Christy, 1983; caridean shrimps: Bauer & Abdalla, 2001; Baeza, 2007). Research in marine invertebrates (e.g. crustaceans) is warranted because it provides opportunities to test predictions fundamental to sexual selection theory and insights on the universality of male sexual competition in shaping sex-specific differences in morphology.

In marine crustaceans, crabs from the family Porcellanidae (porcelain crabs) represent ideal subjects to explore the effect of male sexual competition on the direction and extent of sexual dimorphism because of their recognized anatomical, ecological, and behavioural diversity (Haig, 1960; Baeza, 2007). Among them, adults of *Petrolisthes spinifrons* typically occur as solitary individuals on the sea anemones *Phymactis papillosa* and *Phymanthea pluvia* in the rocky intertidal of the southeastern Pacific (Baeza, Thiel & Stotz, 2001). Territoriality explains the solitary habit of this species; adult crabs use agonistic behaviours to fiercely defend ‘their’ sea anemones against conspecific intruders from the two sexes (Baeza *et al.*, 2001). Protection against visual predation, as achieved by homochromy with their hosts, appears to be one of the main benefits obtained by crabs when dwelling on anemones (Stuardo, 1962; Viviani, 1969). In addition, crabs use anemones as a vantage point for suspension-feeding and consume mucus and feces from hosts (Valdivia & Stotz, 2006). Thus, the high value of these anemones together with their low abundance, small body size (relative to crabs), and low structural complexity favours territoriality in this species (Baeza & Thiel, 2003). Importantly, because of their solitary habit, males are forced to (and do) switch among host individuals in search of sexual partners (Zander, Valdivia & Thiel, 2002). However, the frequency with which males shift among hosts appears to be constrained by the risk of predation that increases substantially for crabs when off hosts (Viviani, 1969; Werlinger, 1989; Baeza & Stotz, 1995; Thiel *et al.*, 2003). Adult females become receptive only during a short period of time immediately after molting and copulation does not last long, as indicated by the extremely low frequency of receptive females sharing their host anemones with mature males (Baeza *et al.*, 2001; Baeza & Thiel, 2003). Furthermore, the absence of a correlation between the body size of males and females comprising these rare

heterosexual pairs implies strong constraints on male–male competition (Baeza, 1999; Baeza & Thiel, 2007). Overall, the mating system of *P. spinifrons* is characterized by low opportunity for male–male competition.

By contrast to that reported for *P. spinifrons*, the sympatric congeneric crab *Petrolisthes mitra* occurs as aggregations (up to 25 individuals) in the morphologically complex and abundant sea urchin *Tetrapygus niger* (Baeza & Thiel, 2000). These groups are comprised of crabs of the two sexes and all life stages (Baeza & Thiel, 2000). Similar to *P. spinifrons* and other urchin-dwelling crabs (Reeves & Brooks, 2001), *P. mitra* seek protection from predation on their urchin hosts. However, host high abundance and large host body size together with considerable host structural complexity does not favour territoriality in this species (Baeza & Thiel, 2003). Males and females move freely and frequently within and among neighbor urchins so that the groups of *P. mitra* on individual hosts are continuously reshuffled (Zander, 2000). Adult males move more intensively than females among urchins. However, male crabs reduce their activity when a receptive female is present in the same host (Zander, 2000). Male crabs follow a mating strategy based on ‘search and interception’ of females (*sensu* Christy, 1987). However, mate guarding (*sensu* Parker, 1974b) is also part of the male mating repertoire. Once a receptive female is found, males protect ‘their’ females from competitors, utilizing their chelipeds and legs so that females become ‘caged’ before, during, and for some unknown period of time after insemination (J. A. Baeza, person. observ.). Importantly, males securing (embracing) recently molted (receptive) females in the field are the largest compared to other adult males in the surroundings (J. A. Baeza, person. observ.). Overall, the mating system of *P. mitra* is characterized by frequent and intense male sexual competition and large males appear to have a mating advantage over smaller males for female monopolization (Baeza & Thiel, 2000; Zander, 2000; J. A. Baeza, person. observ.).

Considering the mating system of the two species above, we predict differences in the extent of sexual dimorphism between these two closely-related crabs. In the urchin-dwelling *P. mitra*, we expect males to have a larger body and larger weaponry (cheliped) than females. Considerable sexual dimorphism in this species should occur because large males have a mating advantage over smaller males for the monopolization of receptive females (Baeza & Thiel, 2000; Zander, 2000). In turn, in the anemone-dwelling crab *P. spinifrons*, we do not expect sexual dimorphism in terms of body size and weaponry because males rarely compete for receptive females (Baeza *et al.*, 2001; Baeza & Thiel, 2003). Nonetheless, weapons (chelipeds) should be well developed both in males and

females of *P. spinifrons* because of their importance in determining the winner during agonistic interactions for monopolization of their scarce anemone hosts.

The present study aimed to explore the role of male sexual competition and intraspecific competition for hosts in explaining differences in sexual dimorphism, in terms of body size and weaponry, using two closely-related species of marine crabs as model system.

MATERIAL AND METHODS

MODEL SPECIES AND THEIR PHYLOGENETIC STATUS

Although originally placed within the genus *Petrolisthes*, Haig (1960) erected the genera *Liopetrolisthes* and *Allopetrolisthes* to contain the two species investigated in the present study: *P. mitra* and *P. spinifrons*, respectively. However, recent molecular phylogenetic analyses suggest that the genera *Liopetrolisthes* and *Allopetrolisthes* are not natural entities and that the two species studied here actually pertain to the genus *Petrolisthes* (Stillman & Reeb, 2001; Baeza, 2007; J. A. Baeza, person. data). Therefore, we treat them as *Petrolisthes* in the present study.

COLLECTION OF PORCELAIN CRABS

Individuals of the porcelain crabs *P. spinifrons* and *P. mitra* were collected by hand from several rocky intertidal sites near Coquimbo (29°57'S, 71°21'W) and El Temblador (29°28'S, 71°18'W) from January to December 1996 and from March 2009 to January 2010. Sampling of crabs usually took place during the lowest tides of each month. During collections, we focused on retrieving all crabs observed in the field, including the largest and smallest individuals, to ensure that there was no bias towards any specific body size range or either of the two sexes. Collected crabs were placed in a large plastic container and transported alive inside buckets to the wet laboratories of the Universidad Católica del Norte, Coquimbo, Chile.

In the laboratory, the carapace width (CW, mm) and/or carapace length (CL, mm) and the length of the left and right cheliped (QL) of all crabs from the two species were measured with a caliper (precision = 0.01 mm). Also, the sex of each crab was determined based on the male gonopore (located at the coxae of the fifth pair of walking legs in males but not in females) and pleopods (long and setose in females and modified as gonopods in males).

Differences in colour pattern were observed in *P. mitra* (samples from 1996) but not in *P. spinifrons*. We explored whether or not the frequency of occurrence of the different colour patterns varied with body size in males of *P. mitra* in an attempt to provide

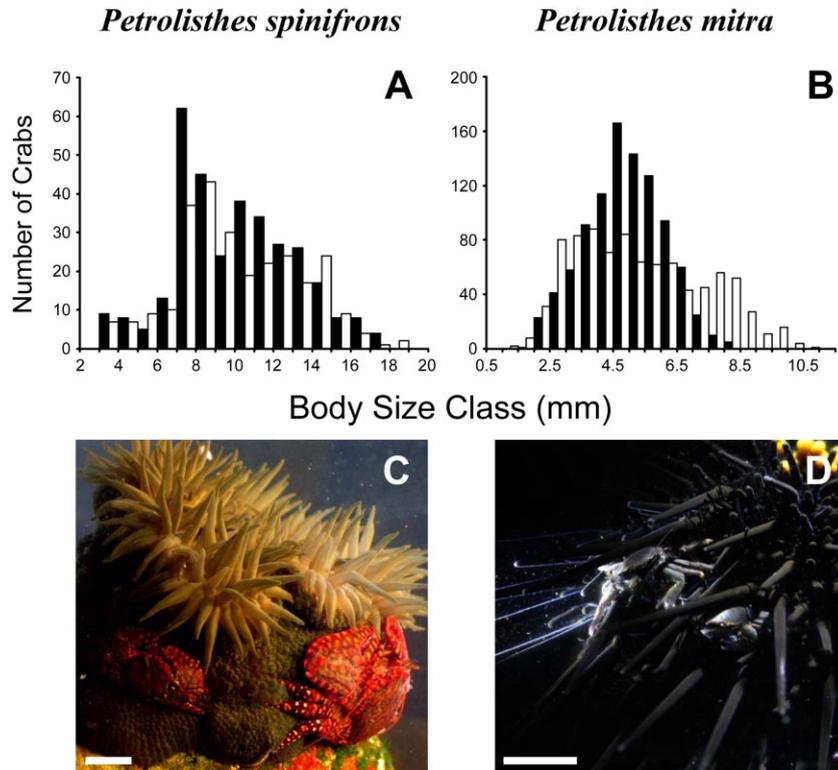


Figure 1. Size frequency distribution (A, B, respectively) of *Petrolisthes spinifrons* and *Petrolisthes mitra* (C, D, respectively). In the images, the two porcelain crabs are observed on their respective hosts: the sea anemone *Phymactis papillosa* and the sea urchin *Tetrapygus niger* (photo credits: Ivan Hinojosa). White and black bars denote males and females, respectively. Scale bars in (A) and (B) = 10 mm.

support for the existence of two male ontogenetic phases in this species (see Results). In other crustaceans with two or more ontogenetic (growth) phases, each phase can be distinguished from the other by body coloration (Kuris *et al.*, 1987). In the present study, we classified *P. mitra* crabs as pertaining to one out of three different colour patterns: (1) dark brown; both carapace and legs are dark brown with a broad yellowish longitudinal stripe on the carapace; (2) pink; both carapace and legs have marbles and stripes in blue and reddish colour; and (3) pink–brown; carapace as in the dark brown colour type but legs as in the pink colour type (Haig, 1960; Urbina-Weber, 1991).

SEXUAL DIMORPHISM IN PORCELAIN CRABS

We tested whether the two studied species exhibited sexual dimorphism in body size by comparing the average body size of male and female conspecifics using a *t*-test or Kruskal–Wallis test depending on whether or not the variances between the compared data sets were homogenous.

In porcelain crabs from the family Porcellanidae, including species from the genus *Petrolisthes*, the first

pair of thoracic appendages bears large chelipeds (Fig. 1C, D) that serve as weapons during intrasexual interactions (Molenock, 1975; Baeza, Stotz & Thiel, 2002). We examined whether the cheliped increased linearly with body size in males and females of the two studied crab species. The relationship between the length of the propodus of the largest cheliped (see Results) and body size of crabs, estimated as carapace width (in mm), was examined using the allometric model: $y = ax^b$ (Hartnoll, 1978, 1982). The slope b of the log–log least-squares linear regression represents the rate of exponential increase ($b > 1$) or decrease ($b < 1$) of the cheliped with a unit of increase in body size of crabs. To determine whether the relationship deviates from linearity, a *t*-test was used to examine whether the estimated slope b deviates from the expected slope of unity (SAS Institute, 2004). If the cheliped grows more or less than proportionally with a unit increase in body size of crabs, then the slope should be greater or smaller than the unity, respectively (Hartnoll, 1978).

In males of *P. mitra*, visual examination of the relationship between carapace width and cheliped length suggested the existence of more than one ontogenetic (growth) phase as reported before for other

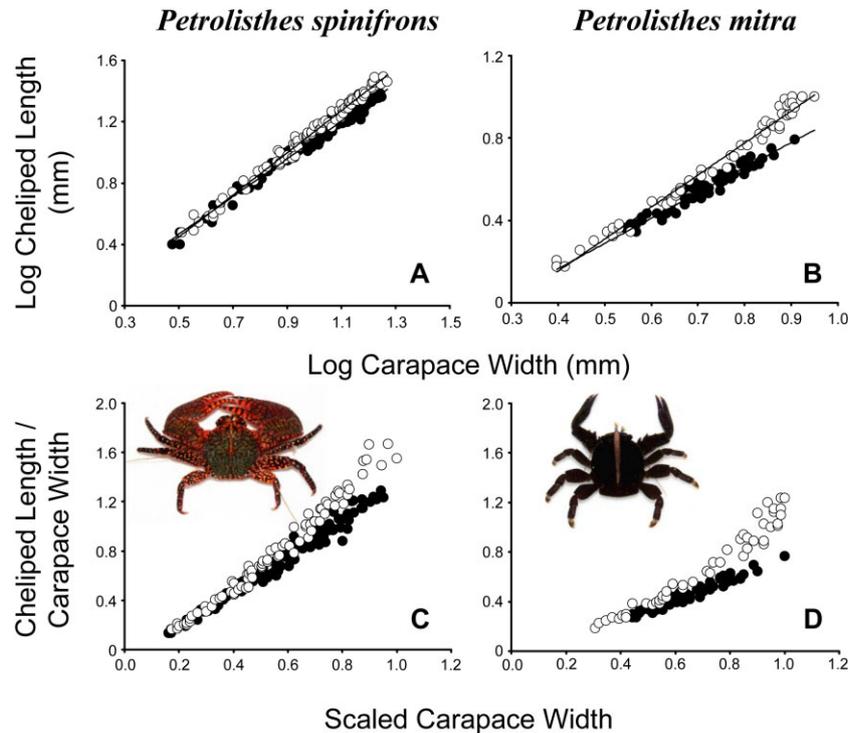


Figure 2. Relative growth of the major cheliped in males and females of *Petrolisthes spinifrons* and *Petrolisthes mitra*. The length of the propodus of the cheliped as a function of carapace width in males and females of *Petrolisthes spinifrons* and *P. mitra* are shown in (A) and (B), respectively. Lineal regression equations obtained previous log–log transformations of the data are shown for each sex in Table 1. Measurements are in mm. The relationship between cheliped and body size in males and females of *P. spinifrons* and *P. mitra* when the different measurements are scaled relative to the carapace width of the largest crab in our sample are shown in (C) and (D), respectively. The typical colour pattern of *P. spinifrons* and the brown colour pattern of *P. mitra* are also shown. White and black dots denote males and females, respectively.

crustaceans. We determined whether or not it was possible to statistically differentiate crabs into different ontogenetic phases in accordance with a protocol modified from Sampedro *et al.* (1999), Gonzalez-Gurriaran & Freire (1994) and Corgos & Freire (2006). First, we used maximum likelihood hierarchical clustering analysis with the variables carapace width and cheliped length to reveal any possible segregation among males that would objectively suggest distinctive ontogenetic phases. For this purpose, we used PROC CLUSTER and the option ML in SAS, version 9.1 (SAS Institute, 2004). Next, in the case that this first analysis did segregate males into different categories (clades), we used a bivariate linear discriminant analysis to cross-validate our findings. This discriminant analysis permits cross-validation of our results because it works assigning individuals to a specific growth phase that, in this case, was first suggested by visual examination of the data and then was objectively distinguished by hierarchical clustering analysis (Sampedro *et al.*, 1999). During the analysis, individuals are assigned to different groups in terms of a reference variable (i.e.

CW) and another morphometric variable (i.e. cheliped length). For this purpose, we used PROC DISCRIM in SAS (SAS Institute, 2004). If the analyses above indicated the existence of different growth phases in males of *P. mitra*, then we additionally performed a different regression analysis for each group identified to obtain a slope.

RESULTS

Sexual dimorphism with respect to body size differed between the two species (Fig. 1). In *P. spinifrons*, the carapace length of male and female crabs varied, respectively, between 3.25 and 18.6 mm (mean \pm SD; 10.12 ± 3.19) and between 3.0 and 17.7 mm (10.01 ± 3.07). Significant differences in CL between the sexes were not detected [*t*-test (variances were homogeneous); $t_{1,595} = 0.46$, $P = 0.6469$], indicating the absence of sexual dimorphism with respect to body size in *P. spinifrons*. By contrast, significant differences in CL between the sexes were detected in *P. mitra* [Kruskal–Wallis test (variances were heterogeneous); $K-W = 394289$, $N = 837$ and 893 for males and females,

Table 1. Growth of major cheliped length (y) relative to carapace width (x) in males and females of *Petrolisthes spinifrons* and *Petrolisthes mitra*

Sex	Phase	Regression	r^2	SE _s	t_s	P	Allometry
<i>Petrolisthes spinifrons</i>							
Males	All	$y = 1.37x - 0.24$	0.99	0.02	21.9	< 0.0001	+
Females	All	$y = 1.23x - 0.15$	0.98	0.02	9.37	< 0.0001	+
<i>Petrolisthes mitra</i>							
Males	All	$y = 1.55x - 0.47$	0.98	0.03	22.6	< 0.0001	+
Males	First OP	$y = 1.38x - 0.37$	0.98	0.04	10.38	< 0.0001	+
Males	Second OP	$y = 1.78x - 0.67$	0.80	0.19	4.19	0.0004	+
Females	All	$y = 1.23x - 0.33$	0.95	0.03	7.07	< 0.0001	+

In males of *P. mitra*, the allometric analysis was also conducted separately for the two different ontogenetic stages [first and second ontogenetic phase (OP)] revealed by clustering and discriminant analyses. The regression equations, coefficients of determination, standard errors of the slopes (SE_s), and the allometric status (+ = positive allometry) of each studied variable are shown (y and x = length of the merus of the major cheliped and carapace width, respectively).

respectively, $P = 0.0476$]. On average, males were larger than females. The carapace length of male and female crabs of *P. mitra* varied, respectively, between 1.2 and 10.6 mm (mean \pm SD; 5.23 ± 2.03) and between 1.5 and 8.4 mm (4.87 ± 1.24).

Heterochely was observed in crabs regardless of their species and sex; one of the chelipeds was invariably larger than the second in the pair. In *P. spinifrons*, the largest of the chelipeds was observed on the right side of the body 58.23% of the time in males (46 out of 79 individuals examined for heterochely) and 53.04% of the time in females (61 out of 115 individuals). These frequencies did not differ significantly from an expected random distribution of 1 : 1 both in males and females (binomial test, $P = 0.1611$ for males and $P = 0.5459$ for females). In *P. mitra*, the largest of the chelipeds was observed on the right side of the body 71.7% of the time in males (38 out of 53 individuals) and 52.9% of the time in females (36 out of 68 individuals). These frequencies differed significantly from an expected random distribution of 1 : 1 in males but not in females (binomial test, $P = 0.0012$ for males and $P = 0.5875$ for females).

In the two studied species, a positive correlation between body size and the length of the propodus of the major cheliped was detected for crabs of both sexes ($P < 0.001$ in all cases; Fig. 2). However, the major cheliped differed with respect to the status and/or degree of allometry depending on the species and sex of the crabs.

In *P. spinifrons*, the largest cheliped presented positive allometry both in males and females; the slope of the relationship between crab body size and largest cheliped size was significantly greater than unity (Fig. 2, Table 1). Importantly, cheliped length was slightly but significantly greater in males than in females at any given size [analysis of covariance

(ANCOVA), effect of sex: $F = 17.79$, d.f. = 1, 120, $P < 0.0001$] and cheliped relative growth was more pronounced in males than in females (Sex \times CW interaction: $F = 51.03$, d.f. = 1, 120, $P < 0.0001$) (Fig. 2, Table 1).

In *P. mitra*, the major cheliped presented positive allometry both in males and females. The major cheliped was larger in males than in females at any given size (ANCOVA, effect of sex: $F = 14.93$, d.f. = 1, 193, $P = 0.0002$). Also, cheliped relative growth was greater in adult males than in adult females (Sex \times CW interaction: $F = 38.02$, d.f. = 1, 193, $P < 0.0001$) (Fig. 2, Table 1).

Sexual dimorphism with respect to cheliped size was much more pronounced in *P. mitra* than in *P. spinifrons* (Fig. 2). This difference between species becomes evident when the carapace width and major cheliped length of each crab is scaled relative to the body size of the largest crab observed in each species. In *P. spinifrons*, the length of the major cheliped of the largest males and females were approximately 1.6 and 1.2 times the width of their own carapace ($\Delta = 0.4$). In *P. mitra*, the length of the major cheliped of the largest males and females in our sample were approximately 1.2 and 0.6 times the width of their own carapace ($\Delta = 0.6$) (Fig. 2). A second comparison similar to that above demonstrates that adult males and females of *P. spinifrons* invested more to chelipeds than adult males and females of *P. mitra* (Fig. 2). This is indicated by the value of the quotient between cheliped length and carapace width that was greater in *P. spinifrons* than in *P. mitra* when sex is taken into account (males: 1.6 in *P. spinifrons* versus 1.2 in *P. mitra*; females: 1.2 in *P. spinifrons* versus 0.6 in *P. mitra*) (Fig. 2).

In *P. mitra*, visual examination of the relationship between carapace width and major cheliped length

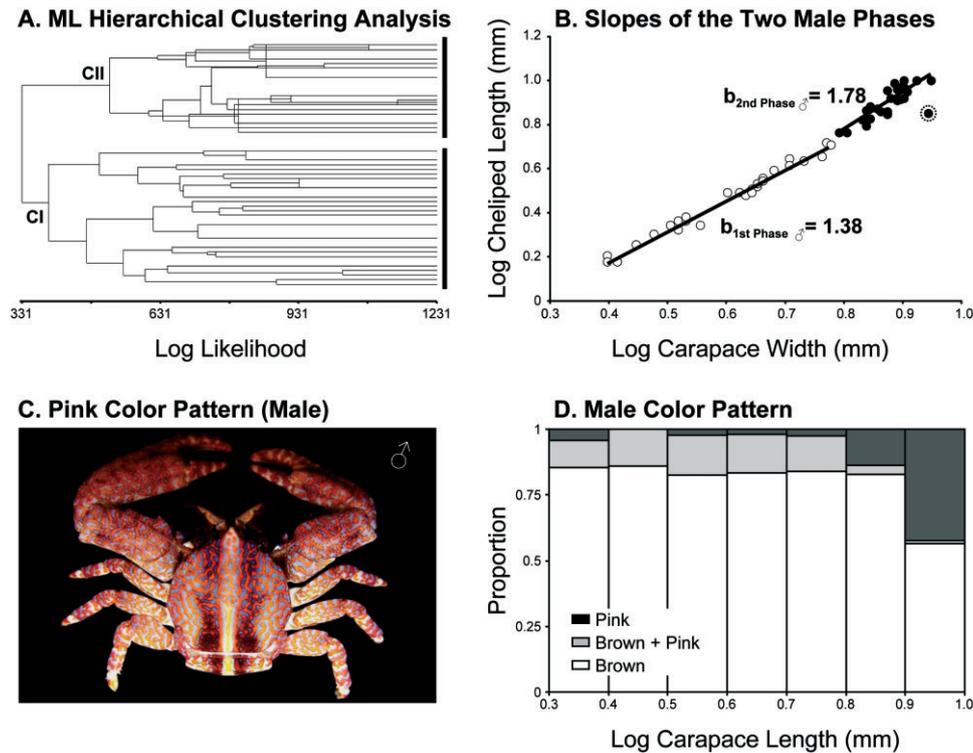


Figure 3. Different male morphotypes in *Petrolithes mitra*. A, two distinctive well supported clades obtained with the maximum likelihood clustering analysis. The analysis segregate male crabs into two major groups comprised of males below and above 7.8 mm CW. B, the two slopes describing the relationship between major claw and carapace width in males from the two different ontogenetic phases (clades) previously determined using clustering analysis. Black and white dots denote males from the first and second ontogenetic phase, respectively. The circled dot represents an outlier that was not considered when the slope of the relationship between major claw and carapace width was calculated for crabs pertaining to the second ontogenetic phase. C, pink colour pattern observed most frequently in male crabs of the second ontogenetic stage. D, the frequency of occurrence of the three colour patterns observed in individuals of different size classes.

suggested the existence of more than one ontogenetic growth phase in males but not in females (Fig. 2). Maximum likelihood clustering analysis segregated male crabs into two distinctive well supported clades (Fig. 3A). A first clade comprised relatively small males with a body size in the range 3.9–7.7 mm CW (CI in Fig. 3A). The second clade comprised the largest crabs in our collection, with a body size in the range 7.9–9.4 mm CW (CII in Fig. 3A). Thus, this hierarchical clustering analysis supported with a high likelihood the existence of two ontogenetic phases in males of *P. mitra*, referred to here as the first ontogenetic male stage (probably immature juvenile crabs plus young adults) and the second ontogenetic stage (probably old adult males) (Fig. 3). Discriminant analysis cross-validated our finding, with all but one of the males being correctly assigned to one of the two ontogenetic stages previously recognized by hierarchical clustering analysis (one of the largest males in our sample have a cheliped much smaller than expected,

was considered an outlier, and was not included in the stage-specific analysis of allometry; see below). The carapace width at which males change from the first growth phase to the old adult phase was approximately 8.0 mm CW. In general, in males of *P. mitra*, the level of allometry of the major cheliped increased with size and/or age, with crabs pertaining to the first ontogenetic phase undergoing an allometric growth of the major cheliped less pronounced than that of the larger and older adult males pertaining to the second ontogenetic phase (Fig. 3B, Table 1).

Concomitantly with differences in relative growth of the major cheliped, the two ontogenetic growth phases detected in the present study in males of *P. mitra* can be distinguished by the frequency with which crabs assumed different colour patterns. Most frequently, male crabs smaller than approximately 8.0 mm CL featured a dark-brown coloration (Fig. 1). In only a few occasions, a pink or pink–brown coloration was observed in these small crabs. In turn, crabs

above 8.0 mm CL (second ontogenetic phase) display a pink colour pattern with more frequency than that observed in male crabs smaller than approximately 8.0 mm CL (Fig. 3C, D).

DISCUSSION

In the present study, differences in the extent of male sexual competition were expected to drive differences in sexual dimorphism between two closely-related species of porcelain crabs. Supporting this prediction, in the urchin-dwelling crab *Petrolisthes mitra*, in which male sexual competition is recurrent, sexual dimorphism was considerable, in terms of body size and weaponry (chelipeds), whereas, in the anemone-dwelling crab *P. spinifrons*, in which male sexual competition is trivial, sexual dimorphism in terms of body size was not detected and differences in cheliped relative size were modest. The relationship established in the present study between the extent of male–male competition and sexual dimorphism in porcelain crabs supports the notion that intrasexual selection is most relevant in shaping differences in morphology between the sexes.

Importantly, processes other than male–male competition that can drive the observed differences in sexual dimorphism between the studied crabs cannot be discarded. For example, female mate choice is predicted to favour large body size in males if male body size conveys honest information to receptive females regarding their genetic quality ('good genes'; Hunt *et al.*, 2004). Similarly, if male body size represents a reliable trait that correlates well with the quality/quantity of resources that females can attain from male mating partners, females are expected to choose large males, and such a preference should favour large body size in males (Shuster & Wade, 2003). Thus, if female mate choice is more relevant in *P. mitra* than in *P. spinifrons*, we expect considerable sexual dimorphism in terms of body size in the former but not the latter species. Importantly, the same conditions that limit male–male competition are also expected to diminish the extent of female mate choice in *P. spinifrons*. In this anemone-dwelling crab, high predation risk when off sea anemones is expected to decrease encounter rates among conspecifics, and thus to reduce not only the level of male–male competition, but also female mate choice (Baeza & Thiel, 2007). By contrast to what happens with *P. spinifrons*, the host characteristics of *P. mitra* does not limit competition among males for receptive females and also provides ample opportunities for females to behave in manners that allow them to choose male mating partners of 'high quality' (e.g. large body size). We argue in favour of new integrative studies exploring the effect of different sexual selection components

(e.g. pre- and post-copula male–male competition, pre- and post-copula female mate choice) in explaining differences in sexual dimorphism in the studied species.

Sexual dimorphism is substantial in the urchin-dwelling crab *Petrolisthes mitra* but is limited in the anemone-dwelling crab *P. spinifrons*. In the present study, we also predicted considerable allocation to weaponry (chelipeds) both in males and females of the anemone-dwelling *P. spinifrons* (but no or minimal sexual dimorphism) because of their importance in determining the winner during agonistic interactions for monopolization of their scarce anemone hosts. In agreement with this hypothesis, investment to chelipeds was considerable in *P. spinifrons* and greater than that observed in the urchin-dwelling *P. mitra*. It should pay for both males and females of *P. spinifrons* to invest heavily in armament because it increases resource holding potential and the chances of monopolizing host individuals via overt aggression. By contrast, in *P. mitra*, natural selection (but not sexual selection) both in males and females for large body sizes and fighting structures (major claws) might be relaxed because of the low intensity of intraspecific competition for abundant hosts (Baeza & Thiel, 2003). Theory predicts that resource (host) scarcity, host small size (relative to that of the symbionts), and host low structural complexity increase host-resource value and favour host monopolization by symbiotic crustaceans (Baeza & Thiel, 2003). Previous studies on the host use pattern of the two studied species agree with the theoretical considerations above. *Petrolisthes spinifrons*, a species that inhabits relatively small, structurally simple, and scarce hosts is territorial; both males and females guard their host individuals against conspecific intruders from the two sexes (Baeza *et al.*, 2002). In turn, host monopolization behaviours do not occur in *P. mitra*, which dwells as dense aggregations on the structurally complex, relatively large and naturally abundant sea urchin *T. niger* (Baeza & Thiel, 2000). In general, the relationship established in the present study between host abundance, intensity of intraspecific competition for hosts, and development of weaponry in porcelain crabs provides empirical support for a resource-monopolization theory that predicts the evolution of weapons and territorial strategies when resources are scarce and/or inexpensive to guard (in terms of energy and time) (Caldwell & Dingle, 1975; Baeza & Thiel, 2003; Emlen, 2008).

In addition to differences in sexual dimorphism in body size and allocation to weaponry, another important difference between the studied species is the existence of two distinctive ontogenetic phases in males of *P. mitra* but not in males of *P. spinifrons*. The

two different ontogenetic phases (morphs) in *P. mitra* can be distinguished from one another by the frequency with which individuals assume different colour patterns and on the basis of cheliped relative size and its allometric status. To the best of our knowledge, this is the first time that more than one male morphotype is reported in the family Porcellanidae. Species with more than one male morphotype are known in several other clades of marine crustaceans [isopods: *Paracerceis sculpta*: Shuster & Wade, 2003; amphipods: *Leucothoides potsii*: Thomas & Barnard, 1983; shrimps: *Macrobrachium rosenbergii*: Kuris *et al.*, 1987; spider (Majoidea) crabs: *Maja squinado* and *Chionoecetes opilio*: Sainte-Marie, Raymond & Brêthes, 1995; Sampedro *et al.*, 1999; squatlobsters: *Munida rugosa*: Claverie & Smith, 2009]. Invariably, alternative mating strategies has been demonstrated for every species of crustacean with two or more male morphs and in which reproductive strategies have been studied (e.g. *P. sculpta*: Shuster & Wade, 2003; *M. rosenbergii*: Ra'anán & Sagi, 1985). It remains to be addressed whether or not the different male morphs of *P. mitra* herein detected feature alternative mating strategies. Importantly, sexual selection theory also predicts that intense male sexual competition favours alternative reproductive tactics in males (Andersson, 1994). The different male morphotypes observed in *P. mitra* but not in *P. spinifrons* (with strong and weak male-male competition, respectively) also supports the above notion.

OUTLOOK

It has been shown that sexual dimorphism differs substantially between two closely-related species of porcelain crabs. Our observations fit well with sexual selection theory that predicts the evolution of sexual dimorphism in species with separate sexes (Shuster & Wade, 2003; Bauer, 2004; Baeza & Thiel, 2007). Nonetheless, alternative mechanisms explaining such differences are plausible and remain to be explored (e.g. female mate choice). Other symbiotic crabs from the family Porcellanidae, including species from the genera *Clastocoechus*, *Minyocerus*, *Neopetrolisthes*, *Petrolisthes*, *Porcellana*, and *Polyonyx*, among others, inhabit hosts (e.g. corals, sea stars, polychaetes, hermit crabs) with differing biology and ecology (Haig, 1960, 1965; Baeza, 2007). Because of the differing ecology of the host species, crabs in this family are expected to display dissimilar mating systems and patterns of sexual dimorphism. Crabs from the family Porcellanidae might be used as model systems to study the importance of environmental conditions (e.g. host traits) in shaping the sex-specific morphology and reproductive behaviour in marine invertebrates.

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REFERENCES

- Andersson M.** 1994. *Sexual selection*. Princeton, NJ: Princeton University Press.
- Andrade MCB.** 1996. Sexual selection for male sacrifice in the Australian redback spider. *Science* **240**: 70–72.
- Baeza JA.** 1999. Territoriality and the agonistic behaviour of *Allopetrolisthes spinifrons* (H. Milne Edwards, 1837) (Decapoda: Anomura: Porcellanidae): ontogenetic changes and temporal variability. Unpublished Marine Biology Thesis, Universidad Católica del Norte, Chile.
- Baeza JA.** 2007. The origins of symbiosis as a lifestyle in marine crabs (genus *Petrolisthes*) from the eastern Pacific: does interspecific competition play a role? *Revista de Biología Marina y Oceanografía* **42**: 7–21.
- Baeza JA, Stotz W, Thiel M.** 2002. Agonistic behaviour and development of territoriality during ontogeny of the sea anemone dwelling crab *Allopetrolisthes Spinifrons* (H. Milne Edwards, 1837) (Decapoda: Anomura: Porcellanidae). *Marine and Freshwater Behaviour and Physiology* **35**: 189–202.
- Baeza JA, Stotz WB.** 1995. Estructura poblacional del cangrejo comensal *Allopetrolisthes spinifrons* (H. Milne Edwards, 1837) (Decapoda: Porcellanidae) sobre su hospedador habitual *Phymactis clematis* (actinaria) y en dos nuevos hospedadores. *Revista de Biología marina* **30**: 255–264.
- Baeza JA, Thiel M.** 2000. Host use pattern and life history of *Liopetrolisthes mitra*, an associate of the black sea urchin *Tetrapygus niger*. *Journal of the Marine Biological Association of the United Kingdom* **80**: 39–45.
- Baeza JA, Thiel M.** 2003. Predicting territorial behavior in symbiotic crabs using host characteristics: a comparative study and proposal of a model. *Marine Biology* **142**: 93–100.
- Baeza JA, Thiel M.** 2007. The mating system of symbiotic crustaceans. A conceptual model based on optimality and ecological constraints. In: Duffy JE, Thiel M, eds. *Evolutionary ecology of social and sexual systems: crustaceans as model organisms*. Oxford: Oxford University Press, 249–255.
- Baeza JA, Thiel M, Stotz WB.** 2001. The life history of *Allopetrolisthes spinifrons*, a crab associate of the sea anemone *Phymactis clematis*. *Journal of the Marine Biological Association of the United Kingdom* **81**: 69–76.

- Bauer RT. 2004.** *Remarkable shrimps*. Norman, OK: Oklahoma University Press.
- Bauer RT, Abdalla JH. 2001.** Male mating tactics in the shrimp *Palaemonetes pugio* (Decapoda, Caridea): precopulatory mate guarding vs. pure searching. *Ethology* **107**: 185–199.
- Butler MA, Losos JB. 2002.** Multivariate sexual dimorphism, sexual selection, and adaptation in Greater Antillean *Anolis* lizards. *Ecological Monographs* **72**: 541–559.
- Caldwell RL, Dingle H. 1975.** Ecology and evolution of agonistic behavior in stomatopods. *Die Naturwissenschaften* **62**: 214–222.
- Carothers JH. 1984.** Sexual selection and sexual dimorphism in some herbivorous Lizards. *American Naturalist* **124**: 244–254.
- Christy JH. 1983.** Female choice in the resource-defense mating system of the sand fiddler crab, *Uca pugilator*. *Behavioral Ecology and Sociobiology* **12**: 169–180.
- Christy JH. 1987.** Competitive mating, mate choice and mating associations of brachyuran crabs. *Bulletin of Marine Science* **41**: 177–191.
- Claverie T, Smith IP. 2009.** Morphological maturity and allometric growth in the squat lobster *Munida rugosa*. *Journal of the Marine Biological Association of the United Kingdom* **89**: 1189–1194.
- Clutton-Brock TH. 2007.** Sexual selection in males and females. *Science* **318**: 1882–1885.
- Clutton-Brock TH, Harvey PH, Rudder B. 1977.** Sexual dimorphism, socionomic sex ratio and body weight in primates. *Nature* **269**: 797–800.
- Corgos A, Freire J. 2006.** Morphometric and gonad maturity in the spider crab *Maja brachydactyla*: a comparison of methods for estimating size at maturity in species with determinate growth. *ICES Journal of Marine Science* **63**: 851–859.
- Darwin C. 1871.** *The descent of man and selection in relation to sex*. London: John Murray.
- Emlen DJ. 2008.** The evolution of animal weapons. *Annual Review of Ecology, Evolution, and Systematics* **39**: 387–413.
- Emlen ST, Oring LW. 1977.** Ecology, sexual selection, and the evolution of mating systems. *Science* **197**: 215–223.
- Gonzalez-Gurriaran E, Freire J. 1994.** Movement patterns and habitat utilization in the spider crab *Maja squinado* (Herbst) (Decapoda, Majidae) measured by ultrasonic telemetry. *Journal of Experimental Marine Biology and Ecology* **184**: 269–291.
- Haig J. 1960.** The Porcellanidae (Crustacea Anomura) of the Eastern Pacific. *Allan Hancock Pacific Expeditions* **24**: 1–440.
- Haig J. 1965.** The Porcellanidae (Crustacea Anomura) of the Western Australia, with descriptions of four new Australian species. *Journal of the Royal Society of Western Australia* **48**: 97–118.
- Hartnoll RG. 1978.** The determination of relative growth in crustacean. *Crustaceana* **34**: 281–292.
- Hartnoll RG. 1982.** Growth. In: Abele LG, ed. *The biology of crustacea* 2. New York, NY: Academic Press, 111–196.
- Huber BA. 2005.** Sexual selection research on spiders: progress and biases. *Biological Reviews* **80**: 363–385.
- Hunt J, Bussière LF, Jennions MD, Brooks R. 2004.** What is genetic quality? *Trends in Ecology and Evolution* **19**: 329–333.
- Kuris AM, Ra'anan Z, Sagi A, Cohen D. 1987.** Morphotypic differentiation of male Malaysian giant prawns, *Macrobrachium rosenbergii*. *Journal of Crustacean Biology* **7**: 219–237.
- Lailvaux SP, Irschick DJ. 2007.** The evolution of performance-based male fighting ability in Caribbean *Anolis* lizards. *American Naturalist* **170**: 573–586.
- Lawrence SE. 1992.** Sexual cannibalism in the praying mantid, *Mantis religiosa*: a field study. *Animal Behaviour* **43**: 569–583.
- Lindenfors P, Tullberg BS, Biuw M. 2002.** Phylogenetic analyses of sexual selection and sexual size dimorphism in pinnipeds. *Behavioral Ecology and Sociobiology* **52**: 188–193.
- Molenock J. 1975.** Evolutionary aspects of communication in the courtship behavior of four species of anomuran crabs (*Petrolisthes*). *Behaviour* **53**: 1–29.
- Parker GA. 1974a.** Assessment strategy and the evolution of fighting behavior. *Journal of Theoretical Biology* **47**: 223–243.
- Parker GA. 1974b.** Courtship persistence and female-guarding as male time investment strategies. *Behaviour* **48**: 157–184.
- Ra'anan Z, Sagi A. 1985.** Alternative mating strategies in male morphotypes of the freshwater prawn *Macrobrachium rosenbergii* (de man). *The Biological Bulletin* **169**: 592–601.
- Reeves MN, Brooks WR. 2001.** Host selection, chemical detection, and protection of the symbiotic pinnotherid crabs *Dissodactylus crinitichelis* and *Clypeasterophilus rugatus* associated with echinoderms. *Symbiosis* **30**: 239–256.
- Richmond BG, Jungers WL. 1995.** Size variation and sexual dimorphism in *Australopithecus afarensis* and living hominoids. *Journal of Human Evolution* **29**: 229–245.
- Robinson MH, Robinson B. 1973.** Ecology and behavior of the giant wood spider *Nephila maculata* (Fabricius) in New Guinea. *Smithsonian Contributions to Zoology* **149**: 1–76.
- Sainte-Marie B, Raymond S, Brêthes JC. 1995.** Growth and maturation of the benthic stages of male snow crab, *Chionoecetes opilio* (Brachyura, Majidae). *Canadian Journal of Fisheries and Aquatic Sciences* **52**: 903–924.
- Sampedro MP, González-Gurriarán E, Freire J, Muiño R. 1999.** Morphometry and sexual maturity in the spider crab *Maja squinado* (Decapoda: Majidae) in Galicia. *Spain Journal of Crustacean Biology* **19**: 578–592.
- SAS Institute. 2004.** *SAS/STAT software*, Version 9.1. Cary, NC: SAS Institute.
- Shuster SM. 1986.** The reproductive biology of *Paracerceis sculpta* (Crustacea: Isopoda). PhD Thesis, University of California, Berkeley.
- Shuster SM, Wade MJ. 1991.** Equal mating success among male reproductive strategies in a marine isopod. *Nature* **350**: 608–610.

- Shuster SM, Wade MJ. 2003.** *Mating systems and strategies*. Princeton, NJ: Princeton University Press.
- Stillman JH, Reeb CA. 2001.** Molecular phylogeny of eastern Pacific porcelain crabs, genera *Petrolisthes* and *Pachycheles*, based on the mtDNA 16S rDNA sequence: phylogeographic and systematic implications. *Molecular Phylogenetics and Evolution* **19**: 236–245.
- Stuardo J. 1962.** El Comensalismo de *Allopetrolisthes spinifrons* (H. Milne-Edwards). *Gayana Zoologica* **6**: 5–8.
- Szekely T, Reynolds JD, Figuerola J. 2000.** Sexual size dimorphism in shorebirds, gulls, and alcids: the influence of sexual and natural selection. *Evolution* **54**: 1404–1413.
- Thiel M, Zander A, Valdivia N, Baeza JÁ, Rueffler C. 2003.** Host fidelity of a symbiotic porcellanid crab: the importance of host characteristics. *Journal of Zoology* **261**: 353–362.
- Thomas JD, Barnard JL. 1983.** Transformation of the *Leucothoides* morph to the *Anamixis* morph (Amphipoda). *Journal of Crustacean Biology* **3**: 154–157.
- Urbina-Weber L. 1991.** Synonymy and characterization of *Liopetrolisthes mitra* (Dana, 1852) and *Liopetrolisthes patagonicus* (Cunningham, 1871) n. comb. *Gayana Zoologica* **55**: 13–22.
- Valdivia N, Stotz W. 2006.** Feeding behaviour of the porcellanid crab *Allopetrolisthes spinifrons*, symbiont of the sea anemone *Phymactis papillosa*. *Journal of Crustacean Biology* **26**: 308–315.
- Viviani CA. 1969.** Los Porcellanidae (Crustacea, Anomura) chilenos. *Beitrage zur Neotropischen Fauna* **6**: 40–56.
- Werlinger C. 1989.** Symbiotic relationship between *Allopetrolisthes spinifrons* (Crustacea, Porcellanidae) and *Phymactis clematis* (Coelenterata, Anthozoa,). MSc Thesis, Universidad de Concepción, Concepción, Chile.
- Zander A. 2000.** Is das Zusammenleben von dem Porzellankrebs *Liopetrolisthes mitra* und dem Seeigel *Tetrapygus niger* an der chilenischen Küste ein Fall von Parasitismus, Kommensalismus oder Symbiose? Unpublished Thesis for Staatsexamen, University of Kiel.
- Zander A, Valdivia N, Thiel M. 2002.** Uso del hospedador por *Allopetrolisthes spinifrons* (Porcellanidae), simbiote de *Phymactis clematis* (Anthozoa). XXII Congreso de Ciencias del Mar, 28–31 May, Valdivia, Chile.