Iheringia
Série Zoologia

e-ISSN 1678-4766
www.scielo.br/isz

Museu de Ciências Naturais

Article

Spatial partitioning between juveniles and adults of the freshwater anomuran crab *Aegla parana* (Crustacea Aeglidae) from southern Brazil

Ana M. Schafaschek & Setuko Masunari

Laboratory for Crustacean Research, Universidade Federal do Paraná, 80050-540 Curitiba, PR, Brazil. (anaschafaschek@gmail.com)

Received 15 April 2021
Accepted 13 January 2022
Published 01 July 2022
DOI 10.1590/1678-4766e2022e2022007

ABSTRACT. In order to understand the role of lower order tributaries in the population structuring of the freshwater anomuran crab *Aegla parana* Schmitt, 1942, a study on the distribution of demographic categories was carried out along Negro River and in its tributary Totó River that belong to Upper Iguaçu Basin, southern Brazil. Two collection points were established along the main channel of Negro River, in a 7.00 km long stretch, and three points in the entire creek Totó River with 6.61 km long. The animals were captured with Surber net and baited traps and had the carapace length (CL) measured. A total 146 crabs were obtained from Negro River and 361 from Totó River, performing 507 analyzed aeglids. From the point 1 of Negro River, males measured 27.68 ± 12.68 mm CL and females 18.98 ± 5.88 mm CL; from point 2 of the same river, the values were 24.45 ± 13.70 mm CL and 27 ± 8.50 mm CL, respectively. There was a positive and direct relationship between the mean CL of the aeglids from Totó River and the distance of the collection points from its source. Males: point 1 (source of the creek): 7.90 ± 1.23 mm CL; point 2: 9.55 ± 3.06 mm CL; point 3: 9.91 ± 2.62 mm CL. Females: point 1 (source): 6.68 ± 1.70 mm CL; point 2: 9.01 ± 1.94 mm CL; point 3: 10.49 ± 2.57 mm CL. The sexually immature aeglids are distributed mainly in the lower order tributary (= Totó River), and the mature ones in the main channel of Negro River, indicating that this population perform ontogenetic migrations from tributary to the main river. The spatial partition can be explained under three aspects that are quite contrasting between Negro River and Totó River: 1. substrate architecture; 2. depth of the water column and 3. quality of available food.

KEYWORDS. Available food, habitat depth, ontogenetic migrations, substrate architecture.

Aegla Leach, 1820 is the only genus of the family Aeglidae that is composed of living species, whose lifecycles are entirely restricted to freshwater environments of southern South America. They have a high degree of endemism and few species with wide distribution may constitute a complex of species, such as *Aegla parana* Schmitt, 1942 (Santos *et al.*, 2017). The interesting and unique freshwater anomuran crab *A. parana* lives mainly in the Iguaçu Basin, southern Brazil. The species is omnivorous, but they can be strong predators.

The displacement of animals is an important population process to understand the temporal and spatial fluctuations in the abundance of a group. Studies suggest that these fluctuations are strongly influenced by ontogenetic changes in the species behavior in addition to the effects of landscape heterogeneity and habitat limitation (Morales & Ellner, 2002). As aeglids are active walkers (Ayres-Peres *et al.*, 2011), certainly, they are under these influences.

The animals' ability to distinguish suitable and unsuitable habitats is the first limitation to be overcome for colonization of new areas, because they had to find new resources offering security for offspring by avoiding competitions (Kokko & López-Sepulcre, 2006). Interactions between life history, physiology, behavior and habitat can make individual displacement an exceptionally complex phenomenon (Patterson *et al.*, 2008).

On the other hand, such patterns of displacement of individuals (daily migrations) and populations (dispersion of the species) may reflect an ecological response to different degree of environmental heterogeneity (Levin *et al.*, 1984; Cohen & Levin, 1991; Bayer *et al.*, 2010). Within a population, daily commuting is generally related to the foraging activity. In addition, it is possible to identify those related to the reproductive phases, which may be the searching for females or displacement of females to other most suitable regions for the survival of offspring (Cohen & Levin, 1991; Lucas *et al.*, 2001; Bertelsen, 2013).

Negro River is the type locality (Schmitt, 1942), has a depth of up to 5.0 m during the rainy season and its affluent Totó River only 0.80 m at its mouth. In addition, the main river has a sandy bottom on which large boulders rest, while the bottom of the stream is covered with pebbles and small boulders that shelter small animals.

Due to this difference in the architecture of the bottom, Negro River hosts most adult crabs (large individuals) while Totó River, most juvenile ones (small individuals). This spatial partitioning can be explained by the abundance of large bivalves such as *Diplodon* sp. in the Negro River, favoring the existence of large aeglids, as they have enough strength to break the shell and ingest the soft part of the mollusk. On the other hand, in the Totó River there are abundant aquatic insects and larvae that are small and, therefore, are suitable for feeding small aeglid crabs.

Therefore, as the crab grow, there is a migration to the main river, where mating is likely to take place. These animals have direct development and the newly hatched larvae spend a few hours on the mother's back.

We do not know if the migration to the Totó River occurs before the larvae hatching (ovigerous females would be the migrants) or if the juveniles migrate towards the tributaries or lower order streams.

The present study aimed to understand the role of the low order tributaries in structuring the population of *A. parana* from the Negro River, Upper Iguaçu Basin. This work clearly shows that the preservation of the adult populations of *Aegla parana* is directly related to the environmental quality of the tributaries.

MATERIALS AND METHODS

Description of the collection sites. The aeglids were obtained from Negro River and its tributary Totó River, Upper Iguaçu River Basin, southern Brazil, both located within the Atlantic Forest biome. Negro River is a large lotic system and constitutes the legal border between the states of Paraná and Santa Catarina (Fig. 1); it was a navigation route in the previous centuries. It is 350 Kilometer (km) long (KÖENE, 2013) and reaches approximately 5 meters (m) deep and 61 m wide at the peak of the rainy season (January and February) (Fig. 2). On the other hand, the tributary Totó River is a small lotic system (Fig. 3), with a total length of 6.61 km, from its source to the mouth at Negro River. It is approximately 1.0 m wide at the source and gradually increases until 6.20 m at its mouth, with depths of approximately 5 centimeter (cm) and 80 cm, respectively.

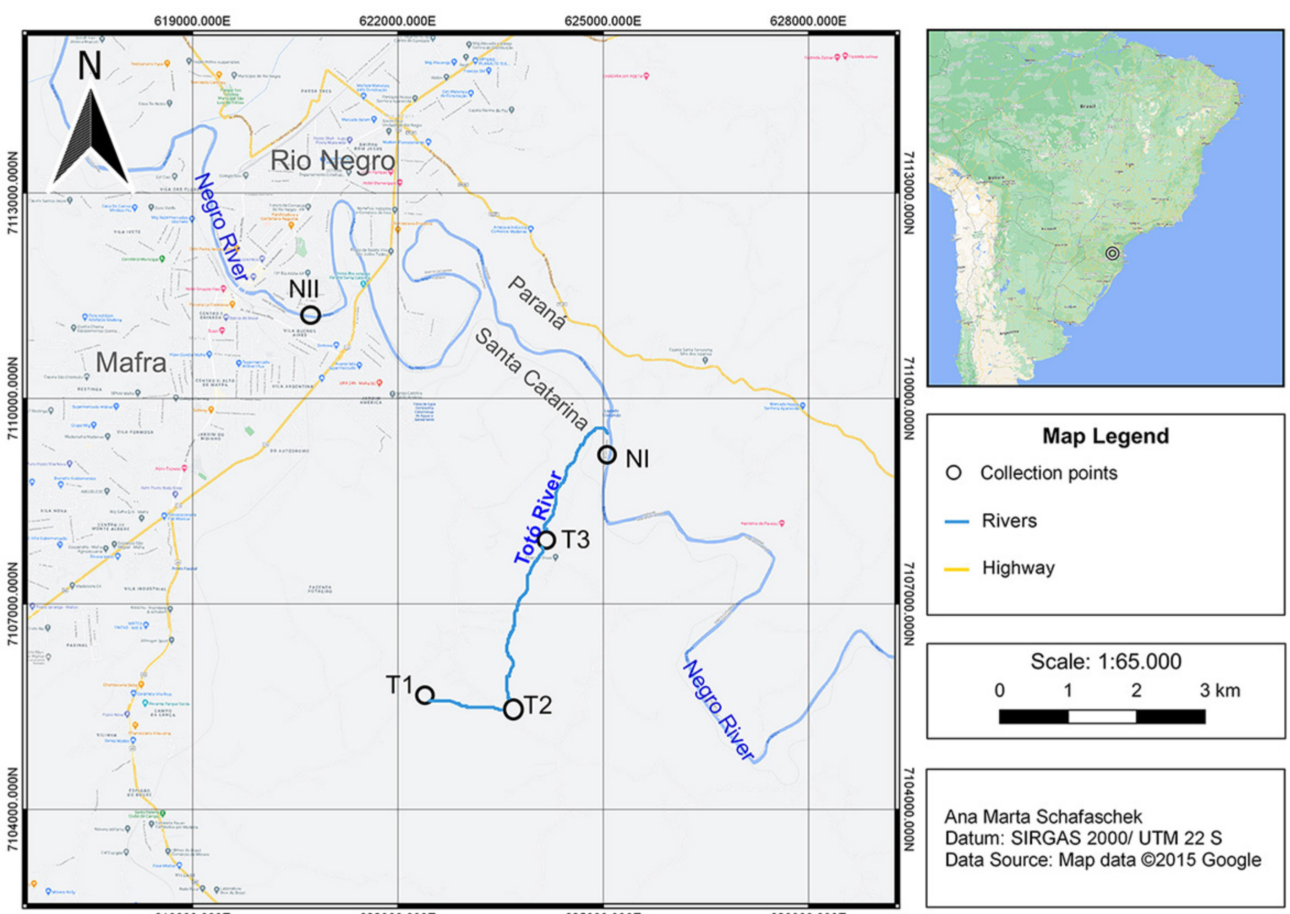

Fig. 1. Map with localization of the Negro River that is the border between the municipalities of Rio Negro and Mafra and between the states of Paraná and Santa Catarina, southern Brazil. In the Negro River two collection points (NI and NII) were established and in its tributary Totó River, three collection points (T1, T2 and T3). Negro River flows from southeast to northwest.

Fig. 2. Negro River, partial view. It was a navigation route in the previous centuries.

Fig. 3. Totó River, partial view. The river bed is dominated by pebble carpet.

The substrate architecture of these two lotic systems is quite contrasting. While the Negro River substrate is predominantly composed of sandy substrate over which isolated large boulders are based, Totó River substrate is composed of countless pebbles and small boulders interspersed with sand and leaf litter (except at the source where sandy substrate is predominant). Due to the high discharge of Negro River, the water flow of its main channel is continuous all year round (Fig. 1); only its marginal area emerges during the dry season. On the other hand, the substrate of Totó River is dominated by uniform pebble bed interrupted by few flagstones, small polls and two waterfalls.

Two collection points (NI and NII) were established along the 7.00 km in the middle course of Negro River, this stretch flows within the urban and rural area of the municipalities of Rio Negro, Paraná state, and Mafra, Santa Catarina state (between 26°08'07.6"S, 49°44'59.8"W and 26°06'49.2"S, 49°47'29.7"W); NI is located in the rural area of Mafra while NII in its urban area (Fig. 1).

Another three collection points (T1, T2 and T3) were established along the entire course of Totó River that runs entirely in the rural area of Mafra: T1 (26°09'43.7"S, 49°46'27.7"W), T2 (26°09'56.5"S, 49°45'57.0"W) and T3 (26°08'34.2"S, 49°45'31.4"W) (Fig. 1). T1 is located at the source of the tributary, T2 and T3 at 1.10 km and 4.76 km from the source, respectively, and the two waterfalls of 5 m and 3 m high are between T2 and T3.

Collection of aeglids. The aeglids were captured with a Surber sampler (500 µm mesh) and baited lobsterpot type traps locally called "covo", in December 2017, February, April and July 2018. Ten baited traps were set and overnighted for 10-12 hours in each collection point and they were inspected for captured animals in the next morning. Since these traps selectively capture large aeglids, collections were complemented with Surber sampler positioned against the direction of the water flow to obtain juveniles that were not collected by traps. The sampling effort for Surber samples was two people for one hour. The collected specimens were transported to the laboratory and frozen until laboratory procedures. The biological material of this research was deposited in Museu de História Natural Capão da Imbuia, Curitiba, PR (MHNCI_INV_0014).

Benthic macroinvertebrates captured together with aeglids in the Surber net were also analyzed for the purpose of knowing the type of food resource available in each lotic system.

Laboratory procedure and statistical analysis. The aeglids were identified according to BOND-BUCKUP (2003) and sexed based on the position of the gonopore openings that are located in the coxae of the third pair of pereiopods in females and in the fifth pair of pereiopods in males (MARTIN & ABELE, 1988). The discrimination between juveniles and adults were performed according to the morphological sexual maturity specified for *A. parana* in SCHAFASCHEK & MASUNARI (2019): males smaller than 23.15 millimeters (mm) carapace length and females smaller than 17.85 mm carapace length are immature crabs.

Males and females had their carapace length (CL) measured from the apex of the rostrum to the mid-posterior border, with a digital caliper (individuals > 20 mm CL) or with Dino-Lite Pro AM413 digital microscope (individuals ≤ 20 mm CL).

For each sample point, the mean, median and standard deviation of CL were calculated. A correlation analysis of the CL values and the distance between the sampling points and the source of Totó River was performed with R Studio 3.4.0.

The analysis of variance between the average CL obtained at the different sample points for both sexes was performed using the *Kruskal-wallis* test ($p<0.05$); the pairs of means were compared using the *Dunn post hoc* test.

Macroinvertebrates were identified according to MERRIT & CUMMINS (1996) for insects, SIMONE (2006) for molluscs and MAGALHÃES (2003) for freshwater decapod crustacean. They were grouped according to their taxonomic group and weighed (wet weight) with a precision scale (Clink 500g / 0.1g). The bivalves were weighed without the shells.

RESULTS

A total of 507 aeglids (222 females and 285 males) were collected, among them 207 males (CL range: 4.92 – 19.95 mm CL) and 154 females (5.18 - 20.31 mm) from Totó River and 78 males (CL range: 6.90 - 50.25 mm) and 68 females (10.37-39.36 mm CL) from Negro River (Tab. I).

Tab. I. *Aegla parana* Schmitt, 1942. Absolute frequency of juveniles and adults of both sexes obtained in Negro River and Totó River, southern Brazil. Adults males CL ≥ 23.15 mm and adults females CL ≥ 17.85 mm (SCHAFASCHEK & MASUNARI, 2019).

	Negro River		Totó River	
	Male	Female	Male	Female
Juvenile	42	15	207	150
Adult	36	53	0	4
Total	78	68	207	154

The males median CL from T1 (Totó River) was 7.98 mm and females' 6.78 mm (excluded a female with 18.55 mm CL); from T2, 8.56 mm CL and 8.89 mm CL, respectively and from T3, 9.61 mm CL and 10.37 mm CL, respectively. One ovigerous female with 19.39 mm CL was captured in T3 of this tributary. The values from NI (Negro River) was 23.16 mm CL for males and 17.54 mm CL for females, and from NII, 21.30 mm CL and 28.33 mm CL, respectively (Figs 4, 5).

There was a positive and direct relationship between the aeglids median CL and respective distance from the collection sites until the source of Totó River. The equations were $y = 1.1125x + 8.3236$ $R^2 = 0.6492$ for males and $y = 1.4469x + 6.7887$ $R^2 = 0.9167$ for females (Fig. 6). Also, a positive and direct relationship between the ratio biomass/macroinvertebrate number and these distances: the equation was $y = 0.3536x - 0.2447$ $R^2 = 0.844$ (Fig. 6).

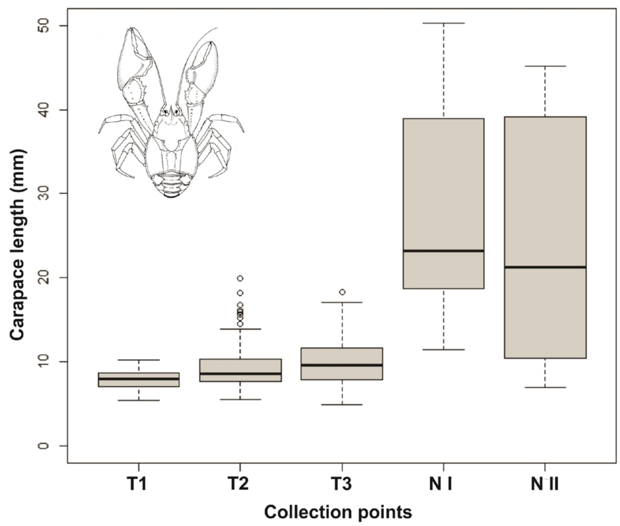

Fig. 4. *Aegla parana* Schmitt, 1942. Aeglids median CL and respective distance from the collection sites. Median (horizontal thick line), first quartile (horizontal bottom line), third quartile (horizontal top line) and minimum and maximum range (vertical dotted line) of carapace length (mm) of males obtained from the three points of Totó River (T1, T2, T3), and from the two points of Negro River (NI, NII).

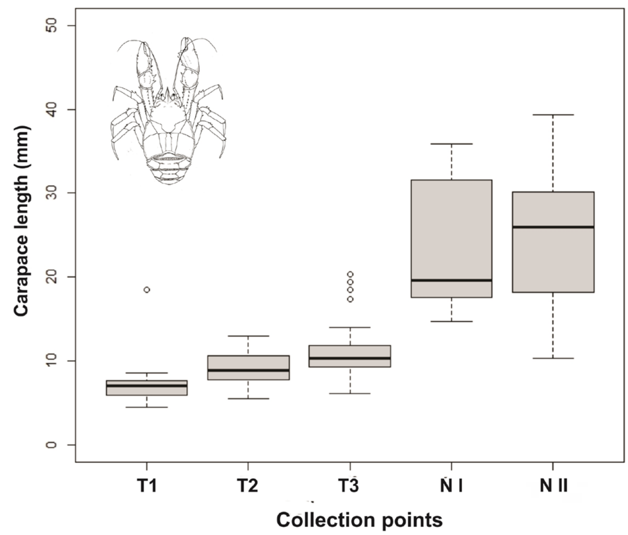

Fig. 5. *Aegla parana* Schmitt, 1942. Aeglids median CL and respective distance from the collection sites Median (horizontal thick line), first quartile (horizontal bottom line), third quartile (horizontal top line) and minimum and maximum range (vertical dotted line) of carapace length (mm) of females obtained from the three points of Totó River (T1, T2, T3), and from the two points of Negro River (NI, NII).

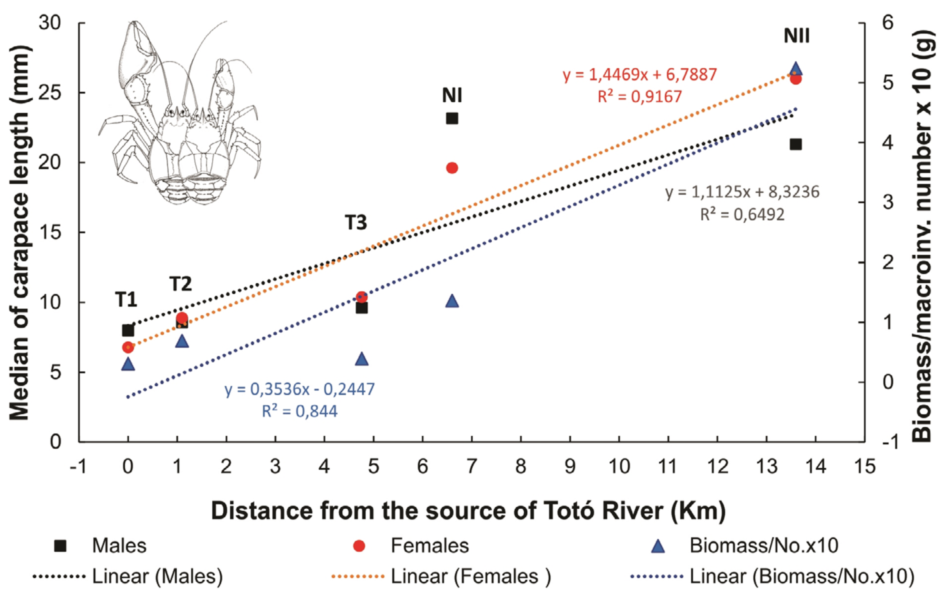

Fig. 6. *Aegla parana* Schmitt, 1942. Relationship between the median carapace length of males and females and the distance of the collection points from the source of Totó River. The relationship between the ratio biomass/number of macroinvertebrates and these distances is also presented. T1, T2, T3, NI, NII, collection points.

There was significant difference among the mean CL of aeglids from Totó River. The Dunn post hoc test showed that T1 is different from T3 for males (Tab. II) and all the sampled points are different from each other for females (Tab. III).

A total of 16 taxonomic groups of macroinvertebrates were collected from Totó River and 11 groups from Negro River, composed of 343 and 180 individuals, respectively. Their biomass, however, totalized 16.5 gram (g) and 87.0 g, respectively, and the ratios biomass/absolute number of macroinvertebrates were: T1=0.031, T2=0.069, T3=0.039, NI=0.137 and NII=0.524 (Tab. IV). This indicated that most macroinvertebrates living in Totó River are small-sized and light animals (aquatic insects) and those from Negro River are mostly represented by big and heavy animals such as the molluscans *Diplodon* sp. and *Corbicula* sp. (Bivalvia).

Tab. II. *Aegla parana* Schmitt, 1942. Analysis of the sample pairs for the significance of the means carapace length of males from Totó River in relation to the distance from the resource. Dunn post hoc test. (*) for $p \leq 0.05$.

	T1	T2	T3
T1		0.07855	0.00657*
T2	0.07855		0.07025
T3	0.00657*	0.07025	

Tab. III. *Aegla parana* Schmitt, 1942. Analysis of the sample pairs for the significance of the means carapace length of females from Totó River in relation to the distance from the spring. Dunn post hoc test. (*) for $p \leq 0.05$.

	T1	T2	T3
T1		0.002346*	1.15E-07*
T2	0.002346*		4.68E-05*
T3	1.15E-07*	4.68E-05*	

Tab. IV. Macroinvertebrates. Biomass (g) and absolute number (inside parenthesis) of the taxonomic groups obtained from Totó and Negro River, southern Brazil.

Taxonomic group	Totó River			Negro River	
	T1	T2	T3	NI	NII
ANNELIDA					
Oligochaeta		0.8 (4)	0.9 (8)		1.6 (11)
CRUSTACEA					
Amphipoda	0.2 (16)				
Isopoda	0.1 (1)		0.1 (1)		
Decapoda - *Trychodactylus fluviatilis*		1.7 (8)			
INSECTA					
Diptera	0.2 (1)				0.2 (7)
Hemiptera		0.8 (1)	0.1 (2)		0.6 (12)
Odonata		1.7 (25)	0.6 (12)	0.6 (11)	0.4 (12)
Trichoptera			0.2 (29)		0.4 (24)
Blattodea-Blattaria			0.5 (5)		
Coleoptera			0.7 (21)		0.1 (1)
Plecoptera			0.1 (1)		0.2 (6)
Ephemeroptera	0.3 (8)		0.6 (133)	0.1 (2)	0.2 (3)
MOLLUSCA					
Cyanocyclas paranacencis		1.0 (26)			
Diplodon sp.			2.5 (1)	0.7 (4)	53.5 (33)
Littoridina sp.			0.7 (29)		0.1 (4)
Corbicula sp.			2.7 (6)	1.2 (2)	27.1 (48)
TOTAL	0.8 (26)	6.0 (70)	9.7 (247)	2.6 (19)	84.4 (161)
Biomass/Number	0.031	0.069	0.039	0.137	0.524

DISCUSSION

The well-known preference of aeglids for low order tributaries (BOND-BUCKUP & BUCKUP, 1994; BUENO & BOND-BUCKUP, 2000; MARCHIORI *et al.*, 2014; SANTOS *et al.*, 2017) was also observed in the present study: approximately double of small aeglids (N=343 crabs) of *Aegla parana* were captured from the tributary Totó (6.6 km long) in comparison to the 7.0 km analyzed stretch of Negro River (N=180 large crabs). Furthermore, the small aeglids from Totó tributary that had the maximum median of 9.61 mm CL for males and 10.37 mm CL for females (see Figs 4 and 5), were sexually immature crabs, as males attain sexual maturity at 23.15 mm CL, and females, at 17.85 mm CL (SCHAFASCHEK & MASUNARI, 2019). On the other hand, most of aeglids obtained from Negro River were sexually mature crabs.

This spatial partitioning between immature and mature *A. parana* can be explained under three distinct physical and biological characteristics observed in Negro River and Totó River: 1. substrate architecture, 2. water column depth and 3. quality of available food.

The substrate architecture is quite contrasting between the tributary and the main river (compare Figs 2 and 3). While in the creek aeglid juveniles have at their disposal numerous microhabitats resulting from the multiplication of substrate composed of pebbles and small boulders, in the main river the sandy substrate with low physical heterogeneity showed to be suitable for large aeglid adults that are powerful swimmers and walkers. This relationship was already observed by SWIECH-AYOUB & MASUNARI (2001) who recorded a higher proportion of juveniles in marginal areas of the Quebra Perna River (Ponta Grossa, PR), where the juveniles find shelter among the branches and leaves of vegetation, pebbles and boulders in the shallow biotopes. On the other hand, large adults were predominant in areas of sandy substrate with few boulders.

It is widely known that the degree of habitat complexity (or physical heterogeneity) has direct relationship with the abundance of species. The degree of complexity is assessed by the shape, size and spatial arrangement of the elements in a habitat (DOWNING, 1991). Although the large number of articles addressed this subject (see review in MCCOY & BELL, 1991), the methods used to quantify and qualify habitat complexity are varied and controversial, and the difficulty in quantifying this factor with a common and universal measure still remains unsolved (TOKESCHI & ARAKAKI, 2012). In this context, it can be considered that the bottom of Totó River provides larger contact surface promoted by numerous small pebbles; in addition, these pebbles weaken the creek water current offering a safe shelter for aeglid juveniles.

On the other hand, the bottom of Negro River that is mainly composed of sandy substrate and boulder outcrops of varied size showed to be a suitable benthic environment for the large aeglid adults. These powerful crabs can actively hunt for alive preys or avoid eventual predator (BURNS, 2011) and, therefore, they do not need refuges underneath pebbles.

The depth of the tributary Totó River and the main channel of Negro River was also quite contrasting, especially at the source of the tributary (5 cm deep), where the water column is too shallow for the colonization of advanced juveniles or adults. On the other hand, the deep water column of the Negro River (5 m during the rainy season) seems to be adequate to accommodate populations composed of large adult aeglids. The narrow band of pebbles in the marginal area, however, can shelter juvenile aeglids.

The third aspect that may be involved in the spatial partitioning of the population of *A. parana* is the composition of the macroinvertebrates that constitute a food source. Aeglids are omnivorous, generalist consumers, feeding on all available resources in the environment (CASTRO-SOUZA & BUCKUP, 2004). Among the known food items are submerged plants, oligochaets (BAHAMONDE & LÓPEZ, 1961), aquatic insect larvae (RODRIGUES & HEBLING, 1978; COLPO *et al.*, 2012), vegetable debris, algae, sand grains, microcrustaceans (BUENO & BOND-BUCKUP, 2004), aeglid fragments, molluscs and fish scales (SANTOS *et al.*, 2008), rotifers (WILLINER, 2010) and decomposing leaves (COGO & SANTOS, 2013).

Similar to the juvenile aeglids, the macroinvertebrates can find a suitable biotope among complex substrate in Totó River. Most of them were aquatic insect (see Tab. III) whose adaptations include the ability to live over surface of hard substrate and/or to protect themselves in small spaces promoted by numerous pebbles (MERRIT & CUMMINS, 1996). These aquatic insects constitute a food suited to the size of juvenile aeglids beyond to be a renewable food source.

On the other hand, the substrate of low heterogeneity of Negro River harbored great number of the filter-feeding macroinvertebrates (bivalve molluscs) (see Tab. III) in the sandy area. These large bivalves probably are preyed by the large *A. parana* as observed in the aeglid *Aegla abtao* Schmitt, 1942 that preyed on a population of the bivalve *Diplodon chilensis* (Gray, 1828), these crabs were capable to crush the molluscan shell (LARA & MORENO, 1995). In the marginal area, pebbles sheltered significant number of aquatic insects that would also constituted a food source for juvenile aeglids.

The direct relationship between the median CL of *A. parana* and the distance between the collection sites and the source of Totó River (see Fig. 3) indicates that an ontogenetic migration can occur from the tributary to the main river.

Migration in aquatic animals can be mainly related to reproductive strategies, such as fishes that perform migrations upstream to lay their eggs, or the freshwater prawns *Atya gabonensis* Glebel, 1875, *Atya scabra* (Leach, 1815) and *Macrobrachium carcinus* (Linnaeus, 1758) whose adults live in rivers can move down to estuaries for release larvae that demand brackish water for the development (AMARAL *et al.*, 2008).

Although migrations within the same river or stream are known for the aeglids *Aegla manuniflata* Bond-Buckup & Santos, 2009 (AYRES-PEREZ *et al.*, 2011) and *Aegla odebrechtti paulensis* Schmitt, 1942 (actually *Aegla paulensis*) (LÓPEZ, 1965), no record of ontogenetic migrations of aeglids from the tributaries to the main river is available in the literature.

Acknowledgments. We are thankful to *Coordenação de Aperfeiçoamento de Pessoal de Nível Superior* (CAPES) from Brazil for the Master Course scholarship for the first author; to *Sistema de Autorização e Informação em Biodiversidade* (SISBIO) for collection license No. 16140-1; to Lucas Schafaschek, Célia Schafaschek, Regina Schafaschek, Márcio Henrique Fernandes, Juliana Mara Padilha and Karine Keler for helping us in the aeglid samplings.

REFERENCES

AMARAL, A. C. Z.; RIBEIRO, C. V.; MANSUR, M. C. D.; SANTOS, S. B. DOS; PAIVA, A. W. E.; MATTEWS-CASCON, H.; LEITE, F. P. P.; MELO, G. A. S. DE; COELHO, P. A.; BUCKUP, L.; VENTURA, C. R. R. & TIAGO, C. G. 2008. A Situação de Ameaça dos Invertebrados Aquáticos no Brasil. *In*: MACHADO, A. B. M.; DRUMMOND, G. M.; PAGLIA, A. P. eds. **Livro Vermelho da Fauna Brasileira Ameaçada de Extinção**. Brasília, Ministério do Meio Ambiente, p. 156-165.

AYRES-PERES, L.; ARAUJO, P. B. & SANTOS, S. 2011. Description of the agonistic behavior of *Aegla longirostri* (Decapoda: Aeglidae). **Journal of Crustacean Biology 31**:379-388.

AYRES-PERES, L.; COUTINHO, D.; BAUMART, J. S.; GONÇALVES, A. S.; ARAUJO, P. B. & SANTOS, S. 2011. Radio-telemetry techniques in the study of displacement of freshwater anomurans. **Nauplius 19**:41-54.

BAHAMONDE, N. & LÓPEZ, M. T. 1961. Estudios biológicos en la populación de *Aegla laevis laevis* (Latreille) de el Monte (Crustacea, Decapoda, Anomura). **Investigaciones Zoo**lógicas **Chilenas 7**:19-58.

BAYER, H. L.; HAYDON, D. T.; MORALES, J. M.; FRAIR, J. L.; HEBBLEWHITE, M.; MITCHELL, M. & MATTHIOPOULOS, J. 2010. The interpretation of habitat preferences metrics under use availability designs. **Transactions of the Royal Society B 365**:2245-2254.

BERTELSEN, R. D. 2013. Characterizing daily movements, nomadic movements, and reproductive migrations of *Panulirus argus* around the Western Sambo Ecological Reserve (Florida, USA) using acoustic telemetry. **Fisheries Research 144**:91-102.

BOND-BUCKUP, G. 2003. Família Aeglidae. *In*: MELO, G. A. S. ed. **Manual de identificação dos Crustacea Decapoda de** água **doce do Brasil.** São Paulo, Editora Loyola, p. 21-116.

Bond-Buckup, G. & Buckup, L. 1994. A família Aeglidae (Crustacea, Decapoda, Anomura). **Arquivos de Zoologia 2**:159-346.

Bueno, A. A. P. & Bond-Buckup, G. 2000. Dinâmica populacional de *Aegla platensis* Schmitt (Crustacea, Decapoda, Aeglidae). **Revista Brasileira de Zoologia 17**:43-49.

Bueno, A. A. P. & Bond-Buckup, G. 2004. Natural Diet of *Aegla platensis* and *Aegla lingulata* Bond-Buckup & Buckup (Crustacea, Decapoda, Aeglidae) from Brazil. **Acta Limnologica Brasiliensia 16**:115-127.

Burns, J. W. 2011. The Distribution and Life History of South American Freshwater Crabs (*Aegla*) and Their Role in Trout Streams and Lakes. **Transactions of the American Fisheries Society 101**:595-607.

Castro-Souza, T. & Bond-Buckup, G. 2004. The trophic niche of two sympatric *Aegla* Leach species (Crustacea, Aeglidae) in a tributary of hydrographic basin of Pelotas River, Rio Grande do Sul, Brazil. **Revista Brasileira de Zoologia 21**:805-813.

Cogo, G. B. & Santos, S. 2013. The role of aeglids in shredding organic matter in neotropical streams. **Journal of Crustacean Biology 34**:1-8.

Cohen, D. & Levin, S. 1991. Dispersal in patchy environments: the effects of temporal and spatial structure. **Theoretical Population Biology 39**:63-99.

Colpo, K. D.; Ribeiro, L. C.; Wesz, B. & Ribeiro, L. O. 2012. Feeding preference of the South American endemic anomuran *Aegla platensis* (Decapoda, Anomura, Aeglidae). **Naturwissenschaften 99**:333-336.

Downing, J. A. 1991. The effect of habitat structure on the spatial distribution of freshwater invertebrate populations. *In*: Bell, S. S.; McCoy, E. D. & Mushinsky, H. R. eds. **Habitat Structure: The Physical Arrangement of Objects in Space.** London, Chapman and Hall, p. 87-106.

Köene, R. 2013. A relação entre as inundações e as características geomorfológicas do Rio Negro/PR. **Geografia Ensino & Pesquisa 17**:175-190.

Kokko, H. & López-Sepulcre, A. 2006. From individual dispersal to species ranges: Perspectives for a changing world. **Science 313**:789-791.

Lara, G. P. & Moreno, C. A. 1995. Efectos de la depredación de *Aegla obtao* (Crustacea, Aeglidae) sobre la distribución espacial y abundancia de *Diplodon chilensis* (Bivalvia, Hyriidae) em el Lago Panguipulli, Chile. **Revista Chilena Historia Natural 68**:123-129.

Levin, S. A.; Cohen, D. & Hastings, A. 1984. Dispersal strategies in patchy environments. **Theoretical Population Biology 26**:165-191.

López, M. T. 1965. Estudios biológicos en *Aegla odebrechtii paulensis* Schmitt (Crustacea, Decapoda, Anomura). **Boletim de Zoologia da Faculdade de Filosofia, Ciências e Letras da Universidade de São Paulo 25**:301-314.

Lucas, M. C.; Baras, E.; Thom, T. J.; Duncan, A. & Slavik, O. 2001. **Migration of freshwater fishes**. Bodmin, Blackwell Science. 420p.

Magalhães, C. 2003. Famílias Pseudothelphusidae e Trichodactylidae. *In*: Melo, G. A. S. ed. **Manual de identificação dos Crustacea Decapoda de água doce do Brasil**, Editora Loyola, São Paulo, p. 143-287.

Marchiori, A. B.; Bartholomei-Santos, M. L. & Santos, S. 2014. Intraspecific variation in *Aegla longirostri* (Crustacea: Decapoda: Anomura) revealed by geometric morphometrics: evidence for ongoing speciation? **Biological Journal of the Linnean Society 112**:31-39.

Martin, J. W. & Abele, L. G. 1988. External morphology of the genus *Aegla* (Crustacea: Anomura: Aeglidae). **Smithsonian Contributions to Zoology 453**:1-46.

McCoy, E. D. & Bell, S. S. 1991. Habitat structure: The evolution and diversification of a complex topic. *In*: Bell, S. S.; McCoy, E. D. & Mushinsky, H. R. eds. **Habitat Structure: The Physical Arrangement of Objects in Space.** London, Chapman and Hall, p. 3-27.

Merrit, R. W. & Cummins, K. W. 1996. **An introduction to the aquatic insects of North America**. Dubuque, Kendall/Hunt. 862p.

Morales, J. M. & Ellner, S. P. 2002. Scaling up animal movements in heterogeneous landscapes: the importance of behaviour. **Ecology 83**:2240-2247.

Patterson, T. A.; Thomas, L.; Wilcox, C.; Ovaskainen, O. & Matthiopoulos, J. 2008. State–space models of individual animal movement. **Trends in Ecology and Evolution 23**:87-94.

Rodrigues, W. & Hebling, N. J. 1978. Estudos biológicos em *Aegla perobae* Hebling e Rodrigues, 1977 (Decapoda, Anomura). **Revista Brasileira de Biologia 38**:383-390.

Santos, S.; Ayres-Peres, L.; Cardoso, R. C. F. & Sokolowicz, C. C. 2008. Natural diet of the freshwater anomuran *Aegla longirostri* (Crustacea, Anomura, Aeglidae). **Journal of Natural History 42**:1027-1037.

Santos, S.; Bond-Buckup, G.; Buckup, L.; Bartholomei-Santos, M. L.; Pérez-Losada, M.; Jara, C. G. & Crandall, K. A. 2017. Three new species of Aeglidae (*Aegla* Leach, 1820) from Paraná State, Brazil. **Journal of Crustacean Biology 35**:839-849.

Schafaschek, A. M. & Masunari, S. 2019. Morphological sexual maturity of the freshwater anomuran crab *Aegla parana* (Crustacea, Decapoda, Aeglidae) from Negro River Sub-basin, Upper Iguaçu Basin, southern Brazil. **Iheringia**, Série Zoologia **109**:e2019029.

Schmitt, W. L. 1942. The species of *Aegla*, endemic South American fresh-water crustaceans. **Proceedings of the United States National Museum 91**:431-520.

Simone, L. R. L. 2006. **Land and Freshwater Molluscs of Brazil**. São Paulo, FAPESP. 340p.

Swiech-Ayoub, B. P. & Masunari, S. 2001. Flutuação temporal e espacial de abundância e composição de tamanho de *Aegla castro* Schmitt (Crustacea, Anomura, Aeglidae) no Buraco do Padre, Ponta Grossa, Paraná, Brasil. **Revista Brasileira de Zoologia 18**:1003-1017.

Tokeschi, M. & Arakaki, S. 2012. Habitat complexity in aquatic systems: fractal sand beyond. **Hydrobiologia 685**:27-47.

Williner, V. 2010. Foregut ossicles morphology and feeding of the freshwater anomuran crab *Aegla uruguayana* (Decapoda, Aeglidae). **Acta Zoologica 91**:408-415.