

Population Structure and Reproduction of *Pseudione elongata africana* (Bopyridae, Isopoda)

Gil Penha-Lopes, Joana F. Marques, Miguel C. Leal*, Ana F. Carvalho and José Paula

Centro de Oceanografia, Laboratório Marítimo da Guia, Faculdade de Ciências, Universidade de Lisboa, Avenida Nossa Senhora do Cabo 939, 2750-374 Lisboa, Portugal.

**Present address: Departamento de Biologia & CESAM, Universidade de Aveiro, Campus Universitário de Santiago, 3810-193 Aveiro, Portugal.*

Keywords: *Pseudione elongata africana*, parasite, population structure, reproduction, mangrove ecosystems, Mozambique

Abstract—The population structure and reproductive fitness of *Pseudione elongata africana* parasitizing the shrimp *Palaemon concinnus* were studied in two mangroves in Mozambique. About 100 host specimens were sampled every 15 days for 12 months at Costa do Sol, a peri-urban mangrove near Maputo, and at Saco, a near pristine mangrove at Inhaca Island. Parasites were removed from the branchiostegites of the shrimp and measured. Ovigerous females were selected and the eggs and embryos removed from the brood pouch and counted after staging their level of development. At Costa do Sol, the total length of female parasites (FPTL) was about 17% higher than at Saco. Ovigerous females were also more abundant at Costa do Sol in both the dry and wet seasons. The average brood size ranged from 89 to 207 eggs mm⁻¹ FPTL in the Saco and 177 to 357 eggs mm⁻¹ at Costa do Sol. These data provide baseline information on the population structure and reproduction of this parasite in east African mangroves. Comparative data on these parameters in peri-urban and more isolated mangroves may also lay the groundwork for the use of parasite reproduction as an indicator of anthropogenic pressure.

INTRODUCTION

Mangrove ecosystems are adversely affected by anthropogenic activities such as deforestation and the dumping of waste in peri-urban areas (Duke *et al.*, 2007; Kruitwagen *et al.*, 2008), despite their widely recognized socioeconomic and environmental importance (Nagelkerken *et al.*, 2008; Walters *et al.*, 2008). Most studies on anthropogenic contaminants in mangrove ecosystems have focused on the measurement

of their concentrations in water, sediment and organisms (see review by Kruitwagen *et al.*, 2008). Recent studies in East Africa have, however, also focused on ecosystem biodiversity (e.g. Cannicci *et al.*, 2009) and the population structure and fitness (Penha-Lopes *et al.*, 2010a; 2010b), behaviour (Bartolini *et al.*, 2009; Bartolini, 2010; Penha-Lopes *et al.*, 2010a) and the physiology of various fauna (Amaral *et al.*, 2009a; 2009b) to assess the degree of pollution in peri-urban mangroves.

Parasites have long been considered important bio-indicators of pollution (MacKenzie, 1999; Marcogliese *et al.*, 2002) and ecosystem health (Hudson *et al.*, 2006). However, few studies have considered parasitism in monitoring and environmental assessment programmes, mostly due to a lack of information regarding their biology and quantification of their responses to contaminants (Blonar *et al.*, 2009). Moreover, parasite interactions with stressors have different outcomes: parasitism might be favoured by some stressors, causing a decrease in host immune-competence, host defence mechanisms and susceptibility (Sures, 2004); other stressors may decrease parasitism by killing the parasite or interfering with its transmission (Lafferty & Kuris, 1999), reducing host fitness or even leading to parasite mortality (Jobling & Tyler, 2003; Lafferty, 2008).

Recently, the shrimp *Palaemon concinnus* Dana, 1852, was identified as a potential bio-indicator of anthropogenic perturbation in East African mangroves due to its high abundance in mangrove creeks and low importance in local fisheries (Penha-Lopes *et al.*, 2010b). Previous research demonstrated that the shrimp were larger at Costa do Sol, a peri-urban mangrove in the Maputo area of Mozambique, where they had a more protracted reproductive season, a higher percentage of ovigerous females, larger brood sizes and higher egg quality (measured using fatty acid indicators) compared to shrimp in more pristine mangroves. The higher loading of organic detritus in the peri-urban mangrove and consequent stimulation of primary production (bacteria and microalgae) may thus provide the shrimp with more abundant and diverse food, increasing several population fitness parameters.

However, it was also observed that *P. concinnus* was usually infested by *Pseudione elongata africana* Kensley, 1968, an ectoparasitic isopod belonging to the family Bopyridae. The parasite life-cycle comprises a free swimming epicaridean larva that attaches itself to an intermediate host (a calanoid copepod) (Dale & Anderson,

1982), then metamorphoses into another free swimming stage (cryptoniscus). After leaving the copepod, the cryptoniscus infects the definitive host, usually a decapod crustacean. Pseudioninae are the largest subfamily within the Bopyridae and many parasitize caridean shrimps, decreasing the hosts' respiratory capacity as they fill their branchial cavity and compress the gill lamellae. Other effects of bopyrid isopod infection are a reduction in reproductive potential, castration, behavioural changes and impaired growth of the host (Paradiso *et al.*, 2004). Penha-Lopes *et al.*, (2010b) showed that the prevalence of this parasite in *P. concinnus* is significantly higher in peri-urban compared to pristine mangroves and that the parasite is ultimately able to castrate the host.

Information on the population structure and reproductive dynamics of parasites in mangrove fauna is limited and this study expands our knowledge in this field. It also addresses the question as to whether *P. elongata africana* parasitizing *P. concinnus* are affected by anthropogenic pressure in a peri-urban mangrove.

MATERIALS and METHODS

Study area and sampling design

Sampling was conducted in Mozambique in two mangrove ecosystems that differed, namely a peri-urban mangrove at Costa do Sol (25°55'S; 32°35'E) and a pristine mangrove in the Saco (26°00'S; 32°55'E) of Inhaca Island (Fig.1). The characteristics of the mangroves are described by Cannicci *et al.* (2009) and Penha-Lopes *et al.* (2009b). The Costa do Sol mangrove is located ~7 km north of Maputo city in Maputo Bay, covers about 2 km², is bordered by a residential area and has been affected by domestic sewage, aquaculture residues and solid waste from various sources over the last decades. The Saco mangrove covers an area of about 2.1 km², is enclosed in a small, shallow bay in the south of Inhaca Island and is unperturbed by major sewage input or other contaminants (PUMPSEA, 2008). Higher organic content, pathogens and

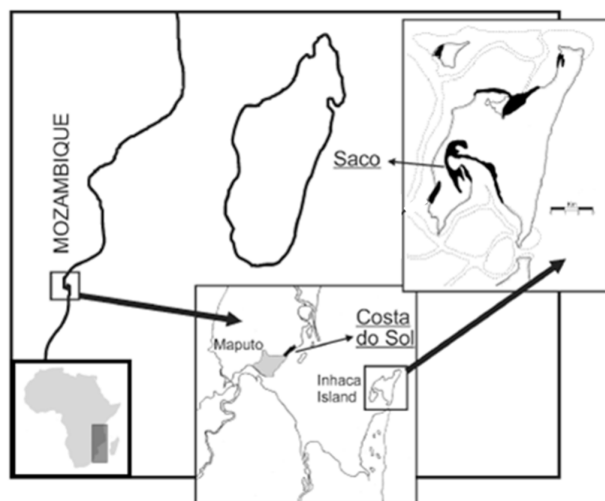


Figure 1. Location of study sites in southern Mozambique.

nutrient concentrations, especially nitrites and nitrates, were observed in sediment pore-water at Costa do Sol compared to Saco (Salvador, 2007; PUMPSEA, 2008).

Sampling was conducted during every spring low tide (roughly every 14 days) in both mangroves, from August 2005 to August 2006. About 100 specimens of *P. concinnus* were collected using a 1 mm mesh net on each sampling occasion. Sampling was performed at each site (Costa do Sol and Saco) in the area bordering the main channels of the mangroves. Data obtained during the PUMPSEA (2008) project (see Fig. 2) indicated that the wet season occurs in the region from December to May and the dry season from June to November. Higher temperatures and heavy rain occur in the wet season, promoting an increase in nutrient concentrations in the water column (Paula *et al.*, 1998) and mangrove sediments. The dry season tends to be cooler with sporadic rainfall.

Parasite prevalence and host population structure

Parasite prevalence, calculated according to Bush *et al.* (1997), and host population structure (see host-parasite in Fig. 3) were analysed in a previous study (Penha-Lopes *et al.*, 2010b). Shrimp were preserved in buffered 4% formaldehyde diluted with seawater for

laboratory examination. Specimens were identified, counted and their sex determined according to the presence or absence of a masculine appendix on the second pleopod pair (Grave & Al-Maslamani, 2006). Their carapace length (CL) was measured under a binocular microscope with a micrometer to the nearest 0.02 mm.

The results (Penha-Lopes *et al.*, 2010b) indicated that the mean prevalence of *P. elongata africana* in male and non-ovigerous female hosts was usually higher at Costa do Sol ($15.71 \pm 6.62\%$) than in the Saco ($9.70 \pm 4.87\%$). The average CL of the shrimps was also higher at Costa do Sol (5.18 ± 0.06 mm) than at Saco (4.41 ± 0.13 mm), the

ovigerous females being larger than the non-ovigerous females and males. We only considered the population structure of the shrimps parasitized by *P. elongata africana* in the present study, constituting a subsample of the earlier material.

Parasite population structure and fecundity

The presence of *P. elongata africana* in the right or left gill chambers of the host was recorded. The total length of the female parasites (FPTL, Fig. 3) was measured to the nearest 0.01 mm and the presence of male parasites on the ventral surface of females between the pleopods was recorded as well as the presence of eggs in the female brood pouch (Fig. 3). The eggs were counted in ovigerous masses and categorised in four developmental stages (egg, embryo I, embryo II, and epicaridium larva) according to the criteria of Beck (1980). While parasite fecundity was determined in terms of the number of eggs and stage I embryos in the brood, the potential fertility was based on the number of stage II embryos and epicaridium larvae in each brood (adapted from the definitions proposed by Penha-Lopes *et al.*, 2009). Only intact ovigerous masses, i.e. those in which the eggs/embryos/larvae were completely covered by the oostegites

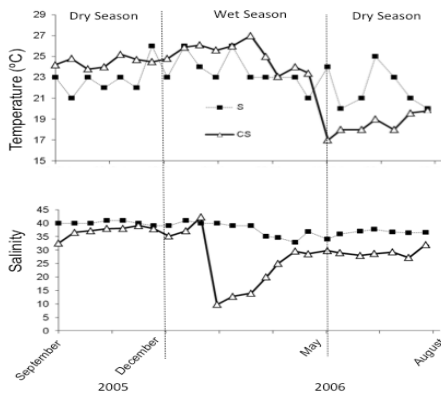


Figure 2. Temperature and salinity measured at spring low tide in the Costa do Sol and Saco mangroves over a period of 12 months (2 measurements per month). S = Saco; CS = Costa do Sol.

of the female and the branchiostegite of the host, were analysed. Fecundity and potential fertility were calculated for the wet and dry seasons, mangrove sites and host sex.

The size at sexual maturity of *P. elongata africana* was obtained from a logistic growth curve fitted to the percentage of sexually mature females and female parasite total length (FPTL) according to the equation:

$$P = \frac{1}{1 + \exp(a + b \cdot FPTL)}$$

where P is the proportion of mature females and a (the y-intercept) and b (the slope) are coefficients derived from the

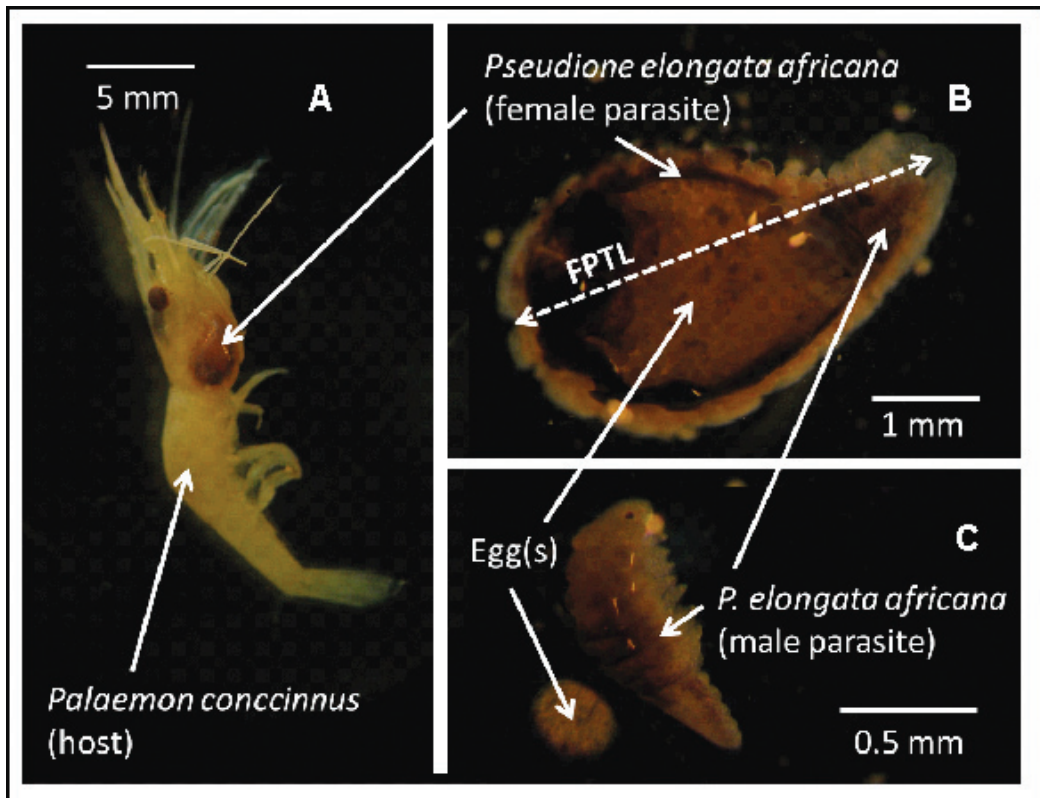


Figure 3. Morphological features of male and female *Pseudione elongata africana* removed from the branchial chamber of the host shrimp *Palaemon concinnus*. A) Dorso-lateral view of infected *P. concinnus* showing deformation of the branchiostegite due to the presence of a female bopyrid in the gill chamber; B) ventral view of female bopyrid showing the marsupium filled with eggs and male bopyrid attached between the pleopods to the female's abdomen; C) male bopyrid and a parasite egg. FPTL = female parasite total length.

logistic equation (for more details see Penha-Lopes *et al.*, 2007). The size at sexual maturity (FPTL₅₀) corresponding to that at which 50% of females reach sexual maturity was calculated according to:

$$FPTL_{50} = -\left(\frac{a}{b}\right)$$

Statistical analyses

Host size carapace length (CL), female parasite total length (FPTL) and the percentage of ovigerous parasite females were subjected to two-way ANOVA at both mangrove sites and in both seasons. Egg numbers were analysed using three-way ANOVA in which the previous factors were considered with the presence of the bopyrid males. Results were considered statistically significant at $p < 0.05$.

The relationship between CL and FPTL and between FPTL and egg/embryo/larval abundance was estimated at each site and in each season using least squares linear regression. Due to the low sample size of ovigerous females (<5% of total sample size), egg abundance data were grouped for each site in both seasons.

RESULTS

Parasite-host population structure

The female of *Pseudione elongata africana* fills most of the branchial chamber of the host, producing a characteristic bulge in its branchiostegite (Fig. 3). The dorsal surface of the female is directed outward against the host's branchiostegite, with the female's anterior region and mouth in contact with the host's posterodorsal edge. The male parasite is tightly wedged among the pleopods of the female (Fig. 3).

All the shrimp considered in this study ($n = 194$) were parasitized by a female bopyrid. Male parasites were found, on average (\pm SE), in 29.12% (± 11.01) and 25.09% (± 5.98) of the hosts in Saco and Costa do Sol, respectively. The average male prevalence at Costa do Sol was much higher in the wet season than

during the dry season (wet: 37.08 \pm 5.19%, dry: 10.10 \pm 5.89%), while the prevalence was similar for both seasons (wet: 29.57 \pm 10.63%, dry: 28.52 \pm 3.69%) in the Saco. While parasites were found more often in the host's left gill chamber in the Saco, no such difference was observed at Costa do Sol (average \pm SE in the Saco, right = 41.55 \pm 7.83%; at Costa do Sol, right = 48.88 \pm 3.44%).

The host CL and FPTL were significantly different between sites and seasons but no significant interaction was detected between these factors (Table 1). Larger hosts (average \pm SE) were observed at Costa do Sol during the wet season compared to the Saco, and to those observed during the dry season (Saco: wet = 4.55 \pm 0.05 mm; dry = 4.01 \pm 0.07 mm; Costa do Sol: wet = 5.27 \pm 0.07 mm; dry = 4.74 \pm 0.09 mm). Similar trends were observed in FPTL (Saco: wet = 4.49 \pm 0.08 mm; dry = 3.93 \pm 0.10 mm; Costa do Sol: wet = 5.17 \pm 0.07 mm; dry = 4.60 \pm 0.11 mm). FPTL increased relative to host size (Fig.4), with no significant differences observed between seasons and sites (slopes: $F = 1.57$, $df = 188$, $p = 0.21$; intercepts: $F = 1.17$, $df = 189$, $p = 0.28$); only a single regression equation was thus calculated.

Bopyrid reproduction dynamics

A higher percentage of ovigerous parasite females was observed at Costa do Sol compared to the Saco (Table 2). Values were also significantly lower during the dry season compared to the wet season (Table 3). A higher percentage of ovigerous females carrying early-stage eggs was usually found at both sites within each season, with the exception of females in the Saco in the wet season (Table 2). The ratio between bopyrid brood size and FPTL was greater during the wet season and at Costa do Sol (average \pm SE; 357.67 \pm 27.55 and 177.08 \pm 27.29 for the wet and dry seasons, respectively) compared to the Saco (207.78 \pm 34.26 and 88.64 \pm 16.70 for the wet and dry seasons, respectively). Lower values of this ratio were found when males were absent (with males: 382.38 \pm 59.00; without males: 353.911 \pm 40.07).

Linear regressions provided similar results for the different egg stages at Saco (slopes: $F = 3.28$, $df = 37$, $p = 0.08$; intercepts: $F = 0.13$, $df = 38$, $p = 0.71$) and Costa do Sol (slopes: $F = 0.98$, $df = 75$, $p = 0.33$; intercepts: $F = 0.00$, $df = 76$; $p = 0.98$) and one slope was thus calculated for the data at both sampling sites. The results indicated that brood size increased with FPTL (Fig. 5) for both sites and seasons and independently. The slopes obtained for the Saco and Costa do Sol differed significantly ($F = 5.95$, $df = 105$, $p < 0.05$). The size at sexual maturity for bopyrid females at Saco and Costa do Sol was 4.15 and 4.58 mm respectively.

DISCUSSION

In addition to the higher parasite prevalence reported in a previous study for Costa do Sol (Penha-Lopes *et al.*, 2010b), the present study revealed that at, Costa do Sol, i) bopyrid females were larger, ii) they had a higher number of eggs per female parasite and iii) ovigerous females were more abundant.

Parasite-Host population structure

The higher parasite prevalence at Costa do Sol may be associated with a higher susceptibility of the shrimps to parasitism due to a decrease in their immunological defences at contaminated sites (Sures, 2006). This may also be due to a higher abundance of intermediate hosts (calanoid copepods) which have been found in estuarine creek waters subjected to industrial and domestic wastes in India and Spain (Ramaiah & Nair, 1997; Uriarte & Villate, 2005). However, the relationship between eutrophication and pollution is not linear (Lafferty, 2008) and the toxic effects of high nutrient inputs may also lead to decreased parasite infection rates.

Although the parasite prevalence was not high all year round (usually between 10-30%, Penha-Lopes *et al.*, 2010b), the values obtained for *P. elongata africana* were, in some instances, much higher than those reported for other Pseudioninae. For example, the prevalence of *Parapenaeopsis styliifera* (H. M. Edwards, 1837) in *Parapenaeon*

japonica (Thielemann, 1910) in coastal waters of Pakistan was 0.80-7.44% (Ayub & Ahmed, 2004); that of *Pseudione affinis* (G.O. Sars, 1882) in several shrimp species in the Mediterranean Sea was 0.37-3.43% (Paradiso *et al.*, 2004); and that of *Pseudione tuberculata* Richardson, 1904 in *Lithodes santolla* (Molina, 1782) in San Juan Bay, Chile, was <25% (Cañete *et al.*, 2008). This variability in the record may be attributable to the different sample sizes; the number of specimens examined in the present study was higher than that of Ayub & Ahmed (2004) and Cañete *et al.* (2008). However, since all the studies referred to were conducted in coastal areas, the differences might also be related to the complexity of estuarine environments.

Only a single infection by a female parasite or parasite pair was noted per shrimp, as reported for other bopyrid species infecting the gill chambers of marine shrimps (Ayub & Ahmed, 2004; Paradiso *et al.*, 2004), although some bopyrid females were only infested by a single dwarf male. This observation indicates the ability of a single castrator to consume all the reproductive energy of the host, and may lead to severe intraspecific and interspecific competition (Lafferty & Kuris, 2009). The much lower prevalence of *P. elongata africana* males (~30%) in *P. concinnus* compared to females is probably related to the first cryptoniscus entering the final host (in this case *P. concinnus*) metamorphosing into a female, and subsequent ones into males. The higher incidence of male parasites during the wet season may be due to a lag before the second cryptoniscus infection (that developing into males), suggested for several bopyrids (Oliveira & Masunari, 2006) such as *Aporobopyrus curtatus* (Richardson) which infects the crab *Petrolisthes armatus* (Gibbes) in southern Brazil; in this, the first cryptoniscus infestation occurs from November to May, whereas the second lasts until July. In addition, the higher male prevalence might be related to synchronous development in both the hosts and parasites, as suggested for other bopyrid-crustacean host systems (Oliveira & Masunari, 2006) and found during the reproductive cycle of *P.*

Table 1. Results of two-way ANOVA conducted on *Palaemon concinnus* carapace length (CL) and female *Pseudione elongata africana* total length (FPTL) at Costa do Sol and in the Saco. Factors were site (Costa do Sol vs Saco) and season (Wet vs Dry). Degrees of freedom (df), mean squares difference (MS), F values and probability (P) are provided for each factor.

Source	df	CL			FPTL		
		MS	F	p	MS	F	p
Site	1	35.94	131.74	<0.0001	30.77	76.82	<0.0001
Season	1	13.26	48.60	<0.0001	14.24	35.55	<0.0001
Site*Season	1	0.02	0.054	0.82	0.01	0.01	0.91
Residuals	190	0.27			0.40		
Total	193						

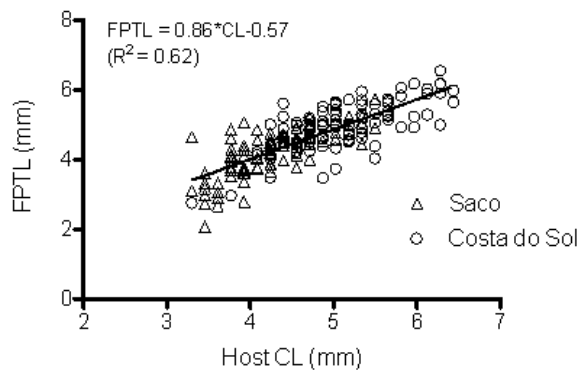


Figure 4. Linear regression between *Palaemon concinnus* carapace length (Host CL) and female *Pseudione elongata africana* total length (FPTL) in the Saco and at Costa do Sol (n=194).

concinnus in south East African mangroves (Penha-Lopes *et al.*, 2010b).

Significant differences were observed in gill chamber selection by the parasites in host shrimp in the Saco as opposed to the Costa do Sol. The exclusive or greater preference of Pseudioninae for the left gill chamber is reported in the literature (see Cañete *et al.*, 2008), although reasons for this relative to host physiology or immunology are still unknown, pointing to the need for further studies on the mechanism of infection in these host-parasite systems.

Parasitized hosts are usually smaller than non-infected hosts. However, the former sometimes grow faster and to larger sizes, leading to a phenomenon termed gigantism (Lafferty & Kuris, 2009). Penha-Lopes *et al.*, (2010b) noted this phenomenon in the shrimp population under study. Not only were

shrimp with parasites larger but the bopyrid females also grew together with the shrimps, occupying most of the cephalothorax. A high correlation between the size of female bopyrids and that of their hosts indicates that the latter is usually infested early in life and that the parasite grows with the host (Cash & Bauer, 1993; Munoz & George-Nascimento, 1999). While it has been suggested that bopyrid parasites reduce the metabolic performance of their hosts, particularly their respiratory function and gonad development (Calado *et al.*, 2006; Paradiso *et al.*, 2004), laboratory experiments

have revealed that they do not significantly affect the activity patterns of their definitive hosts (Chaplin-Ebanks & Curran, 1949), which is in agreement with the larger size of parasitized shrimps found in this study. Nevertheless, parasites were not recorded in any ovigerous *P. concinnus*, suggesting that bopyrid parasites have a significant effect on shrimp physiology, particularly reproduction (Penha-Lopes *et al.*, 2010b).

At Costa do Sol, the host population was larger than in the Saco. We further know that the first-mentioned host population used a higher amount of energy for reproduction (Penha-Lopes *et al.*, 2010b), as do many other decapod species in this region (Penha-Lopes *et al.*, 2009; Torres *et al.*, 2009). The fact that some castrators are not efficient enough to consume all the energy liberated

Table 2. Mean (\pm SE) percentages of ovigerous and non-ovigerous bopyrid females at both sites in the wet and dry seasons. Ovigerous females were divided into early (egg and stage I embryo) and late embryo (stage II embryo and epicaridium larva) stages.

Sites	Seasons	Non-ovigerous females	Ovigerous females		
			Total	Early embryo stages	Late embryo stages
Saco	Dry	58.6 (3.4)	41.4 (3.4)	27.5 (3.1)	13.9 (1.2)
	Wet	40.4 (6.7)	59.6 (6.7)	19.2 (13.5)	40.4 (6.7)
Costa do Sol	Dry	38.9 (4.0)	61.1 (4.0)	50.1 (5.8)	11.0 (6.9)
	Wet	23.7 (3.8)	76.3 (3.8)	62.0 (4.2)	14.3 (3.9)

by interruption of the host's reproduction, allowing residual energy to be used by the castrated hosts for growth (Lafferty & Kuris, 2009), may also provide an explanation for the presence of larger hosts in the peri-urban mangrove. Hence, Penha-Lopes *et al.*, (2010b) explanation that a greater abundance of food sources at Costa do Sol leads to larger hosts needs further clarification.

On the other hand, castrator parasites also benefit from a larger host size, providing them increased survival possibilities as they may attain a larger size (Minchella, 1985). Such a benefit was observed in the present study, suggesting that differences in female parasite size in the two mangroves could be used to indicate the level of eutrophication, this being higher at Costa do Sol compared to the Saco (Cannicci *et al.*, 2009).

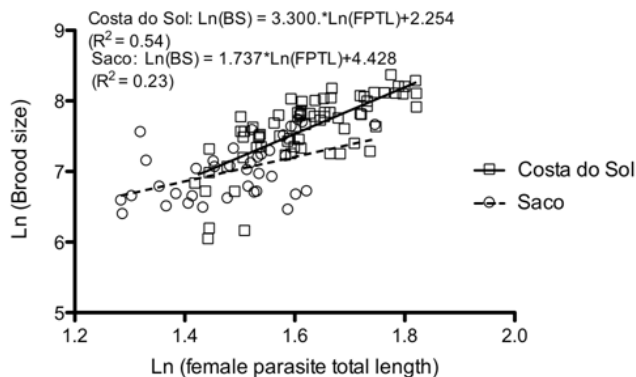


Figure 5. Linear regressions for female *Pseudione elongata africana* brood size (BS) versus total length (FPTL) in the Saco ($n = 37$) and at Costa do Sol ($n=72$). Data were Ln transformed to reveal a linear relationship between the variables as the brood size was expected to vary exponentially with female size.

Bopyrid reproduction dynamics

At Costa do Sol, nearly 40% of the *P. concinnus* females were ovigerous while, in the Saco, their fecundity rarely rose above 10-15% (Penha-Lopes *et al.*, 2010b). A higher percentage of ovigerous females was also commonly observed during the wet and warmer season (Penha-Lopes *et al.*, 2010b), this being common in other crustaceans inhabiting tropical estuaries (Litulo, 2005a; Litulo, 2005b; Litulo, 2005c; Litulo, 2005d; Penha-Lopes *et al.*, 2009; Torres *et al.*, 2009). At Costa do Sol, most of the bopyrid females were ovigerous (>60% in the dry season and ~80% in the wet season) whereas, in the Saco, these percentages were rarely above 40% and 60% respectively in the dry and wet seasons. This suggests that the parasite has a longer reproductive period relative to that of the host, especially in the Saco, where reproduction was restricted to the wet season.

Trouvé & Morand (1998) noted that a higher fecundity in some parasitic species may be explained by their larger size. While food supply is usually not a problem for parasites, parasitic isopods may be under pressure to produce more offspring, leading to their evolution to a large size (Poulin, 1995).

Fecundity in *P. elongata africana* was positively correlated with female size, as reported for other bopyrids (Romero-Rodríguez & Román-Contreras, 2008). In this

Table 3. Results of two-way ANOVA of the percentage of ovigerous *Pseudione elongata africana* females collected at Costa do Sol and in the Saco. Factors were site (Costa do Sol vs Saco) and season (Wet vs Dry). Degrees of freedom (df), mean squares difference (MS), F values and probability (P) are provided for each factor.

Source	df	% Ovigerous females		
		MS	F	P
Site	1	1304.86	16.86	<0.01
Season	1	1001.33	12.94	<0.01
Site*Season	1	8.09	0.096	0.76
Residuals	12	77.38		
Total	15			

Table 4. Results of three-way ANOVA performed on the ratio between the number of eggs and female *Pseudione elongata africana* length (eggs/FPTL) collected at Costa do Sol and in the Saco. Factors were site (Costa do Sol vs Saco); season (Wet vs Dry); and male presence. Degrees of freedom (df), mean squares difference (MS), F values and probability (P) are provided for each factor.

Source	Df	eggs/FPTL		
		MS	F	P
Site (Si)	1	1182561	33.38	<0.001
Season (Se)	1	1086687	30.67	<0.001
Male presence (Mp)	1	191212	5.40	<0.05
Si*Se	1	22292	0.63	0.43
Si*Mp	1	24955	0.70	0.40
Se*Mp	1	440	0.01	0.91
Si*Se*Mp	1	8145	0.23	0.63
Residuals	186	35432		
Total	193			

regard, Cash and Bauer (1993) suggested that female parasites create a voluminous bulge in the host's carapace during moulting to increase its capacity for eggs laid in the ovigerous chamber. Values for parasite fecundity in this study were slightly higher than those reported for bopyrids of smaller size, e.g. *Bopyrina ocellata* (Czerniavsky, 1868) in which ovigerous females are 1.5-3.1 mm in size and bear 330-1 410 eggs, and *Bopyrinella thorii* (Richardson, 1904) in which ovigerous females are 3.9-9.1 mm in size and bear 83-1 036 eggs (Romero-Rodríguez & Román-Contreras, 2008), but lower than those reported for large epicarideans, e.g. *Argeia pugettensis* Dana, 1852 in which ovigerous females are 3.9-9.1 mm and bear 1600-38 300 eggs, and *Anuropodione carolinensis* Markham, 1973,

females of which are 5-16 mm in size and bear 9 500-28 000 eggs (Wenner & Windsor, 1979).

The higher number of eggs reported in bopyrid females at Costa do Sol was most probably due to the larger host shrimp size (and consequently female parasite size), and the host's habitat is not as important for isopod reproduction potential as host body size (Munoz & George-Nascimento, 1999). Nevertheless, when comparing the number of eggs in females of identical size at both sites, those from Costa do Sol bore almost double the number of eggs compared to the Saco. This indicates that reproductive fitness is higher at Costa do Sol compared to the Saco (Penha-Lopes *et al.*, 2010b; Penha-Lopes *et al.*, 2009). A higher quantity and quality of food (PUMPSEA, 2008) and different

environmental parameters such as salinity and temperature (Fig. 2) may be the most important factors affecting the reproductive potential of this ectoparasite. Thus, as with the matter of female parasite size, variability in the reproduction of *P. elongata africana* relative to these parameters also bears further consideration for usefulness as an indicator of anthropogenic pressure.

Acknowledgments—The authors thank E. Nhaca for assistance in the field and two anonymous reviewers for their helpful comments that improved the manuscript. Scholarship support from Fundação para a Ciência e Tecnologias gratefully acknowledged (SFRH/BD/25277/2005 and SFRH/BPD/65977/2009 to GPL, SFRH/BD/63783/2009 to MCL, and SFRH/BPD/26999/2006 to JFM). This study formed part of PUMPSEA (Peri-urban mangrove forests as filters and potential phytoremediators of domestic sewage in East Africa), contract number (INCO-CT2004-510863), funded by the 6th framework of the European Commission. The project was also funded by Fundação para a Ciência e Tecnologia (Pest-OE/MAR/UI0199/2011). The experimental procedures complied with the laws of Mozambique.

References

- Amaral V, Penha-Lopes G, Paula J (2009a) Effects of vegetation and sewage load on mangrove crab condition using experimental mesocosms. *Estuarine Coastal and Shelf Science* 84: 300-304
- Amaral V, Penha-Lopes G, Paula J (2009b) Insights on RNA/DNA ratio of mangrove crabs as indicators of habitat quality. *Aquatic Conservation* 19: 56-62
- Ayub Z, Ahmed M (2004) Study on the host-parasite relationship of *Parapenaemon stylifera* (H. Milne Edwards) and *Parapenaemon japonica* (Thielemann) (Isopoda: Bopyridae). *Hydrobiologia* 524: 225-228
- Bartolini F, Cimó F, Fusi M, Dahdouh-Guebas F, Penha-Lopes G, Cannicci S (2010) The effect of sewage discharge on the ecosystem engineering activities of two East African fiddler crab species: Consequences for mangrove ecosystem functioning. *Marine Environmental Research*: 10.1016/j.marenvres.2010.1010.1002
- Bartolini F, Penha-Lopes G, Limbu S, Paula J, Cannicci S (2009) Behavioural responses of mangrove fiddler crabs (*Uca* spp.) to urban sewage loadings: results of a mesocosm approach. *Marine Pollution Bulletin* 58: 1860-1867
- Beck JT (1980) Life history relationships between the bopyrid isopod *Probopyrus pandalicola* and one of its caridean shrimp hosts *Palaemonetes paludosus*. *American Midland Naturalist* 103: 135-154
- Blanar CA, Munkittrick KR, Houlihan J, Maclatchy DL, Marcogliese DJ (2009) Pollution and parasitism in aquatic animals: A meta-analysis of effect size. *Aquatic Toxicology* 93: 18-28
- Bush AO, Lafferty KD, Lotz JM, Shostak AW (1997) Parasitology meets ecology on its own terms: Margolis *et al* revisited. *Journal of Parasitology* 83: 575-583
- Calado R, Vitorino A, Dinis MT (2006) Bopyrid isopods do not castrate the simultaneously hermaphroditic shrimp *Lysmataamboinensis* (Decapoda: Hippolytidae). *Diseases of Aquatic Organisms* 73: 73-76
- Cañete JI, Cárdenas CA, Oyarzún S, Plana J, Palacios M, Santana M (2008) *Pseudione tuberculata* Richardson, 1904 (Isopoda: Bopyridae): a parasite of juveniles of the king crab *Lithodes santolla* (Molina, 1782) (Anomura: Lithodidae) in the Magellan Strait, Chile. *Revista de Biología Marina y Oceanografía* 43: 265-274

- Cannicci S, Bartolini F, Dahdouh-Guebas F, Fratini S, Litulo C, Macia Jr A, Mrabu E, Penha-Lopes G, Paula J (2009) Effects of urban wastewater impact on crab and mollusc assemblages in equatorial and subtropical mangroves of East Africa. *Estuarine Coastal and Shelf Science* 84: 305-317
- Cash CE, Bauer RT (1993) Adaptations of the branchial ectoparasite *Probopyrus pandalicola* (Isopoda, Bopyridae) for survival and reproduction related to ecdysis of the host, *Palaemonetes pugio* (Caridea, Palaemonidae). *Journal of Crustacean Biology* 13: 111-124
- Chaplin-Ebanks SA, Curran MC (1949) The effect of the parasitic isopod *Probopyrus pandalicola* (Packard, 1879), on the tidal activity patterns of the grass shrimp, *Palaemonetes pugio* Holthuis. *Crustaceana* 78: 1053-1061
- Dale WE, Anderson G (1982) Comparison of morphologies of *Probopyrus bithynis*, *P. floridensis*, and *P. pandalicola* larvae reared in culture (Isopoda, Epicaridea). *Journal of Crustacean Biology* 2: 392-409
- Duke NC, Meynecke JO, Dittmann S, Ellison AM, Anger K, Berger U, Cannicci S, Diele K, Ewel KC, Field CD, Koedam N, Lee SY, Marchand C, Nordhaus I, Dahdouh-Guebas F (2007) A world without mangroves? *Science* 317: 41-42
- Grave S, Al-Maslmani I (2006) A new species of *Palaemon* (Crustacea, Decapoda, Palaemonidae) from Qatar. *Zootaxa* 1187: 37-46
- Hudson PJ, Dobson AP, Lafferty KD (2006) Is a healthy ecosystem one that is rich in parasites? *Trends in Ecology & Evolution* 21: 381-385
- Jobling S, Tyler CR (2003) Endocrine disruption, parasites and pollutants in wild freshwater fish. *Parasitology* 126: S103-S107
- Kruitwagen G, Pratap HB, Covaci A, Wendelaar Bonga SE (2008) Status of pollution in mangrove ecosystems along the coast of Tanzania. *Marine Pollution Bulletin* 56: 1022-1031
- Lafferty KD (2008) Ecosystem consequences of fish parasites. *Journal of Fish Biology* 73: 2083-2093
- Lafferty KD, Kuris AM (1999) How environmental stress affects the impacts of parasites. *Limnology and Oceanography* 44: 925-931
- Lafferty KD, Kuris AM (2009) Parasitic castration: the evolution and ecology of body snatchers. *Trends in Parasitology* 25: 564-572
- Litulo C (2005a) Population biology of the fiddler crab *Uca annulipes* (Brachyura: Ocypodidae) in a tropical East African mangrove (Mozambique). *Estuarine, Coastal and Shelf Science* 62: 283-290
- Litulo C (2005b) Population dynamics and reproduction of the hermit crab *Calcinus gaimardii* (Anomura: Diogenidae) at Inhaca Island, southern Mozambique. *Journal of Natural History* 39: 3359-3367
- Litulo C (2005c) Population structure and reproduction of the hermit crab *Dardanus deformis* (Anomura: Diogenidae) in the Indian Ocean. *Journal of the Marine Biological Association of the United Kingdom* 85: 883-887
- Litulo C (2005d) Population structure and reproductive biology of the fiddler crab *Uca urvillei* (Brachyura: Ocypodidae) in Maputo Bay (south Mozambique). *Journal of Natural History* 39: 2307-2318
- Mackenzie K (1999) Parasites as pollution indicators in marine ecosystems: a proposed early warning system. *Marine Pollution Bulletin* 38: 955-959
- Marcogliese D, Nbsp J (2002) Food webs and the transmission of parasites to marine fish. *Parasitology* 124: 83-99

- Minchella DJ (1985) Host life-history variation in response to parasitism. *Parasitology* 90: 205–216
- Munoz G, George-Nascimento M (1999) Reciprocal reproductive effects in the symbiosis between ghost shrimps (Decapoda : Thalassinidea) and bopyrid isopods (Isopoda : Epicaridea) at Lenga, Chile. *Revista Chilena de Historia Natural* 76(2) 72: 49-56
- Nagelkerken I, Blaber SJM, Bouillon S, Green P, Haywood M, Kirton LG, Meynecke JO, Pawlik J, Penrose HM, Sasekumar A, Somerfield PJ (2008) The habitat function of mangroves for terrestrial and marine fauna: A review. *Aquatic Botany* 89: 155-185
- Oliveira E, Masunari S (2006) *Pseudione tuberculata* Richardson, 1904 (Isopoda: Bopyridae): a parasite of juveniles of the king crab *Lithodes santolla* (Molina, 1782) (Anomura: Lithodidae) in the Magellan Strait, Chile. *Revista Brasileira de Zoologia* 23: 1188-1195
- Paradiso ML, Bottari T, Marino F, Boyko CB, Rinelli P, Giannetto S (2004) Presence and Histopathology of the parasitic isopod *Pseudione affinis* (Epicaridea, Bopyridae) on pandalid shrimps from the central Mediterranean Sea. *Crustaceana* 77: 397–405
- Paula J, Pinto I, Guambe I, Monteiro S, Gove D, Guerreiro J (1998) Seasonal cycle of planktonic communities at Inhaca Island, southern Mozambique. *Journal of Plankton Research* 20: 2165-2178
- Penha-Lopes G, Bartolini F, Limbu S, Cannicci S, Mgaya Y, Paula J (2010a) Ecosystem engineering potential of the gastropod *Terebralia palustris* (Linnaeus, 1767) in mangrove wastewater wetlands - a controlled mesocosm experiment. *Environmental Pollution* 158: 258-266
- Penha-Lopes G, Torres P, Cannicci S, Narciso L, Paula J (2010b) Monitoring anthropogenic sewage pollution on mangrove creeks in southern Mozambique: a test of *Palaemon concinnus* Dana, 1852 (Palaemonoidae) as a biological indicator. *Environmental Pollution* 159: 636-645
- Penha-Lopes G, Torres P, Narciso L, Cannicci S, Paula J (2009) Comparison of fecundity, embryo loss and fatty acid composition of mangrove crab species in sewage contaminated and pristine mangrove habitats in Mozambique. *Journal of Experimental Marine Biology and Ecology* 381: 25-32
- Penha-Lopes G, Torres P, Macia A, Paula J (2007) Population structure, fecundity and embryo loss of the seagrass shrimp *Latreutes pymoeus* (Decapoda: Hippolytidae) at Inhaca island, Mozambique. *Journal of the Marine Biological Association of the United Kingdom* 87: 5676-5681
- Poulin R (1995) Evolutionary influences on body size in free-living and parasitic isopods. *Biological Journal of the Linnean Society* 54: 231-244
- Pumpsea (2008) Peri-urban mangrove forests as filters and potential phytoremediators of domestic sewage in East Africa. Final activity report. European Commission: FP6, INCO-CT2004-510863. Instituto de Ciências Aplicadas e Tecnologia, Lisbon, Portugal, 447pp
- Ramaiah N, Nair N (1997) Distribution and abundance of copepods in the pollution gradient zones of Bombay Harbour-Thana creek-Bassein creek, west coast of India. *Indian Journal of Marine Sciences* 26: 20-25

- Romero-Rodríguez J, Román-Contreras R (2008) Aspects of the reproduction of *Bopyrinella thorii* (Richardson, 1904) (Isopoda, Bopyridae), a branchial parasite of *Thor floridanus* Kingsley, 1878 (Decapoda, Hippolytidae) in Bahía de la Ascensión, Mexican Caribbean. *Crustaceana* 81: 1201-1210
- Salvador EM (2007) Assessment of microbial contamination from non-point domestic sewage on two contrasting peri-urban mangroves (Costa do Sol and Ponta Rasa) around Maputo City. In Symposium Guide and Book of Abstracts of The Fifth Western Indian Ocean Marine Science Association Scientific Symposium Durban, South Africa, 102 pp
- Sures B (2004) Environmental parasitology: relevancy of parasites in monitoring environmental pollution. *Trends in Parasitology* 20: 170-177
- Sures B (2006) How parasitism and pollution affect the physiological homeostasis of aquatic hosts. *Journal of Helminthology* 80: 151-157
- Torres P, Penha-Lopes G, Narciso L, Paula J (2009) Fecundity and brood loss in four species of fiddler crabs, genus *Uca* (Brachyura: Ocypodidae), in the mangroves of Inhaca Island, Mozambique. *Journal of the Marine Biological Association of the United Kingdom* 89: 371-378
- Trouvé S, Morand S (1998) Evolution of parasites' fecundity. *International Journal for Parasitology* 28: 1817-1819
- Uriarte I, Villate F (2005) Differences in the abundance and distribution of copepods in two estuaries of the Basque coast (Bay of Biscay) in relation to pollution. *Journal of Plankton Research* 27: 863-874
- Walters BB, Rönnbäck P, Kovacs JM, Crona B, Hussain SA, Badola R, Primavera JH, Barbier E, Dahdouh-Guebas F (2008) Ethnobiology, socio-economics and management of mangrove forests: A review. *Aquatic Botany* 89: 220-236
- Wenner LE, Windsor TN (1979) Parasitism of galatheid crustaceans from the Norfolk Canyon and Middle Atlantic Bight by bopyrid isopods. *Crustaceana* 37: 293-302