Morphological variation of freshwater crabs Zilchiopsis collastinensis and Trichodactylus borellianus (Decapoda, Trichodactylidae) among localities from the middle Paraná River basin during different hydrological periods

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Abstract

Measures of hydrologic connectivity have been used extensively to describe spatial connections in riverine landscapes. Hydrologic fluctuations constitute an important macrofactor that regulates other environmental variables and can explain the distribution and abundance of organisms. We analysed morphological variations among individuals of two freshwater crab species, Zilchiopsis collastinensis and Trichodactylus borellianus (Decapoda, Trichodactylidae) from localities of the middle Paraná River basin during two phases of the local hydrological regime. Specimens were sampled at sites (localities) of Paraná River, Saladillo Stream, Salado River and Coronda River when water levels were falling and rising. The conductivity, pH, temperature and geographical coordinates were recorded at each site. The dorsal cephalothorax of each crab was represented using 16 landmarks for Z. collastinensis and 14 landmarks for T. borellianus. The Canonical Variate Analyses showed differences in shape (for both species) among the crabs collected from the Paraná and Salado Rivers during the two hydrologic phases. We did not find a general distribution pattern for shape among the crab localities. During falling water, the shapes of Z. collastinensis were not related to latitude-longitude.
gradient (i.e., showing greater overlap in shape), while during rising water the shapes were ordered along a
distributional gradient according to geographical location. Contrary, shapes of *T. borellianus* were related
to latitude-longitude during falling water and were not related to distributional gradient during rising
water. The cephalothorax shape showed, in general, no statistically significant covariations with environ-
mental variables for either species. These results show that each freshwater crab species, from different
localities of the middle Paraná River, remain connected; however, these connections change throughout
the hydrologic regime of the floodplain system. This study was useful for delineating how the relation
among shapes of crabs of localities varies during two phases of the hydrological regime and for estimating
the connections and geographical patterns in the floodplain system.

**Keywords**
Geometric morphometrics, Brachyura, floodplain, connectivity

**Introduction**

Measures of hydrologic connectivity have been used extensively to describe spatial
connections in riverine landscapes (Ward 1989, Amoros and Bornette 2002). The
dynamic and hierarchical nature of lotic ecosystems can be conceptualised as a four-
dimensional fluvial hydrosystem, displaying distinct longitudinal, lateral, vertical and
temporal characteristics (Ward 1989).

Floodplain systems vary broadly in their environmental characteristics and hydro-
logical regimes (Ward et al. 2002). The alluvial valley, principally located in the middle
and lower section of Paraná River, is a complex ensemble of lotic and lentic environ-
ments (Drago 2007). The main factor modelling the dynamics of the Paraná River
system and its floodplain is the hydro-sedimentological cycle (Junk et al. 1989, Neiff
1990). Rising and falling water make two complementary phases of the cycle, which
have much influence on the stability of river ecosystems (Neiff 1990). The period of
flood is typically during spring and summer, while the period of low water is in au-
tumn and winter (Drago 2007). In this sense, this hydrological fluctuation constitute
an important macrofactor that regulates environmental variables and can explain the
richness, distribution and abundance of organisms that live in these systems (Junk et
al. 1989, Neiff et al. 2001, Mayora et al. 2013).

The movements of some species are related to the spatial and temporal dynamics
of the floodplain system that they inhabit. Dispersal is defined as the movement of an
organism over a specified distance or from one predefined patch to another (Bennetts
et al. 2003). Depending on the hydrologic regime of the floodplain system, dispersal
tends to homogenise populations between water bodies during high water periods and
to decrease the differences between richness and abundance of organisms at nearby
sites (Gomes et al. 2012). Freshwater invertebrates disperse through active or passive
movements, which can influence colonisation rates, gene flow, and evolutionary diver-
gence (Bilton et al. 2001).

The movements of freshwater decapods are influenced by biotic and abiotic fac-
tors in dynamic floodplain systems, and these factors vary over different spatial and
temporal scales (Williner et al. 2010). The regular movements of floodplain decapods are typically active or passive displacements within lakes, ponds or rivers (Williner et al. 2009). Little is known about the dispersal of the large freshwater crab *Zilchiopsis collastinensis* (Pretzmann, 1968). This burrowing crab spends most of its life on river banks in canyons where the locations of caves varies with the river’s water level (Williner et al. 2009). More is known about the smaller freshwater crab *Trichodactylus borellianus* Nobili, 1896, which inhabits the roots of water hyacinths and moves passively with macrophyte displacements (Collins et al. 2006).

The dispersal and connectivity of freshwater invertebrate populations are difficult to study directly. One way to perform such studies is by assessing the differences or similarities in the shape of the organisms between populations. Morphometric studies are useful for delineating the shapes of various populations and species over geographical ranges and such studies can provide evidence of regional differences in crustaceans (Rufino et al. 2006, Konan et al. 2010, Silva et al. 2010, Srijaya et al. 2010, Bissaro et al. 2013). Geometric morphometrics (GM) can be used to quantify the variation in these forms (Monteiro 1999), generating a set of shape variables that can be used to test statistical hypotheses and providing a means of visually describing patterns of shape differences in the data (Rohlf and Marcus 1993, Adams 1999). Previous studies have used GM to compare populations of freshwater decapods (Giri and Collins 2004, Giri and Loy 2008, Barría et al. 2011, Idaszkin et al. 2013). The aim of this paper was to study and infer about the population connectivity of *Z. collastinensis* and *T. borelli anus* in the context of a floodplain system, through the analysis the morphological variations observed among crabs from localities of the middle Paraná River during two phases of their habitat’s hydrological regime.

**Methods**

*Zilchiopsis collastinensis* and *T. borelli anus* were collected from macrophytes using hand nets and from caves by hand (*Z. collastinensis* only). Samples were collected from sites (localities) along the Paraná River (PR1, PR2, PR3, PR4 and PR5), the Saladillo Stream (SS1 and SS2), the Salado River (SR1 and SR2) and the Coronda River (CR) (Fig. 1). After collection, the specimens were chilled and then preserved with 96% ethanol for further Geometric Morphometrics (GM) analysis. The individuals collected were deposited in the Laboratorio de macrocrustaceos del Instituto Nacional de Limnología (INALI-CONICET-UNL).

Each site was sampled during two different phases of the hydrological regime (i.e., when water levels were falling and rising in the Paraná and Salado River) (Fig. 2). Data on hydrometric levels were obtained from local ports and from the Facultad de Ingeniería y Ciencias Hídricas (Universidad Nacional del Litoral). In addition, conductivity, pH and temperature were measured at each site with a digital sensor (HANNA 198130) (Table 1). The geographical locations according to geographic coordinates of the sampling sites were obtained using GPS tracking (Garmin Dakota 20).
To apply the GM analysis, digital images of each crab’s cephalothorax were taken using a Sony Cyber-shot digital camera with a 12.1 megapixel resolution. The cephalothorax structure of *Z. collastinensis* was represented using 16 digitised landmarks (Type I: LMs #2 to 7; LMs #11 to 16 and Type II: LMs #1, 8, 9 and 10) (Bookstein 1991) (Fig. 3a).

**Figure 1.** Sampling sites (localities): Paraná River (PR1, PR2, PR3, PR4, PR5); Saladillo Stream (SS1, SS2); Salado River (SR1, SR2); Coronda River (CR).

**Figure 2.** Different phases of the hydrological regime according to hydrological level. Paraná River (black line) and Salado River (gray line). The circles indicate the water level in which the crabs were collected from each river (falling and rising water).

To apply the GM analysis, digital images of each crab’s cephalothorax were taken using a Sony Cyber-shot digital camera with a 12.1 megapixel resolution. The cephalothorax structure of *Z. collastinensis* was represented using 16 digitised landmarks (Type I: LMs #2 to 7; LMs #11 to 16 and Type II: LMs #1, 8, 9 and 10) (Bookstein 1991) (Fig. 3a).
For *T. borellianus*, 14 landmarks were digitised (Type I: LMs #2 to 7; LMs #9 to 14 and Type II: LMs #1 and 8) (Fig. 3b). The computer program tpsDig 1.40 was used to digitise these landmarks (Rohlf 2004).

Following the GM analysis, the shape symmetric components associated with position, rotation, translation and size were removed using the Procrustes fit in the program MorphoJ (Klingenberg 2011). Variation in the shape symmetric components was explored via a principal component analysis (PCA) applied to the Procrustes coordinates. Intrapopulation allometry was tested using multivariate regression, with centroid size as the independent variable. The size correction was made by taking into
account the residuals of the common pooled within-group regression in the program MorphoJ. Sexual dimorphism was also tested. However, the results ultimately showed that male and female crabs displayed similar variation in shape among localities for both species, and therefore samples were not segregated by sex in subsequent analyses.

Permutations were used to establish the significance of each statistical test, employing 10,000 permutations for the multivariate regression (Klingenberg 2011).

Variations in the shape symmetric component among sites for each moment of the hydrologic regime were analysed using Procrustes pairwise permutation tests and Canonical Variate Analyses (CVA) with the program MorphoJ (10,000 permutations), with residuals of the pooled within-group regression as the focal dataset.

The covariations among shapes, environmental variables and geographical location (altitude and longitude) were analysed with the software tpsPLS (Rohlf 2006) using a permutation test with 99 randomisations. This program uses a two-block partial least-squares analysis, calculating the covariation and correlation between shape and a set of variables (Rohlf 2006). We used this type of analysis to examine whether shape among crabs of different localities varied as a result of certain environmental variables or geographical location in each river during the two phases of the hydrological regime.

Results

The number of specimens collected and analyzed differed for each site depending on the phase of the hydrological regime (Table 2). The geographical locations of the sampling sites were relatively close together (Table 2).

Variation in shape was ordered along PC1 by site at the two hydrological periods for *Z. collastinensis* (PC1: 72.42% and PC2: 10.00% when water levels were falling; PC1: 74.53% and PC2: 6.98% when water levels were rising) and along PC2 by site for *T. borellianus* (PC1: 44.62% and PC2: 15.72% when water levels were falling; PC1: 41.55% and PC2: 16.59% when water levels were rising).

All crabs from all localities of both species exhibited significant \((p < 0.05)\) allometric relationships between cephalothorax shape and centroid size during two phases of the hydrologic regime.

Differences in shape variation were observed among the crabs of the Paraná and Salado Rivers during the two phases of the hydrologic regime (Figs 4 and 5) (Procrustes pairwise permutation tests with CVA). For *Z. collastinensis*, individuals of localities in the Paraná River were similar in shape when water levels were falling. Additionally, individuals collected from PR1 had shapes similar to those collected in SR2 (Salado River site) (Fig. 4a) (Table 3) and in CR (Fig. 4a) (Table 3). When water levels were rising, individuals collected from localities in the Paraná River were similar in shape (Fig. 4b) (Table 3). No differences in shape were observed among individuals in localities in both rivers compared to those in CR (Fig. 4b) (Table 3). Individuals collected from both rivers were more similar in shape when water levels were falling than when water levels were rising (Fig. 4a and b). When water levels were rising, crabs collected
from localities in the Paraná River had overlapping shapes but these shapes were different from those of crabs collected from the Salado River site (Fig. 4b).

For *T. borellianus*, despite some differences in the results of the CVA for samples collected when water levels were falling, individuals from localities in the Paraná River were similar in shape (Fig. 5a) (Table 3). These were different in shape compared to those in the CR site (Fig. 5a) (Table 3). Shape variation differed when water levels were rising, being the crabs from localities in the Paraná River similar in shape to crabs from CR (Fig. 5b) (Table 3). For both phases of the hydrologic regime, crabs from localities in the Paraná River had overlapping shapes, but those shapes were different from those for crabs in SR2 (Fig. 5a and b).
Figure 5. Graphics of Canonical Variate Analyses (CVA) of cephalothorax shapes of *Trichodactylus borellianus* between localities. Ellipses represent the confidence interval at 90%. Paraná River (PR1, PR2, PR3, PR4); Saladillo Stream (SS1, SS2); Salado River (SR2); Coronda River (CR). a) falling water b) rising water.

Table 3. Procrustes pairwise permutation tests with Canonical Variate Analyses (CVA) of cephalothorax shapes of *Zilchiopsis collastinensis* and *Trichodactylus borellianus* between localities, during two different phases of the hydrological regime of the middle Paraná River basin. The upper right triangle gives the Procrustes distances and the lower left triangle gives the *p*-values from permutation tests for Procrustes distances among shapes of crabs from localities. Paraná River (PR1, PR2, PR3, PR4 and PR5); Saladillo Stream (SS1, SS2); Salado River (SR1, SR2); Coronda River (CR).

| Z. collastinensis | PR1 | PR5 | SR2 | CR |
|------------------|-----|-----|-----|----|
| Falling water    |     |     |     |    |
| PR1              | -   | 0.0104 | 0.0081 | 0.0189 |
| PR5              | 0.3619 | -   | 0.0107 | 0.0191 |
| SR2              | 0.2779 | 0.0065** | -   | 0.0162 |
| CR               | 0.0699 | 0.0402** | 0.0069** | -   |

| Rising water     | PR1 | PR2 | PR3 | SR1 | CR |
|------------------|-----|-----|-----|-----|----|
| PR1              | -   | 0.0125 | 0.0115 | 0.0129 | 0.0134 |
| PR2              | 0.0904 | -   | 0.0143 | 0.0166 | 0.0081 |
| PR3              | 0.2474 | 0.0172** | -   | 0.0131 | 0.0128 |
| SR1              | 0.2887 | 0.0119** | 0.1801 | -   | 0.0128 |
| CR               | 0.1262 | 0.3750 | 0.0642 | 0.1193 | -   |

| T. borellianus   | PR2 | PR3 | PR4 | SS1 | SR2 | CR |
|------------------|-----|-----|-----|-----|-----|----|
| Falling water    |     |     |     |     |     |    |
| PR2              | -   | 0.0158 | 0.0109 | 0.0101 | 0.0127 | 0.0163 |
| PR3              | 0.017* | -   | 0.0185 | 0.0167 | 0.0185 | 0.0173 |
| PR4              | 0.0771 | 0.0057* | -   | 0.007 | 0.0147 | 0.0204 |
| SS1              | 0.1714 | 0.0178* | 0.64 | -   | 0.0147 | 0.0206 |
| SR2              | 0.0136* | 0.0021** | 0.0038** | 0.0054* | -   | 0.0090 |
| CR               | 0.002** | 0.0097** | 0.0001*** | 0.0002*** | 0.1882 | -   |

| Rising water     | PR1 | PR3 | SS2 | SR2 | CR |
|------------------|-----|-----|-----|-----|----|
| PR1              | -   | 0.0097 | 0.0133 | 0.0182 | 0.0088 |
| PR3              | 0.4162 | -   | 0.0146 | 0.0196 | 0.0109 |
| SS2              | 0.0656 | 0.0112* | -   | 0.0098 | 0.0095 |
| SR2              | 0.0006*** | <0.001*** | 0.0645 | -   | 0.0163 |
| CR               | 0.4218 | 0.1778 | 0.1623 | 0.0009*** | -   |

Statistically significant differences, *p* < 0.05, **p** < 0.005, ***p** < 0.001.
Zilchiopsis collastinensis and Trichodactylus borellianus presented particular shape variations that were related to geographical location during the two phases of the hydrologic regime. For instance, the covariation between shape and distribution of Z. collastinensis when water levels were falling was statistically not significant. In this case, individuals from localities in the Paraná River and the Salado River were more similar in shape, as revealed by the CVA (Fig. 4a) (Table 4). However, significant high covariation between cephalothorax shape and geographical location was observed when water levels were rising (Table 4). Crabs from localities along the Paraná River were ordered by shape according latitude-longitude gradient and this pattern was separate from that of individuals from the site of the Salado River (Fig. 6a). In contrast, T. borellianus displayed significant covariation between shape and latitude-longitude when water levels were falling (Table 4), and individual shapes were ordered along a distributional gradient for localities in both rivers (Fig. 6b). Covariation between shape and geographical location was not statistically significant for samples collected when water levels were rising (Table 4). For both species, the crabs of closest sites (based on latitude and longitude) were more similar in shape when covariation was significant (Table 4) (Fig. 6a and b). However, this pattern of covariation was not observed for the two hydrological periods for the two species.

Cephalothorax shape was not significantly related to environmental variables for either species (Table 5), with the exception of when water levels were falling for localities of Z. collastinensis. At this time, conductivity was most related to shape (Fig. 7).

**Discussion**

The relation of cephalothorax shape among localities of two freshwater crabs (Z. collastinensis and T. borellianus) collected from connected rivers was different during two phases of the rivers’ hydrological regimes. In this ecological system, whether water levels were falling or rising impacted the population connectivity for the two species. This suggests that individuals were interchanged among localities by dynamic processes.
Table 5. *Zilchiopsis collastinensis* and *Trichodactylus borellianus*: covariations among crab cephalothorax shapes of localities and environmental variables during two phases of the hydrological regime of the middle Paraná River basin.

| Environmental variables | Cephalothorax shape |  |  |
|-------------------------|---------------------|--|--|
|                         | *Z. collastinensis*  |  | *T. borellianus* |
|                         | %Cov.   | p-value | %Cov.   | p-value |
| **Falling water**       |         |         |         |         |
| Dimension 1             | 0.9769  | 0.01*   | 0.7321  | 0.47    |
| Dimension 2             | 0.9984  | 0.03*   | 0.9708  | 0.20    |
| **Rising water**        |         |         |         |         |
| Dimension 1             | 0.9020  | 0.16    | 0.7050  | 0.53    |
| Dimension 2             | 0.9760  | 0.23    | 0.9702  | 0.14    |

Statistically significant differences, *p* < 0.05.

Figure 6. Results of the tpsPLS applying the two-block partial least-squares analysis. **a** *Zilchiopsis collastinensis* when water levels were rising **b** *Trichodactylus borellianus* when water levels were falling. Paraná River (PR1, PR2, PR3, PR4); Saladillo Stream (SS1); Salado River (SR1, SR2); Coronda River (CR).

Figure 7. Results of the tpsPLS applying the two-block partial least-squares analysis on *Zilchiopsis collastinensis* when water levels were falling. Paraná River (PR1, PR5); Salado River (SR2); Coronda River (CR).
of the rivers. Generally, rivers in floodplain systems exhibit considerable heterogeneity that varies over multiple temporal and spatial scales (Neiff et al. 2001). Variability over short time scales, such as seasonal flooding, affects the viability of in-stream populations through changes in recruitment, survival and dispersal (Poff et al. 1997). In addition, hydrological connectivity plays an important role in the movement of populations by connecting various landscape patches (Ward 1989, Amoros and Bornette 2002, Pringle 2003).

According to the phases when crabs were more similar in shape (falling water for *Z. collastinensis* and rising water for *T. borellianus*), this can be related to the movements through to a dynamic floodplain system. Generally, water flow patterns become more important in systems with floodplains because currents have an effect on faunal distribution and on the movement of aquatic invertebrates (Olden et al. 2004, Grönroos et al. 2013). As a result, the movements of freshwater decapods are induced by both biotic and abiotic factors in a dynamic floodplain system and these movements can occur over different spatial and temporal scales (Williner et al. 2010). The freshwater crab *T. borellianus* moves passively as a function of macrophyte migrations (Collins et al. 2006). *Zilchiopsis collastinensis* was also found to be associated with macrophytes in this study. Water flow within the hydrological regime is one of the primary factors regulating the growth and distribution of aquatic plants in streams and rivers and affects the passive movements of crustaceans (Chambers et al. 1991). This was also reported by Schiesari et al. (2003), who documented the potential role of macrophyte rafts in the dispersal of organisms across banks and possibly over very large distances in Amazonian rivers.

We did not find a general distribution pattern for crab localities at the two phases of the hydrologic regime. Shapes of *Z. collastinensis* were not related to location during falling water, while shapes of *T. borellianus* were not related to location during rising water. This would imply that the crabs’ morphological characteristics were not related to latitude-longitude, with high overlap in shape of crabs among the various localities irrespective the origin of the river. Thus, crabs of even distant localities had similar characteristics in shape. In this sense, the flow of water currents becomes particularly important in floodplain systems because the flow regime organises the river ecosystem and strongly affects population dynamics (Poff et al. 1997, Neiff et al. 2001). Four different density stages were observed for palaemonids and trichodactilids in the Middle Paraná River, coinciding with events in the hydrological cycle (Collins et al. 2006, Williner et al. 2010). Additionally, population increases for the prawn *M. amazonicum* Heller, 1862 in the Amazon River was associated with prawn migrations during floods (Walker and Ferreira 1985). Furthermore, the hydrologic regime of a floodplain system tends to homogenise populations between water bodies during high water periods, attenuating the differences between populations (Gomes et al. 2012). On the other hand, during rising water, the shapes of *Z. collastinensis* were ordered along a distributional gradient according to geographical location. Contrary, shapes of *T. borellianus* were related to latitude-longitude on falling water. During these phases, the crabs of closest sites were the most similar in shape. Similar observations have been reported
for *Macrobrachium vollenhovenii* (Herklots, 1851), for which morphological variations between populations were a function of distance between four rivers in Côte d’Ivoire (Konan et al. 2010). Therefore, morphometric analysis proved to be an important tool for evaluating patterns of shape variation for invertebrates by geographical location (Alibert et al. 2001, Krapivka et al. 2007).

Thus, this relationship between shape and latitudinal-longitudinal (distributional) gradient could be affected by the hydrological connectivity between rivers and by the dynamics of the floodplain system. Studies of morphological variation can elucidate patterns observed in phenotypic and genetic characteristics among populations (O’Reilly and Horn 2004). For example, the low morphological and geographical differentiation for the decapod crab *Pachygrapsus marmoratus* (Fabricius, 1787) was attributable to open gene flow and consequent homogenisation (Silva et al. 2009). Additionally, a study of the crab *Carcinus maenas* (Linnaeus, 1758) suggested that there was a high degree of connectivity with little evidence of reduced gene flow (Silva et al. 2010).

In addition, we found some covariation between shape and environmental variables for *Z. collastinensis* during periods of falling water levels. However, the general pattern observed in this study showed that shape was not related to environmental variables for both species of crabs. In floodplain systems, environmental variables are affected by hydrological fluctuations together with hydrological connectivity. These events can regulate population dynamics and constitute an important macrofactor that regulates other environmental variables and can explain the distribution and abundance of organisms that live in these systems (Ward 1989, Neiff et al. 2001). On the other hand, gene flow among populations can counteract gene frequency changes because of selection, imposing a limit on local adaptation. Migration generally has an important role in evolution, affecting spatial patterns and adaptation to local environments (Hellberg et al. 2002).

In this study, we found that the two species demonstrated particular shape variations in relation to geographical location for the two periods in the hydrologic regime. This pattern can be explained by the different behaviours and life histories of each crab. For instance, *Z. collastinensis* is a large burrowing crab that spends most of its life on the banks of rivers in canyons (Williner et al. 2009). *Trichodactylus borellianus* is a small crab that inhabits water hyacinth roots, and this species’ movements depend on macrophyte migrations (Collins et al. 2006). This indicates that these crabs could have different dispersal rates, as previously suggested by Bohonak and Jenkins (2003) for invertebrates.

Despite the shape differences found for both crab species during the two periods in the hydrologic regime, shape was more similar for individuals in downstream locality where rivers converge during periods of rising water levels. This suggests that there were exchanges in organisms along the upstream-downstream gradient, referred to as a longitudinal connection (Ward 1989).

These results showed that each freshwater crab species (*Z. collastinensis* and *T. borellianus*) from different localities of the middle Paraná River were connected; however, the flow of organisms changed at different phases of the hydrologic regime. More precisely, this is indicative of a specific type of hydrological connectivity (in an ecologi-
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...that results in the water-mediated transfer of matter, energy and organisms within or between elements of the hydrologic cycle. These connections between crabs of localities can change as a function of the hydrologic regime in a floodplain system. This alteration in connectivity is to be expected because hydrological connectivity operates in longitudinal, lateral, vertical and temporal dimensions (Ward 1989), although the vertical and lateral connections were not evaluated in this study. Furthermore, the distinctiveness of floodplain macrosystems is that the level of water affects the dynamics and the relationships among populations (Poff et al. 1997, Neiff et al. 2001).

Even though this study explored the use of geometric morphometrics at a microgeographical scale, genetic analyses are required to better understand the processes of dispersal and population connectivity of freshwater crabs in this dynamic floodplain system. However, the findings of this study are particularly relevant in the context of ecological flows. When rivers are altered by a human activity, a floodplain’s hydrologic dynamics might help to maintain the ecological integrity of decapods, influencing the flow and population connectivity.

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References

Adams DC (1999) Methods for shapes analysis of landmark data from articulate structures. Evolutionary Ecology Research 1: 959–970.
Alibert P, Moureau B, Dommergues JL, David B (2001) Differentiation at a microgeographical scale within two species of ground beetle, Carabus auronitens and C. nemoralis (Coleoptera, Carabidae): a geometrical morphometric approach. Zoologica Scripta 31: 299–311. doi: 10.1046/j.1463-6409.2001.00068.x
Amoros C, Bornette G (2002) Connectivity and biocomplexity in waterbodies of riverine floodplains. Freshwater Biology 47: 761–776. doi: 10.1046/j.1365-2427.2002.00905.x
Barría EM, Sepúlveda RD, Jara CG (2011) Morphologic variation in Aegla Leach (Decapoda: Reptantia: Aeglideae) from central-southern Chile: interspecific differences, sexual dimorphism, and spatial segregation. Journal of Crustacean Biology 31: 231–239. doi: 10.1651/10-3324.1
Bennetts RE, Nichols JD, Lebreton JD (2003) Methods for estimating dispersal probabilities and related parameters using marked animals. In: Clobert J, Danchin E, Dhondt AA, Nichols JD (Eds) Dispersal. Oxford University Press, 3–17.
Bilton DT, Freeland JR, Okamura B (2001) Dispersal in freshwater invertebrates. Annual Review of Ecology 32: 159–181. doi: 10.1146/annurev.ecolsys.32.081501.114016

Bissaro FG, Gomes JL, Madeira di Benedito AP (2013) Morphometric variation in the shape of the cephalothorax of shrimp Xiphopenaeus kroyeri on the east coast of Brazil. Journal of the Marine Biological Association of the United Kingdom 93(3): 683–691. doi: 10.1017/S0025315412000409

Bohonak AJ, Jenkins DG (2003) Ecological and evolutionary significance of dispersal by freshwater invertebrates. Ecology Letters 6: 783–796. doi: 10.1046/j.1461-0248.2003.00486.x

Bookstein FL (1991) Morphometric Tools for Landmark Data. Cambridge University Press, Cambridge, 435 pp.

Chambers PA, Prepas EE, Hamilton HR, Bothwell ML (1991) Current velocity and its effect on aquatic macrophytes in flowing waters. Journal of Applied Ecology 1: 249–257. doi: 10.2307/1941754

Collins PA, Giri F, Williner V (2006) Population dynamics of Trichodactylus borellianus (Crustacea Decapoda Brachyura) and interactions with the aquatic vegetation of the Paraná River (South America, Argentina). Annals of Limnology 42:19–25. doi: 10.1051/limn/2006001

Drago EC (2007) The physical dynamics of the River-lake floodplain system. In: Iriondo MH, Paggi JC, Parma MJ (Eds) The Middle Paraná River: Limnology of a Subtropical Wetland. Springer-Verlag, Heidelberg, 83–122. doi: 10.1007/978-3-540-70624-3_4

Giri F, Collins PA (2004) A geometric morphometric analysis of two sympatric species of the family Aeglidae (Crustacea, Decapoda, Anomura) from the La Plata basin. Italian Journal of Zoology 71: 85–88. doi: 10.1080/11250000409356555

Giri F, Loy A (2008) Size and shape variation of two freshwater crabs in Argentinean Patagonia: the influence of sexual dimorphism, habitat, and species interactions. Journal of Crustacean Biology 28: 37–45. doi: 10.1651/07-2824R.1

Gomes LC, Bulla CK, Agostinho AA, Vasconcelos LP, Miranda LE (2012) Fish assemblage dynamics in a Neotropical floodplain relative to aquatic macrophytes and the homogenizing effect of a flood pulse. Hydrobiologia 685: 97–107. doi: 10.1007/s10750-011-0870-6

Grönroos M, Heino J, Siqueira T, Landeiro VL, Kotanen J, Bini LM (2013) Metacommunity structuring in stream networks: roles of dispersal mode, distance type, and regional environmental context. Ecology and Evolution 3(13): 4473–4487. doi: 10.1002/ece3.834

Hellberg M, Burton R, Neigel J, Palumbi S (2002) Genetic assessment of connectivity among marine populations. Bulletin of Marine Science 70: 273–290.

Idaszkin YL, Márquez F, Nocera AC (2013) Habitat-specific shape variation in the carapace of the crab Cerograpus angulatus. Journal of Zoology 290: 117–126. doi: 10.1111/jzo.12019

Junk WJ, Bayley PB, Sparks RE (1989) The flood pulse concept in river-floodplain systems. In: Dodge DP (Ed.) Proceedings of the International Large River Symposium. Canadian Special Publication of Fisheries and Aquatic Sciences 106: 110–127.

Klingenberg CP (2011) MorphoJ: an integrated software package for geometric morphometrics. Molecular Ecology Resources 11: 353–357. doi: 10.1111/j.1755-0998.2010.02924.x

Konan KM, Adépo-Gourène AB, Ouattaraa A, Nyingy WD, Gourène G (2010) Morphometric variation among male populations of freshwater shrimp Macrobrachium vollenhovenii
Morphological variation of freshwater crabs Zilchiopsis collastinensis...

Herklots, 1851 from Côte d’Ivoire Rivers. Fisheries Research 103: 1–8. doi: 10.1016/j. fishres.2010.01.005

Krapivka S, Toro JE, Alcápán AC, Astorga M, Presa P, Pérez M, Guíñez R (2007) Shell-shape variation along the latitudinal range of the Chilean blue mussel Mytilus chilensis (Hupe 1854). Aquaculture Research 38: 1770–1777. doi: 10.1111/j.1365-2109.2007.01839.x

Mayora G, Devercelli M, Giri F (2013) Spatial variability of chlorophyll-a and abiotic variables in a river–floodplain system during different hydrological phases. Hydrobiologia 717: 51–63. doi: 10.1007/s10750-013-1566-x

Monteiro LR (1999) Multivariate regression models and geometric morphometrics: the search for causal factors in the analysis of shape. Systematic Biology 48: 192–199. doi: 10.1080/106351599260526

Neiff JJ (1990) Ideas para la interpretación ecológica del Paraná. Interciencia 15: 424-441.

Neiff JJ, Poi de Neiff A, Casco S (2001) The effect of prolonged floods on Eichhornia crassipes growth in Paraná River floodplain lakes. Acta Limnologica Brasiliensia 3: 51–60.

Olden JD, Hoffman AL, Monroe JB, Poff NL (2004) Movement behaviour and dynamics of an aquatic insect larva in a stream benthic landscape. Canadian Journal of Zoology 82: 1135–1146. doi: 10.1139/z04-094

O’Reilly KM, Horn MH (2004) Phenotypic variation among populations of Atherinops affinis (Atherinopsidae) with insights from a geometric morphometric analysis. Journal of Fish Biology 64: 1117–1135. doi: 10.1111/j.1095-8649.2004.00379.x

Poff NL, Allan JD, Bain MB, Karr JR, Prestegaard KL, Richter BD, Sparks RE, Stromberg JC (1997) The natural flow regime. BioSience 47: 769–784. doi: 10.2307/1313099

Pringle C (2003) What is hydrologic connectivity and why is it ecologically important? Hydrological Processes 17: 2685–2689. doi: 10.1002/hyp.5145

Rohlf FJ (2004) Tpsdig (Version 1.40). Department of Ecology and Evolution, State University of New York at Stony Brook, New York. http://life.bio.sunysb.edu/morph/

Rohlf FJ (2006) Tpspls (Version 1.18). Department of Ecology and Evolution, State University of New York at Stony Brook, New York. http://life.bio.sunysb.edu/morph/

Rohlf FJ, Marcus LF (1993) A revolution in morphometrics. Trends in Ecology and Evolution 8: 129–132. doi: 10.1016/0169-5347(93)90024-J

Rufino M, Abelló P, Yule AB (2006) Geographic and gender shape differences in the carapace of Liocarcinus depurator (Brachyura: Portunidae) using geometric morphometrics and the influence of a digitizing method. Journal of Zoology 269: 458–465. doi: 10.1111/j.1469-7998.2006.00086.x

Schiesari L, Zuano J, Azevedo-Ramos C, Garcia M, Gordo M, Messias M, Monteiro Vieira E (2003) Macrophyte rafts as dispersal vectors for fishes and amphibians in the Lower Solimoes River, Central Amazon. Journal of Tropical Ecology 19: 333–336. doi: 10.1017/S0266467403003365

Silva IC, Hawkins SJ, Paula J (2009) A comparison of population differentiation in two shore crab species with contrasting distribution along the Portuguese coast, using two morphological methodologies. Marine and Freshwater Research 60: 833–844. doi: 10.1071/MF08215
Silva IC, Alves MJ, Paula J, Hawkins SJ (2010) Population differentiation of the shore crab Carcinus maenas (Brachyura: Portunidae) on the southwest English coast based on genetic and morphometric analyses. Scientia Marina 74: 435–444.

Srijaya TC, Pradeep PJ, Mithun S, Hassan A, Shaharom F, Chatterji A (2010) New record on the morphometric variations in the populations of horseshoe crab (Carcinoscorpius rotundicauda Latreille) obtained from two different ecological habitats of Peninsular Malaysia. Our Nature 8: 204–211.

Walker I, Ferreira MJN (1985) On the populations dynamics and ecology of the shrimp species (Crustacea, Decapoda, Natantia) in the Central Amazonian river Taruma-Mirim. Oecologia 66: 264–270.

Ward JV (1989) The four-dimensional nature of lotic ecosystems. Journal of the North American Benthological Society 8: 2–8. doi: 10.2307/1467397

Ward JV, Tockner K, Arscott DB, Claret C (2002) Riverine landscape diversity. Freshwater Biology 47:517–539. doi: 10.1046/j.1365-2427.2002.00893.x

Williner V, Giri F, Collins PA (2009) Los crustáceos decápodos dulceacuícolas en Argentina. FABICIB 13: 107–125. doi: 10.14409/fabicib.v13i1.846

Williner V, Giri F, Collins PA (2010) Metapopulations of Decapods in the Floodplain of Parana River, South America. In: Alvares MA (Ed.) Floodplains: Physical Geography, Ecology and Societal Interactions. Nova Science Pub, New York, 179–199.