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Chief Editor José Paula

Coral reefs of Mauritius in a changing global climate

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Aims and scope: The *Western Indian Ocean Journal of Marine Science* provides an avenue for the wide dissemination of high quality research generated in the Western Indian Ocean (WIO) region, in particular on the sustainable use of coastal and marine resources. This is central to the goal of supporting and promoting sustainable coastal development in the region, as well as contributing to the global base of marine science. The journal publishes original research articles dealing with all aspects of marine science and coastal management. Topics include, but are not limited to: theoretical studies, oceanography, marine biology and ecology, fisheries, recovery and restoration processes, legal and institutional frameworks, and interactions/relationships between humans and the coastal and marine environment. In addition, *Western Indian Ocean Journal of Marine Science* features state-of-the-art review articles and short communications. The journal will, from time to time, consist of special issues on major events or important thematic issues. Submitted articles are subjected to standard peer-review prior to publication.

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Word from the Editor

The last couple of years have been a time of change for the Western Indian Ocean Journal of Marine Science. The journal has a new and more modern layout, published online only, and the editorial Board was increased to include more disciplines pertaining to marine sciences. While important challenges still lie ahead, we are steadily advancing our standard to increase visibility and dissemination throughout the global scientific community. The central objective of the journal continues focused on the Western Indian Ocean region and serving its growing scientific community.

We are pleased to start the publication of special issues of the journal, launched here with the publication of manuscripts from the University of Mauritius Research Week 2016. The special issues aim to contribute for advancing marine science in the WIO by focusing on specific themes, geographical areas or assembling contributions from scientific meetings. The editorial processes are exactly the same as for regular issues, with double peer-review, and guest editors are considered.

José Paula
Chief Editor

Editorial Note · Coral reefs of Mauritius in a changing global climate

The University of Mauritius Research Week (UoM RW) has been held on an annual basis since 2007 and was organized for the 9th time from 19-23 September 2016. The Research Week is geared towards dissemination of knowledge generated through research activities at the University and by relevant stakeholders in accordance with the UoM's vision of "*Excellence in Research and Innovation*". In line with national priorities, the UoM organizes this event to provide insightful research outcomes not only for the advancement of academic knowledge, but for the benefit of the community at large, through robust policy recommendations.

Out of the multiple submissions made during the UoM RW 2016, a number of manuscripts in the field of ocean/marine sciences were selected to be published in the Western Indian Ocean Journal of Marine Science (WIOJMS), as a special issue entitled "Coral reefs of Mauritius in a changing global climate". This issue is presented in the context of Mauritius being surrounded by a beautiful but delicate coral reef ecosystem, which provides ample ecosystem services contributing to the national economy, but which is subjected to extreme climatic events. Hence, in this special issue several contributions advancing our scientific understanding for sustainable use and management of marine resources in a globally changing marine environment are articulated. The original article by Mattan-Moorgawa *et al.* investigates the photo-physiology of diseased and non-diseased corals. Coral diseases are becoming more common on reefs worldwide due to both local and global stressors. Ramah *et al.* then present a short communication related to substrate affinity by two giant clam species found on the Mauritian coral reefs. Giant clams are under threat worldwide and information on their substrate affinity and habitat aims at providing insightful information towards their sustainable management. In addition, Nandoo *et al.*, in an effort to optimize nucleic acid extraction protocols from marine gastropods, present an original article based on a comparative study using the gastropod genera *Planaxis*, *Cypraea* and *Drupella*. These marine gastropods are ecologically important for coral reefs, especially the coral-eating *Drupella*. Moreover, given the importance of intertidal molluscs, Kaullysing *et al.* document the density and diversity of the benthic molluscs while comparing sheltered and exposed coastal habitats. Appadoo & Beeltah report on the biology of *Platorchestia* sp. (Crustacea, Amphipoda) at Poste La Fayette, Mauritius. Studies on Amphipod diversity and distribution are important especially since studies on marine biodiversity are scarce around Mauritius. Another original article by Ragoonaden *et al*. analyses the recent acceleration of sea level rise in Mauritius and Rodrigues. Such studies are more important than ever in the light of a globally changing marine environment with small island states faced with issues related to rising sea level. Two field notes, based on field observations, are presented by Bhagooli *et al.*, documenting a variety of coral diseases, and *Stylophora pistillata*-like morphotypes occurring around Mauritius Island, respectively. Kaullysing *et al.* also present a field note on coral-eating gastropods observed around Mauritius.

Apart from the local contributors, international collaborators also contribute two original articles in this special issue. Casareto *et al.* characterize the chemical and biological aspects of a coral reef of Mauritius focusing on benthic carbon and nitrogen fixation. These studies related to benthic productivity are important for understanding sustainability of coral reefs and/or lagoonal fisheries. On the other hand, Tokumoto *et al.* document the first detection of membrane progestin receptor (mPR)-interacting compounds from Mauritian coral reef and lagoonal seawater. They used cutting-edge technology to detect key regulators of reproduction in seawater. These contributions in terms of original articles, short communications, and field notes generate new scientific knowledge that may better inform policy and decision making in the field of coral reef studies and management in Mauritius, while contributing to the understanding of coral reefs in the wider Western Indian Ocean region.

Prof. Sanjeev K. Sobhee
Pro-Vice Chancellor (Academia)
The University of Mauritius

Aspects of the biology of *Platorchestia fayetta* sp. nov. (Crustacea, Amphipoda) at Poste La Fayette, Mauritius

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Abstract

Amphipods form an important component of coastal fauna and this study is focused on the biology of semi-terrestrial *Platorchestia fayetta* sp. nov. inhabiting sand and wave-cast algae on the north-eastern coast at Poste La Fayette, Mauritius. The population structure, size class variation, sex ratio and female reproductive status of the species were studied during the summer months (October 2015 - February 2016). The number of *Platorchestia fayetta* sp. nov. decreased considerably throughout the study period. Incubating females were present in all samples collected and ranged between 2.1 to 5.1 mm in size, with the larger ones brooding more embryos. The species can be described as multivoltine having a life history strategy of type I, whereby production of offspring occurred continuously. The average male body size ranged between 4 - 5 mm and was significantly larger than females in most months. Sex ratio was always female biased. This study adds to the knowledge on the biology of the species. Such information is important to understand the population structure of *Platorchestia fayetta* sp. nov. and their interaction with the changing environment.

Keywords: Population structure, size class variation, sex ratio, female reproductive states

Introduction

The talitrids form part of a large family comprising of nearly 300 species of gammaridean amphipods that are terrestrial, semi-terrestrial and aquatic. The terrestrial ones, also known as 'landhoppers', are classified in the genus *Talitroides*, while the semi-terrestrial, estuarine or coastal 'beachfleas' comprise the genera *Orchestia*, *Platorchestia*, *Floresorchestia* and *Eorchestia* or 'sandhoppers' of the genera *Talorchestia* and *Africorchestia* (Milne & Griffiths, 2013). Studies on talitrids of the Western Indian Ocean have been conducted in Madagascar by Ledoyer (1986) where he reported on some species of beach hoppers and provided detailed identification keys for species of the genus *Orchestia*. Some of these species, *Orchestia ancheidos* and *Orchestia anomala* (Cheverux, 1901) have been reviewed and are now classified as *Floresorchestia itampolo* (Lowry & Springthorpe, 2015) and *Floresorchestia andrevo* (Lowry & Springthorpe, 2015). In Mauritius, there has been little research conducted on beach hoppers either on a biological or taxonomical basis. Barnard (1936) studied some terrestrial isopods and amphipods of the island and reported the species *Talitrus gulliveri (*Miers), *Talitroides topitotum* (Burt) and *Orchestia mauritiensis (*Barnard 1936). In a study on shallow-water marine gammaridean amphipods from 34 sites in Mauritius, 69 species have been reported, including one beach hopper *Floresorchestia anomala* (Chevreux 1901) by Appadoo & Steele (1998). Although some taxonomical work was done on these talitrids from the island very little is known about their biology and population structure. This study aims at understanding the population structure and reproductive status of the semi-terrestrial 'beachhopper' *Platorchestia fayetta* sp. nov. described by Green (2015) from Poste La Fayette public beach.

Materials and Methods

Study sites and sampling

Platorchestia fayetta sp. nov. was collected during low tide once per month from October 2015 to February 2016 at Poste La Fayette beach (20°07'39.33"S, 57°45'30.56"E). Samples consisting of beach wrack and sand were collected using a hand shovel and placed in a polyethene plastic bag. Collections made during the warmer months (December, January and February) required digging into the sand.

Laboratory analysis

The samples were brought to the laboratory and sorted by the formalin wash method (Appadoo & Myers, 2004). Amphipods were then immediately separated from the wrack and stored in 70% ethanol. The species was identified using the description of Green & Appadoo (2017), and Green (2015). Samples collected were counted and separated into male, female and juveniles using a stereomicroscope.

The body lengths of male, female and juvenile amphipods were recorded to the nearest 0.1 mm by using a calibrated eye-piece graticule and a stereomicroscope. This was achieved by carefully extending the body of the amphipod through the use of a pair of forceps and measuring the length along the body from the base of the antennae 1 to the base of the telson.

For fecundity analysis, the numbers of eggs or developing embryos in the brood pouch of each incubating female was counted.

Data analysis

Data obtained were processed to compute mean body lengths and parameters related to reproduction. The percentage frequency of males, females and juveniles were computed and recorded in size frequency histograms. The sex ratio for each month was also calculated by dividing the overall number of males present in a particular month by the total number of females present in that same month. ANOVA was used to test for statistical difference in body lengths of males and females. Linear regression was used to investigate the relationship between brood size and female size.

Results

Population structure

The results of the population structure for each month is shown in size frequency histograms (Fig. 2). The *Platorchestia fayetta* sp. nov. population went through significant fluctuations during the study period. Besides the slight increase recorded from October 2015 (N=141) to November 2015 (N=265), the rest of the months (December 2015 to February 2016) showed a considerable decrease in the population. Females dominated the population from October 2015 to February 2016. The percentage of males collected was approximately half of that of females present, while only 15% consisted of new recruits. Out of the 265 *Platorchestia fayetta* sp. nov. collected in November, 75% comprised of females while only 12% were males. The lowest percentage of males (9%) and females (48.3%) was recorded in January.

Size class variation

In October, a peak was recorded in specimens ranging between 4 - 5 mm in size. In December 2015 and January 2016, a shift towards smaller individuals ranging between 2 - 3 mm and 1 - 2 mm respectively was apparent. The February collection consisted

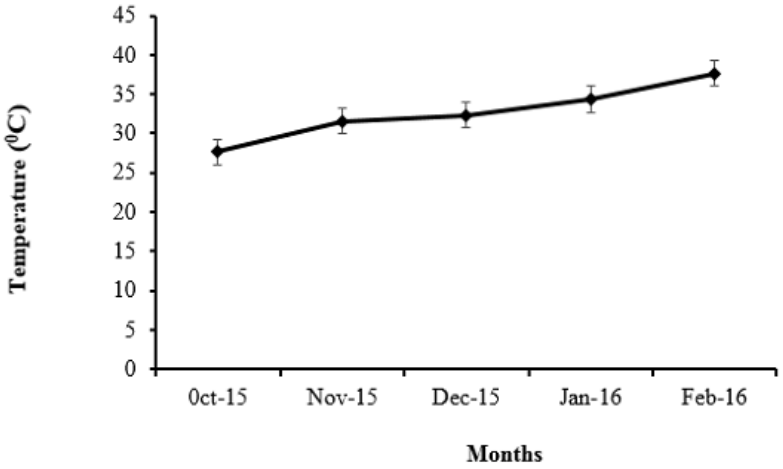

Figure 1. Mean monthly sea temperature variation recorded at Poste La Fayette (October 2015 – February 2016).

mostly of specimens ranging from 3 - 4 mm. The percentage of small-sized *Platorchestia fayetta* sp. nov. was high during the warmer months (Fig.1 and 2) of the study period.

Mean body size and sex ratio (males/ females)

Highest mean lengths of males were recorded in November 2015 (5.03 ± 0.49 mm), and females in January 2016 (4.39 ± 0.43 mm) respectively, while the smallest mean lengths of males (4.29 ± 0.83 mm) and females (2.64 ± 0.58 mm) were recorded in February 2016 and November 2015 respectively.

Results of sex ratio are shown in Table 1, indicating a strongly female-biased population where females outnumbered males throughout the study period.

Female reproductive state and fecundity

The monthly variation in female reproductive states of *Platorchestia fayetta* sp. nov. is shown in Figure 3. Incubating females and females devoid of eggs were present although the percentage of incubating females was relatively low during the study period. The highest percentage of incubating females was recorded in October 2015, and lowest in January 2016.

Egg-bearing females varied greatly in size with a minimum of 2.1 mm and a maximum of 5.1 mm. The largest females were recorded in January 2016 (4.3 ± 0.3 mm). The number of eggs, which depended on the size of females, varied from 5 to 17. Linear regression equations linking brood size (Y) and body length (x) data are presented in Table 2.

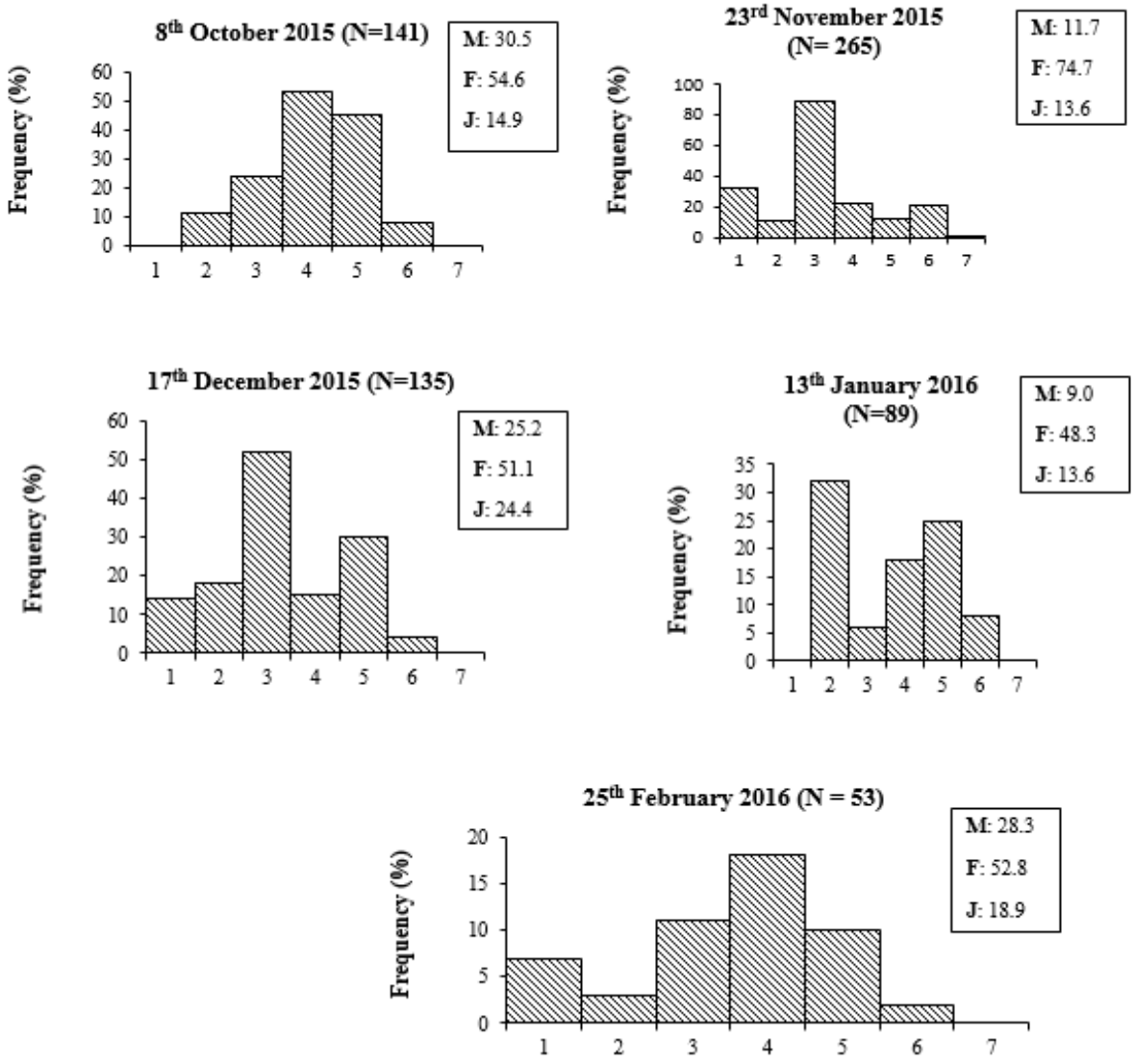

Figure 2. Body size class histograms of *Platorchestia fayetta* sp. nov. for October 2015 to February 2016.

Table 1. *Platorchestia fayetta* sp. nov. body size of males and females, and sex ratio from October 2015 to February 2016.

Months	Male (mean ± S.D)	N	Females (mean ± S.D)	N	Sex ratio (male/female)
October 2015	4.39 ± 0.74	43	3.59 ± 0.56	77	1: 1.79
November 2015	5.03 ± 0.49	31	2.64 ± 0.58	198	1: 6.39
December 2015	4.82 ± 0.17	34	2.78 ± 0.39	68	1: 2
January 2016	4.30 ± 0.64	8	4.39 ± 0.43	43	1: 5.38
February 2016	4.29 ± 0.83	15	3.17 ± 0.67	28	1: 1.87
ANOVA results (monthly size variation)	Male, $F_{(4, 126)} = 3.23$ $P < 0.001$		Female, $F_{(4, 409)} = 0.13$ $P < 0.001$		

Discussion

Population structure of *Platorchestia fayetta* sp. nov.

Continuous reproduction has been reported in other tropical talitrids, *Pseudorchestia brasiliensis* of Rio de Janeiro, Brazil (Cardoso & Veloso, 2001), and *Platorchestia platensis* in Guadeloupe (Ciaviatti *et al*., 1993) and Florida (Garces & Marsh, 1991). Changes in reproductive performance is dependent on the pattern of growth and development suggesting that high latitude populations have larger brood sizes, but fewer numbers of broods, whereas populations found closer to the equator are iteroparous, and mostly multivoltine with smaller embryo size (Wildish, 1988).

Dahl (1946) found that the reproductive period of *P. platensis* lasted from May to November and that the reproduction rate was highest between June and October, suggesting that there is more than a single generation per year. The life history of *P. platensis* is semi-annual (Wildish, 1982) producing at least two generations per year (Morino, 1978; Behbehani & Croker, 1982; Lalitha *et al*., 1990). In the current study it was noted sexual maturity was reached in *Platorchestia fayetta* sp. nov. at small sizes as temperature increased from October 2015 to February 2016. This phenomenon was observed in amphipods such as *Lembos websteri*, *Corophium bonnelli* and *Bathyporeira pilosa* from the Isle of Cumbrae in Scotland (Powell & Moore, 1991). Similar results were discussed by Appadoo & Myers (2004) where *Cymadusa filosa*, *Ampithoe laxipodus* and *Mallacoota schellenbergi* studied in Mauritius showed that sexual maturity in both females (carrying eggs) and males (recognized by secondary sexual characteristics) of each species

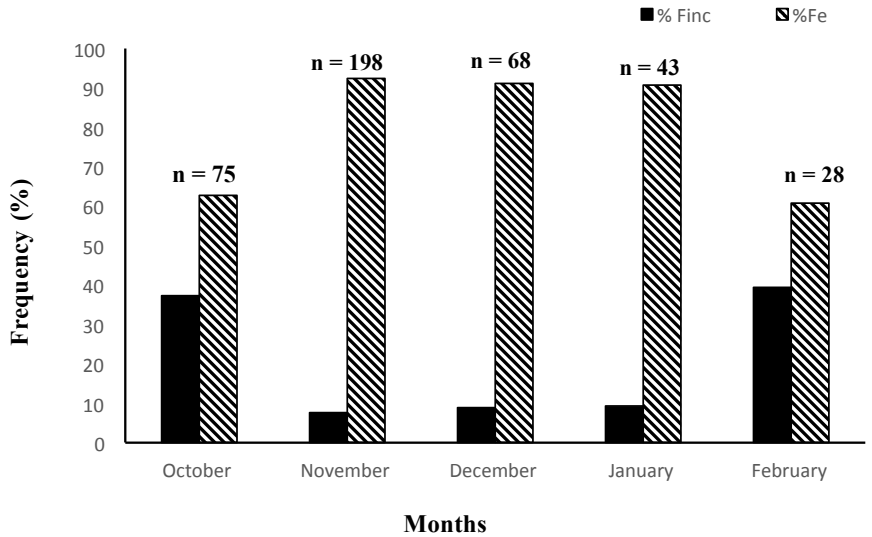

Figure 3. Monthly female reproductive states (F_{inc}: eggs or juveniles present in brood pouch, F_e: mature females devoid of eggs) of *Platorchestia fayetta* sp. nov.

Table 2. Number of eggs in brood pouch (Y) and body size (x) of incubating females of *Platorchestia fayetta* sp. nov. (October 2015 - February 2016).

Months	Size of gravid female (mm)		Number of eggs		*N*	Regression equation	R^2	*P*	Egg quantity of standard female (3mm)
	Range	Mean ± S.D	Range	Mean ± S.D					
October 2015	2.2 – 4.3	3.75 ± 0.6	6 – 11	8.18 ± 6.0	28	Y = -6.05+3.79x	0.33	0.001	5.32
November 2015	3.5 – 5.1	3.99 ± 0.5	9 – 12	10.5 ±1.1	15	Y = 9.11+0.36x	0.06	n.s.	10.19
December 2015	3.0 – 3.2	3.05 ± 0.9	7 – 10	8.3 ± 1.2	6	Y= -16.5+8.21x	0.83	0.012	8.13
January 2016	3.7 – 4.5	4.35 ± 0.3	10 – 17	12 ± 1.0	4	Y = 76.5-14.3x	0.15	n.s.	33.6
February 2016	2.1 – 3.1	2.69 ± 0.4	5 – 10	7.36 ± 1.4	11	Y = 1.73 + 2.09x	0.31	0.07	8.00
Mean year (October 2015 - February 2016)	2.1 – 5.1	3.57 ± 0.5	5 - 17	9.27 ± 2.1	64	Y = 12.9 + 0.03x	0.34	< 0.001	12.99

is reached at a smaller size in warmer months compared to cooler months.

The present study carried out on *Platorchestia fayetta* sp. nov at Poste La Fayette also showed rapid sexual maturity in both males and females. Secondary sexual characteristics were present in males of small body length, and gravid females present in the population were all also of small size. Morino (1978) observed that geographical distribution and variation in seasons resulted in body size changes in *Orchestia platensis,* which provided a direct relationship between temperature and size. Morina (1978) also noted that the molting process in these amphipods takes place at a faster rate at high temperatures when the length of the inter-moult process is decreased. Similar deductions can be made for the species under the present study. The body lengths measured during the study on *Platorchestia fayetta* sp. nov. showed that sexual maturity is reached early due to an increased rate of molting. This could be attributed to the high ambient temperatures recorded at Poste La Fayette which is located in the tropics.

Reproductive status, fecundity and sex ratio

The reproductive period is noted when there is the presence of gravid females and juveniles in the sampled population. Eggs were present in the brood pouches through all months sampled suggesting that the population was reproductive throughout the study. An incubating female in the *Platorchestia fayetta* sp. nov. population can contain up to 17 eggs in her brood pouch. Pardal *et al.* (2000) suggested that seasonal alteration in the quantity of food available can affect the reproductive capacity of a female. One such example was observed in *Platorchestia pietschmanni* in Madagascar (Steele, 1973) suggesting that the species was multivoltine. In addition, the species under study showed a life history strategy of type I, where the production of offspring occurred throughout the study period.

Saint-Marie (1991) found out that the life history patterns of gammaridean amphipods can vary due to the variation in their reproductive strategy which can be separated into semelparity or iteroparity. Their life cycles can be further classified into semi-annual, annual, biannual or perennial and this might be due to biotic factors such as latitude, depth and salinity. Sainte Marie (1991) also determined that semi-annual or annual low latitude populations have high reproductive capacities characterised by multiple broods and minute embryos.

The biological features, percentage of juveniles and ovigerous females, and sex ratio, as well as the variations of within talitrids, have been well investigated in previous papers (Charfi-Cheikhrouha *et al*., 2000; 2001; Bouslama *et al*., 2009). Moore (1981) stated that sex ratios can vary according to season. He suggested that sex ratios can either be skewed towards females as observed during this study, or male biased. He also mentioned that male dominance is observed in cooler months, while warmer months were dominated by females.

Conclusion

This study contributes to understanding the biology of *Platorchestia fayetta* sp. nov. in Mauritius. The main biological characteristic of this species based on this study is that the population is made up of males ranging from 4 - 5 mm, females from 2 - 4 mm, and juveniles from 1 - 2 mm in length. The minimum size of egg-bearing females is 2.1 mm and the brood size ranged from 5 - 17 eggs. The collected population was mostly dominated by females. Females with oostegites were present throughout the study period, suggesting the species is multivoltine.

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References

Appadoo C, Steele DH (1998) Shallow-water marine gammaridean amphipods of Mauritius Island. Crustaceana 71 (6): 633-645

Appadoo C, Myers AA (2004) Reproductive bionomics and life history traits of three gammaridean amphipods, *Cymadusa filosa* Savigny, *Amphithoe laxipodus* Appadoo and Myers and *Mallacoota schellenbergi* Ledoyer from the tropical Indian Ocean (Mauritius). Acta Oecologica 26: 227-238

Barnard KH (1936) Terrestrial isopods and amphipods from Mauritius. Annals of the Natal Museum 8 (1): 1-17

Behbehani MI, Croker RA (1982) Ecology of beach wrack in Northern New England with special reference to *Orchestia platensis*. Estuarine, Coastal and Shelf Science 15: 611-620

Bouslama MF, El gtari M, Charfi-cheikhrouha F (2009) Impact of environmental factors on zonation, abundance, and other biological parameters of two Tunisian populations of *Talitrus saltator* (Amphipoda, Talitridae). Crustaceana 82(2): 141-157

Cardoso RS, Veloso VG (2001) Embryonic development and reproductive strategy of *Pseudorchestoidea brasiliensis* (Amphipoda: Talitridae) at Prainha Beach, Brazil. Journal of Natural History, 35:201211

Chevreux E (1901) Crustacés Amphipodes. Mission scientifique de M. Ch. Alluaud aux Iles Séychelles (Mars, Avril, Mai 1892). Mémoires de La Société zoologique de France, 14: 388-438

Ciavatti G, Louis M, Amanieu M (1993) Stratégie de la reproduction chez une population de *Platorchestia platensis* (Amphipoda: Talitridae) en Guadeloupe (Antilles française). Acta Oecologica 14: 501–519

Charfi-Cheikhrouha F, El gtari M, Bouslama MF (2000) Distribution and reproduction of two sandhoppers, *Talitrus saltator* and *Talorchestia brito* from Zouaraa beach-dune system (Tunisia). Polish Archives Hydrobiology 43 (3-4): 621-629

Dahl E (1946) The Amphipoda of the Sound. Part 1, Terrestrial Amphipoda. Undersökninger över Öresund 29. Lunds Universitets Årsskrift N.F 42: 1-53

Garcés HA, Marsh GA (1991) Studies on the distribution and ecology of *Platorchestia platensis* (Krøyer) at Lake Wyman, Florida. Florida Scientist. Quarterly Journal of the Florida Academy of Sciences 54: 1-10

Green A (2015) A Study on morphology and biology of beach hoppers (Crustacean) in Mauritius, Unpublished BSc Thesis, University of Mauritius, Faculty of Science

Green A, Appadoo C (In Press) A taxonomic update of the coastal talitrids of Mauritius with description of a new species. Zootaxa

Lalitha M, Shyamasundari K, Rao KH (1990) Annual life cycle of the talitrid amphipod, *Orchestia platensis* Krøyer (Crustacea: Amphipoda). Rivista di Idrobiologia 29: 729-745

Ledoyer M (1986) Crustacés amphipodes gammariens. Fauna de Madagascar 59 (2): 599-1112

Lowry JL, Springthorpe RT (2015) The tropical talitrid genus *Floresorchestia* (Crustacea, Amphipoda, Talitridae). Zootaxa 3935 (1): 001-068

Milne R, Griffiths CL (2013) Additions to and revisions of the amphipod (Crustacea: Amphipoda) fauna of South Africa, with a list of currently known species from the region. African Natural History 9: 61-90

Moore PG (1981) The life histories of the amphipods *Lembos websteri* Bate *and Corophium bonnellii* Milne-Edwards in kelp holdfasts. Journal of Experimental Marine Biology and Ecology 49: 1-50

Morino H (1978) Studies on the Talitridae (Amphipoda, Crustacea) in Japan III. Life history and breeding

activity of *Orchestia platensis* Krøyer. Publications of the Seto-Marine Biological Laboratory 24: 245-267

Pardal MA, Marques JC, Metelo I, Lillebo AI, MR (2000) Impact of eutrophication on the life cycle, population dynamics and production of *Ampithoe valida* (Amphipoda) along an estuarine spatial gradient (Mondego Estuary, Portugal). Marine Ecology Progress Series 196: 207-219

Powell R, Moore PG (1991) The breeding cycles of females of seven species of amphipods (Crustacea) from the Clyde Sea area. Journal of Natural History 25: 435-479

Sainte-Marie B (1991) A review of the reproductive binomics of aquatic gammaridean amphipods: variation of life history traits with latitude, depth, salinity and superfamily. Hydrobiologia 223: 189-227

Steele DH (1973) The biology of *Parhyalella pietschmanni* Schellenberg, 1938 (Amphipoda, Hyalellidae) at Nosy Be, Madagascar. Crustaceana 25: 276-280

Wildish DJ (1982) Evolutionary ecology of reproduction in gammaridean Amphipoda. International Journal of Invertebrate Reproduction 5: 1-19