Limnoperna fortunei Colonies: Structure, Distribution and Dynamics

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Abstract Settlement of new recruits of *Limnoperna fortunei* occurs preferentially on areas already colonized by conspecifics, and on surfaces with well-developed periphytic biofilms. Hard substrata (immobile rocks, wood) are preferred by the mussel, but colonization can also take place on muddy areas stabilized by roots or fibrous debris, on floating and submerged plants, and on mussel shells, crustaceans, etc. Colonization starts in crevices, angles and other sites inaccessible to large predators, but it often extends over open areas as well. Mussel beds rarely exceed 7–10 cm in thickness, with most adults being at least partially attached to the substrate. Juveniles often settle on larger shells. Densities of over 200,000 ind./m^2 have been reported occasionally, but such high numbers are invariably dominated by specimens <2 mm in length. Densities of adult mussels (>5-7 mm) are usually below 10,000 ind./m^2. The only site where densities were estimated over an entire

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water body, the reservoir Embalse de Río Tercero, yielded an average of 959 ind./m^2. Mussel colonies are usually most abundant and dense along the coastal fringe, where rock outcrops are common. Deeper areas are covered with clay and silt, and are therefore unfit for mussel colonization. Data at hand are still insufficient for describing multiannual trends in mussel abundance in South America; however, ancillary evidence suggests that, after having peaked 7–10 years after introduction, densities have been waning. Size structure of individuals in mussel colonies depends strongly on the time of the year. During periods of peak recruitment (spring to late summer) juveniles < Size structure of individual > 2 mm in length can represent >90% of the population, whereas during the winter they normally account for 10-15%.

Settlement of Recruits

The ecological and economic impacts of *Limnoperna fortunei* are due in part to life history traits typical of its marine ancestors, but very unusual among freshwater animals. Unlike most freshwater bivalves, *L. fortunei* possesses a series of free-swimming larval stages, the last one of which, the pediveliger, can either swim using its velum or crawl using its foot (Cataldo and Boltovskoy 2000; Cataldo et al. 2005; see Chapter "Larval Development of *Limnoperna fortunei*" in this volume). Upon receiving the proper cues, the pediveliger will settle onto an appropriate surface and secrete byssal threads; once anchored, it will complete its metamorphosis to become a postveliger or plantigrade mussel.

Settlement is an active process in which the pediveliger selects the site and substrate on which to settle (Rodriguez et al. 1993). Pediveligers of *L. fortunei* have been shown to recruit preferentially to sites providing some kind of protection. In his pioneering work on *L. fortunei*, Morton (1977) reported that in Plover Cove Reservoir, Hong Kong, *L. fortunei* larvae always prefer to settle into crevices or joints, as compared to open surfaces, and the same was observed by Boltovskoy and Cataldo (1999) and by Sylvester et al. (2007) for larvae settling onto experimental frames in the Lower Paraná River. This behaviour has been extensively addressed in studies of marine sessile invertebrates and is thought to be effective in escaping predation and dislodgement by physical disturbances such as waves and currents (Walters and Wethey 1996).

Aggregates of conspecifics and surfaces covered with a dense biofilm are also preferred by *L. fortunei* for settlement over clean substrata (Morton 1977, Sardiña et al. 2009; Balazote Oliver 2011). Many studies attest to the fact that larvae of marine mussels and other sessile invertebrates are influenced by specific chemical cues to settle and metamorphose within conspecific colonies (Burke 1986; Had-

Fig. 1 *Limnoperna fortunei* recruits settled on artificial tiles after 1 and 3 months of deployment in the lower Paraná River delta (*bars* denote means of three replicates, error bars are SE). Tiles were deployed on 28 December 2007. (Based on data from Sardiña et al. 2009)
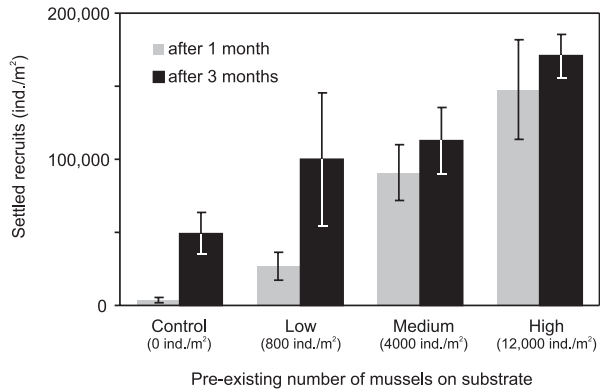
field and Paul 2001; Tamburri et al. 2008). While settlement cues have not yet been identified in *L. fortunei*, there is considerable evidence from field experiments (see below) for the existence of site-specific chemical cues that promote larval settlement in this species.

Using artificial tiles in a 3-month field experiment, Sardiña et al. (2009) found significantly higher numbers of recruits on tiles with conspecific adults than on tiles without conspecifics, and a positive relationship between the number of recruits and the number of adults on the tiles was also observed (Fig. 1). However, a density-dependent response was also detected when the population appeared to reach the carrying capacity (ca. 112,000–170,000 ind./m^2). As the experiment progressed, the rate of larval settlement on tiles highly covered by mussels diminished (Fig. 1). It was suggested that settlement cues provided by attached individuals (adults and newly established settlers) induced larvae to settle preferentially on substrata with conspecifics, as reported for *Dreissena polymorpha* by Chase and Bailey (1996). Sardiña et al. (2009) hypothesized that these chemical cues have threshold concentrations above which settlement is hindered signaling that the site is no longer advantageous for establishment, for example, because of intraspecific competition for limited food resources when population density is too high. Such a mechanism was also suggested for *D. polymorpha* (Hebert et al. 1991; Wood 2013), as well as for many marine invertebrates (Browne and Zimmer 2001).

The presence of a biofilm was also found to enhance settlement of *L. fortunei* postveligers. In a field experiment, artificial tiles on which a biofilm had developed after exposure underwater in laboratory conditions for different periods of time (0, 1, 2, and 4 weeks) were immersed in the lower Paraná River for 2 weeks to test the response of *L. fortunei* larvae to the presence and age of the biofilm. Larvae were found to recruit more actively on tiles initially covered with heavy biofilm (2 and 4 weeks old) than on tiles with weak biofilm (1 week old) or no biofilm at the time of deployment (Fig. 2; Balazote Oliver 2011). This behaviour mimics settlement of *D. polymorpha* larvae under similar conditions (Wainman et al. 1996; Kavouras and Maki 2003).

Fig. 2 Number of *Limnoperna fortunei* recruits settled on artificial substrata after 2 weeks in November 2009 in the lower delta of the Paraná River. Substrata were previously exposed to periphytic colonization for periods of 0–4 weeks. (Based on data from Balazote Oliver 2011)
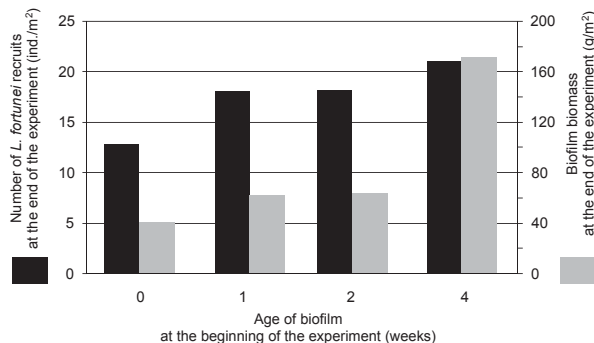
The above experiments, confirmed by subsequent studies (e.g. Nakano et al. 2010; Nakano et al. 2011) elsewhere, indicate that recruitment patterns are governed by two potentially synergistic mechanisms: (1) Conspecifics and biofilms promote larval settlement through specific settlement cues. These chemical cues may not only be released to the medium, but may also act on contact of a larva with a sessile conspecific or biofilm. This conclusion is supported by the results of Morton (1977) and Uryu et al. (1996), who reported strong thigmotaxis in *L. fortunei* larvae, stressing the importance of stimulus of contact for larval settlement. (2) Conspecifics and biofilms provide protection to the newly settled larvae, and thus survival is enhanced compared to barren areas.

These two mechanisms are intimately linked, since enhanced survival rates and other fitness payoffs (e.g. fertilization success in the case of gregarious settlement) would result in the evolutionary acquisition of mechanisms that attract larvae toward a surface covered by conspecifics or biofilms (Sardiña et al. 2009).

Types of Substrata Colonized

Highest mussel densities occur on hard, immobile substrata. In many areas, such substrata are associated with man-made structures, including piers, spur dikes, groynes, pilings, breakwaters, revetments, rock armors, gabions, quay walls, boat hulls, etc., for which reason mussel densities in the vicinity of populated sites are often higher than elsewhere (especially in areas dominated by soft, unconsolidated substrata), and are therefore a poor indicator of overall population numbers.

Colonization by *L. fortunei*, however, is not restricted to hard substrata. In the Paraná River delta mussel clusters occur on soft, silty bottom stabilized with reed or rush roots and fibrous plant debris (Fig. 3a; Boltovskoy et al. 2006). Along the coasts of Salto Grande Reservoir (Argentina/Uruguay), *L. fortunei* thrives on soft silty-sandy areas covered by a thin hardened crust (Fig. 3d). Plants may constitute important sites for attachment, including reed and rush roots (Fig. 3b; Mansur et al. 2003),
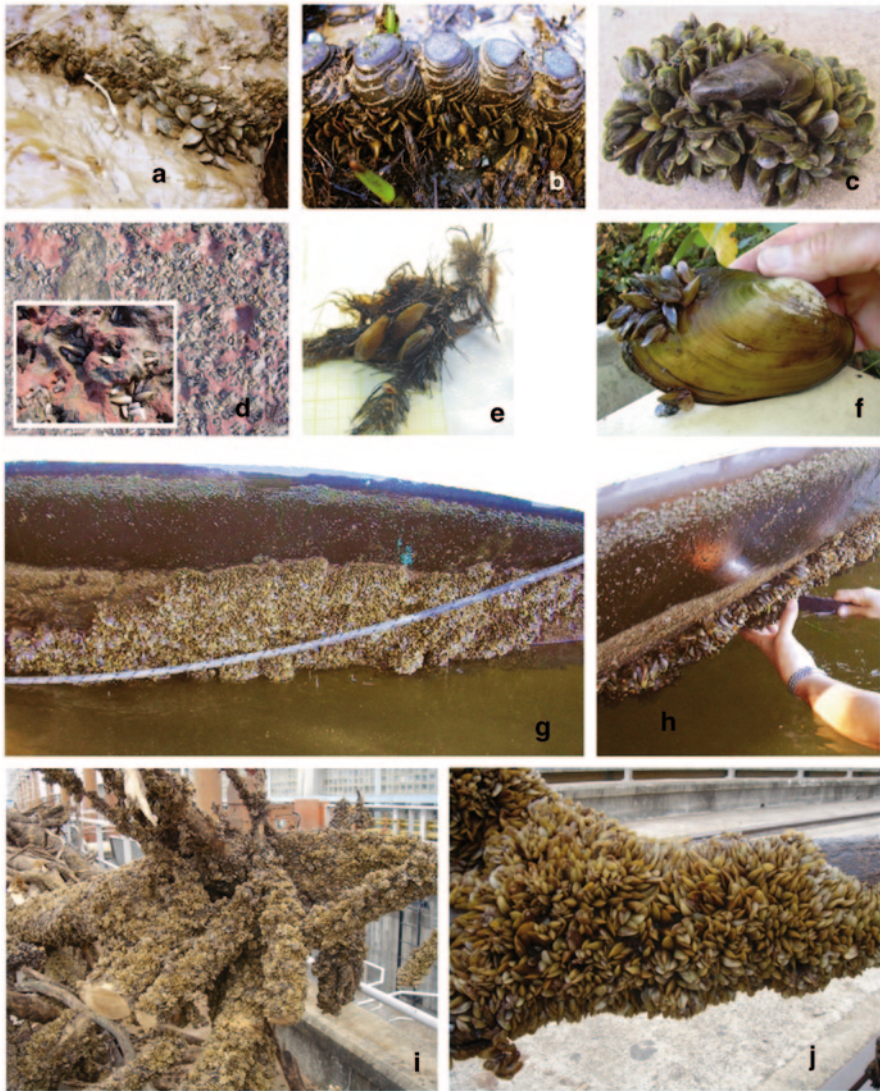
Fig. 3 *Limnoperna fortunei* on different substrata. **a** On muddy bottom, attached to loose fibers of plant debris and roots (lower delta of the Paraná River); **b** attached to reed (*Scirpus californicus*) stems and roots (lower delta of the Paraná River); **c** forming a druse around a large *L. fortunei* specimen (Embalse de Río Tercero reservoir); **d** on hardened crust overlaying soft sediments (Salto Grande Reservoir); **e** attached to roots of water hyacinth (*Eichhornia crassipes*) (Middle Paraná River); **f** Attached to a larger bivalve (Unionidae) (Embalse de Río Tercero reservoir); **g** and **h** entirely covering a GRP (fiberglass reinforced plastic) boat hull (Embalse Río Tercero reservoir); **i** and **j** on tree remains recovered from the bottom of Salto Grande Reservoir. (**a** and **d** from Boltovskoy et al. 2006; **e** from Rojas Molina 2010)

roots, rhizomes and stolons of the water hyacinth (*Eichhornia crassipes*, *E. azurea*; Callil et al. 2006; Marçal and Callil 2008, 2012; Rojas Molina 2010; Rojas Molina et al. 2010; Ohtaka et al. 2011; Fig. 3e), waterweed (*Egeria densa*) stems and leaves (Alvarenga et al. 2005), bahiagrass (*Paspalum* sp.; Darrigran and Ezcurra de Drago 2000), hydrilla or water thyme (*Hydrilla verticillata*; Michelan et al. 2014), etc. Although densities on these plants are usually comparatively low (Table 1), they are most probably very important for the dispersion of the species, especially in areas where hard surfaces are scarce, as in most of the habitats associated with the Paraná and Paraguay rivers.

Mussels and other freshwater invertebrates provided with hard shells or exoskeletons are also used by *L. fortunei* for settling. Shu and Wu (2005) reported that 35% of the bivalves (*Arconaia lanceolata, Larnprotula leai, Larnprotula caveata* and *Larnprotula rochechouarti*) of Poyang Lake (China) are "infected" by the mussel, with an average of 6.6 mussels per clam. Both in Asia and in South America, *L. fortunei* has been observed on several bivalves (*Anodontites trapesialis, A. trapezeus, A. tenebricosus, Diplodon koseritzi, Corbicula fluminea, Leila blainvilliana*), gastropods (*Pomacea canaliculata*), crustaceans (*Aegla platensis, Trichodactylus borellianus*), and even freshwater sponges (*Trochospongilla* sp.) (Darrigran and Ezcurra de Drago 2000; Darrigran 2002; Mansur et al. 2003; Ezcurra de Drago et al. 2004; Lopes et al. 2009; Karatayev et al. 2010; Ohtaka et al. 2010; Rojas Molina and Williner 2013). These associations between *L. fortunei* and live substrata may sometimes represent a significant negative impact for the organisms "infected" (as has been suggested for *D. polymorpha*, e.g., Schloesser et al. 1996; see Chapter "Relationships of *Limnoperna fortunei* with Benthic Animals" in this volume). For the mussel, they can also be of significance; although population densities recorded are low, the availability of isolated hard objects for attachment in areas otherwise barren of adequate settling surfaces may represent important seeding spots or stepping stones for further dispersion.

As opposed to *Dreissena* species, where empty shells have been observed to represent an important source of substrate (Strayer et al. 1996; Burlakova et al. 2006; Strayer and Malcom 2006), dead conspecifics and other bivalve and gastropod remains are seldom significant for *L. fortunei* in South America. This difference with *D. polymorpha* is likely due to the fact that calcium concentrations in South American inland waters are normally much lower than those in Europe and North America (Boltovskoy et al. 2006; Karatayev et al. 2007), and therefore dead mollusc shells dissolve before they are colonized. In some water bodies, dissolution of the shells is so fast that it often precedes decomposition of the soft parts, as indicated by the occurrence of dead, softened shells embedded in abundant organic remains (Boltovskoy et al. 2009b).

Table 1 Maximum densities of *L. fortunei* reported by different surveys

Max. dens. reported (ind./m²)	Site	Substrate	Reference [comments]
85	São Gonçalo channel (Brazil)	Mud	Lopes and Vieira (2012) [probably on hard-surfaced objects lying on the bottom]
100	Pond in Buenos Aires city (Argentina)	Waterweed (*Egeria densa*) stems and leaves	Alvarenga et al. (2005)
108	Upper Paraguay River (Brazil)	Roots of anchored water hyacinth (*Eichhornia azurea*)	Callil et al. (2006)
2500	Middle Paraná River (Argentina)	Artificial (plastic)	Cepero (2003)
3616	Upper Paraguay River (Brazil)	Roots of water hyacinth (*Eichhornia crassipes*)	Marçal and Callil (2012) [mean on *E. crassipes* for 15 lakes: 1327 ind./m²]
22,400	Itaipú Reservoir (Brazil/Paraguay)	Artificial (plastic)	Belz (2006)
31,900	Río Santiago (Río de la Plata estuary, Argentina)	Artificial (plastic netting)	Bonel (2011)
50,000	Salto Grande Reservoir (Argentina/Uruguay)	Rock	Boltovskoy et al. (2006)
65,700	Coronda River (Argentina)	Artificial (plastic netting)	Bonel (2011)
82,151	Río de la Plata estuary (Argentina)	Mudrock	Darrigran and Pastorino (1993)
93,000	Itaipú Reservoir (Brazil/Paraguay)	Artificial (wood)	Takeda and Fujita (2012)
119,000	Itaipú Reservoir (Brazil/Paraguay)	Artificial (dam structures)	Mata (2011)
120,000	Jacuí River delta (Brazil)	Artificial (steel)	Kapusta and Fagondes de Freitas (2012)
124,000	Upper Paraguay River (Brazil)	Rock outcrops	Oliveira and Calheiros (2012)
143,500	Lagoa dos Patos (Brazil)	Rush (*Scirpus californicus*) rhizomes	Mansur et al. (2003)
150,000	Bagliardi Beach, Río de la Plata estuary (Argentina)	Mudrock	Darrigran and Ezcurra de Drago (2000)

Table 1 (continued)

Max. dens. reported (ind./m²)	Site	Substrate	Reference [comments]
170,000	Río de la Plata estuary (Argentina)	Mudrock	Darrigran et al. (2003)
203,000	Lower Paraná River delta (Argentina)	Artificial (PVC)	Sylvester (2006), Sylvester et al. (2007) [92 % below 1 mm]
701,000	Bagliardi Beach, Río de la Plata estuary (Argentina)	Artificial (stone revetments)	Spaccesi and Rodrigues Capítulo (2012) [annual mean based on 12 samples: 227,000]

Location and Structure of Mussel Colonies

Almost invariably, colonization of a new substrate starts in the crevices, holes, corners, angles and other less accessible areas. This tendency to form clusters is not restricted to the larvae (Morton 1977; see above), but is also displayed by dislodged adults, which normally crawl around for some time before reattaching, reattachment being more frequent in the angles than elsewhere (Uryu et al. 1996; see Chapter "Behavior and Taxis of Young and Adult *Limnoperna fortunei*" in this volume). In many cases, colonization is restricted to these protected sites and, regardless of the age of the mussel bed, does not extend beyond them (Fig. 4). In others, however, colonization starts there but eventually covers the entire surface available (Fig. 3g, h; 4 and 5). Aggregation in mussels and other sessile organisms, both freshwater and marine, has been described for numerous species. Experimental studies indicate that this gregarious behaviour confers better protection against water movements and predators, increases the amount of surface available for attachment, and improves the chances of successful fertilization (Côté and Jelnikar 1999; Cheung et al. 2004; Kobak et al. 2010).

Colonization of unprotected, widely open areas is sometimes clearly associated with the abundance and diversity of predators. In most areas of the Paraná River, including its lower delta and the Río de la Plata estuary, dense *L. fortunei* beds develop on many hard substrata, but boat hulls are never colonized (regardless of the presence, age and type of their antifouling coatings), with the exception of restricted crevices and angles around propellers, submerged components of rudder mechanisms and scupper pipe fittings. On the other hand, in the reservoir Embalse de Río Tercero, boat hulls, especially those whose antifouling coating has not been maintained for some time, are completely overgrown (Fig. 3g and h). A major difference between these two habitats is that while the Paraná River hosts anywhere between 200 and >500 fish species (Bonetto 1998; López et al. 2008), in the reservoir only 13 species have been recorded (Freyre et al. 1983). Furthermore, most of the ca. 50 fishes known to consume adult mussels (see Chapter "Trophic Relationships of *Limnoperna fortunei* with Adult Fishes" in this volume and review in Boltovskoy and Correa 2015) are absent from Embalse de Río Tercero. In the Lower Paraná delta, predators (chiefly fishes) eliminate up to 95 % of the mussel

Fig. 4 Different degrees of development of mussel beds on pilings along the coast of the Luján River (lower delta of the Paraná River). (From Boltovskoy et al. 2006)

November 2005   September 2013

Fig. 5 Mussel beds on rock outcrops in the reservoir Embalse de Río Tercero in 2005 and 8 years later, in 2013. (Courtesy of Miguel Hechem)

biomass (Sylvester et al. 2007), which suggests that the lower predation pressure in Embalse de Río Tercero allows mussel beds to develop in unprotected areas (but see below).

Nevertheless, predation is most probably not the only deterrent to mussel colonization. In the Luján River (Lower Paraná delta), concrete pilings located a few hundred meters apart host very different population densities (Fig. 4; Boltovskoy et al. 2006). Widely dissimilar degrees of mussel coverage and extremely high patchiness unassociated with more or less obvious causes, like differences in predation pressure or substrate availability, seem to be common throughout the range of the species. In an attempt to pinpoint the factors responsible for the uneven distribution of mussel beds on mudrock substrata along the coast of the Río de la Plata estuary (Fig. 6), Boltovskoy et al. (unpublished data) monitored changes in nine fixed areas 70×70 cm in size for 36 months. Aside from a general trend toward decreasing mussel densities with increasing air exposure (Fig. 7), none of the variables considered (small-scale topographic differences, insolation, substrate tilt, wave exposure, etc.) were associated with mussel coverage. Thus, there probably are complex biotic and abiotic interactions, as well as intrinsic factors, whose significance still eludes our comprehension.

Fig. 6 *L. fortunei* beds on mudrock along the coast of the upper Río de la Plata estuary

Several authors investigated *L. fortunei*'s preferences for attachment as a function of the orientation of the substrate, but the results are still inconclusive. Morton (1977) suggested that a combination of depth-dependent geotactic and phototactic responses may be responsible for dissimilar settling rates on vertical and horizontal upward- and downward-facing surfaces of experimental substrata. Uryu (1996) performed a series of laboratory experiments which also suggest that geotaxis and phototaxis affect settlement. These experiments yielded interesting data on the behaviour of the mussels, but they may not necessarily constitute an adequate proxy of actual settling rates in nature. For example, horizontal upward-facing surfaces often host much lower mussel densities than vertical and horizontal downward-facing
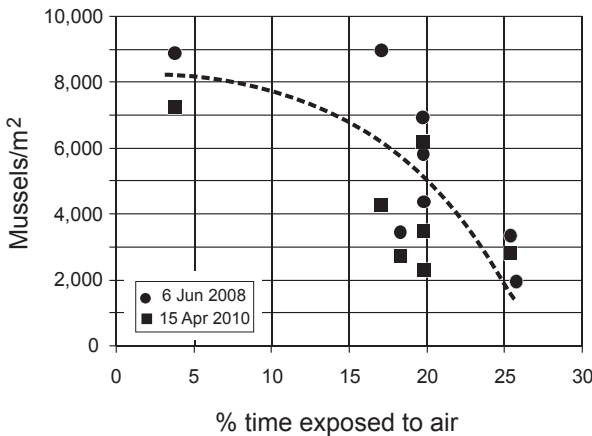

Fig. 7 Relationship between height of substrate (coastal mudrock along the Río de la Plata estuary) and *Limnoperna fortunei* densities on two different sampling dates. Substrate height is given as the mean proportion of overall time when the corresponding site is exposed to air (i.e. above the waterline). Exposure to air is based on a long-term series of historical water-level readings (rather than on calculated tide values, which are very strongly influenced by wind direction, intensity and duration). *Dotted line* indicates suggested trend

Fig. 8 Cross-section of a
rock covered by mussels (**a**)
and top view of a mussel
bed showing small juveniles
attached to the shells of larger
individuals (**b**)
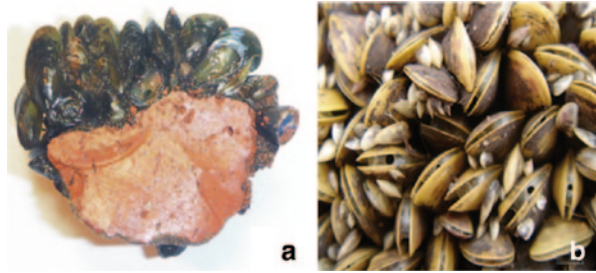
ones because the former retain more sediments (Xu et al. 2013b). Also in pipes, when the lower half accumulates clay and silt, colonization is restricted to the sides and roof of the ducts.

The height of mussel beds can occasionally exceed 10 cm (Xu et al. 2013b), but normally it is around 5–7 cm. Unlike the zebra mussel, whose colonies can attain a vertical thickness of up to 20–30 individuals (Burks et al. 2002), in golden mussel colonies most adults tend to be at least partly attached to the substrate, and although the irregular distribution of the shells does not allow defining the number of mussel layers involved precisely, large (>7–10 mm) specimens supported only by underlying shells are comparatively few (Fig. 8a). On the other hand, juveniles up to 3–4 mm in length are often attached only to the sides of larger conspecifics (Fig. 8b).

As shown by studies of the zebra mussel, this spatial organization may partly reflect the fact that veligers tend to settle onto the surface of colonies, which results in a vertical stratification with larger individuals at the bottom and younger ones at the top (Burks et al. 2002). However, there probably is also active migration of the smaller specimens from deep and intermediate positions toward the top of the mussel bed. Burks et al. (2002) found significant differences between the quality of the interstitial water at the bottom, middle and top of colonies of *D. polymorpha*, whereby oxygen was the lowest and NO_2–N (but not NO_3–N) were the highest at the base. Presumably in response to this gradient, as well as the relative scarcity of food at the base of the colony (Tuchman et al. 2004), mussels were observed to migrate upwards, with significantly higher relocation rates for the smaller (<13 mm) individuals. Concomitantly, mortality rates were higher in the bottom layers of the colony than at the surface. This suggests that as *L. fortunei* individuals grow in size, they are gradually displaced down toward the bottom of the mussel bed. By this time their capacity to detach, migrate and reattach has diminished, while their tolerance to adverse conditions has increased allowing them to survive in this harsher environment. Although environmental conditions at the bottom of the mussel bed are less favourable, direct attachment to the substrate should be more favourable than attachment to the shells of other mussels, since there is a risk of dislodgement when the substrate mussels die.

Differences in colony structure between *L. fortunei* (single-layered) and *D. polymorpha* (multi-layered) may also be due to the very fast postmortem dissolution of dead golden mussel shells in the Ca-poor waterbodies colonized (see Chapter "Parallels and Contrasts Between *Limnoperna fortunei* and Species of *Dreissena*" in this volume). Dead individuals are but a very small proportion of the population (usually less than 5 %), which indicates that dislodgment, dissolution and destruction of dead mussels is fast.

Densities

Reported *L. fortunei* densities on natural and artificial substrata are extremely variable (Table 1). Differences are primarily associated with type of substrate, but also with other factors, including time after initial colonization, season, depth, water quality, etc. Curiously, the highest value reported in the literature is from Bagliardi Beach, in the Río de la Plata estuary, where *L. fortunei* was first detected in South America (Pastorino et al. 1993). Here, on granite revetments, in February 2002, Spaccesi and Rodrigues Capítulo (2012) recorded over 700,000 ind./m^2 (Table 1). The second highest estimate (203,000 ind./m^2) is that of Sylvester (2006) on PVC artificial substrata in the lower delta of the Paraná River.

Assuming that the footprint of a 5–25 mm shell is ca. 10–70 mm^2, and that no space is left between shells, 1 m^2 of substrate can theoretically accommodate around 15,000–100,000 animals. Thus, extremely high densities are obviously largely due to the overwhelming dominance of tiny recent recruits below 1–2 mm in length. Densities above 30,000–50,000 ind./m^2 are almost invariably strongly dominated by very small mussels (Fig. 9), and seasonal changes in mussel densities are chiefly a reflection of recruitment processes (Fig. 10). For example, the second highest density record (203,000 ind./m^2) corresponds to a sample recovered in December 2003 from an artificial substrate where 97 % of the specimens were below 2 mm in length (Sylvester et al. 2007).

Despite the fact that mussel densities have been estimated numerous times in different areas and on different substrata (Table 1), their usefulness as an indicator

Fig. 9 Relationship between mean mussel size and overall mussel density in 11 samples from artificial substrata deployed in the Lower Paraná River delta between December 2002 and June 2004. (Based on data from Sylvester 2006)
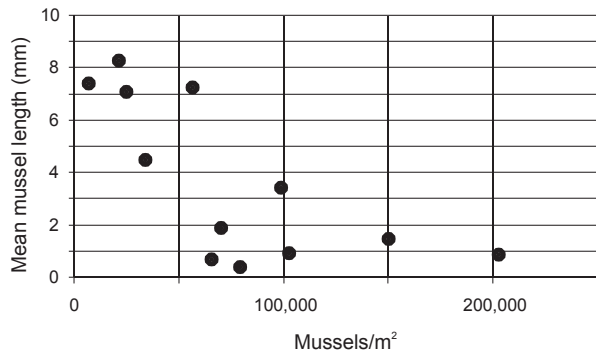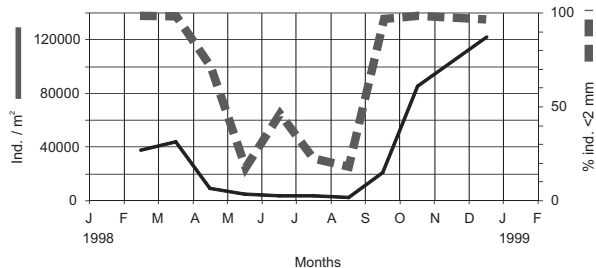

Fig. 10 Changes in mussel total densities and in the proportions of individuals <2 mm in length on artificial substrata deployed in the Lower Paraná River between 20 Jan 1998 and 17 Dec 1998 (Based on data from Boltovskoy and Cataldo 1999)
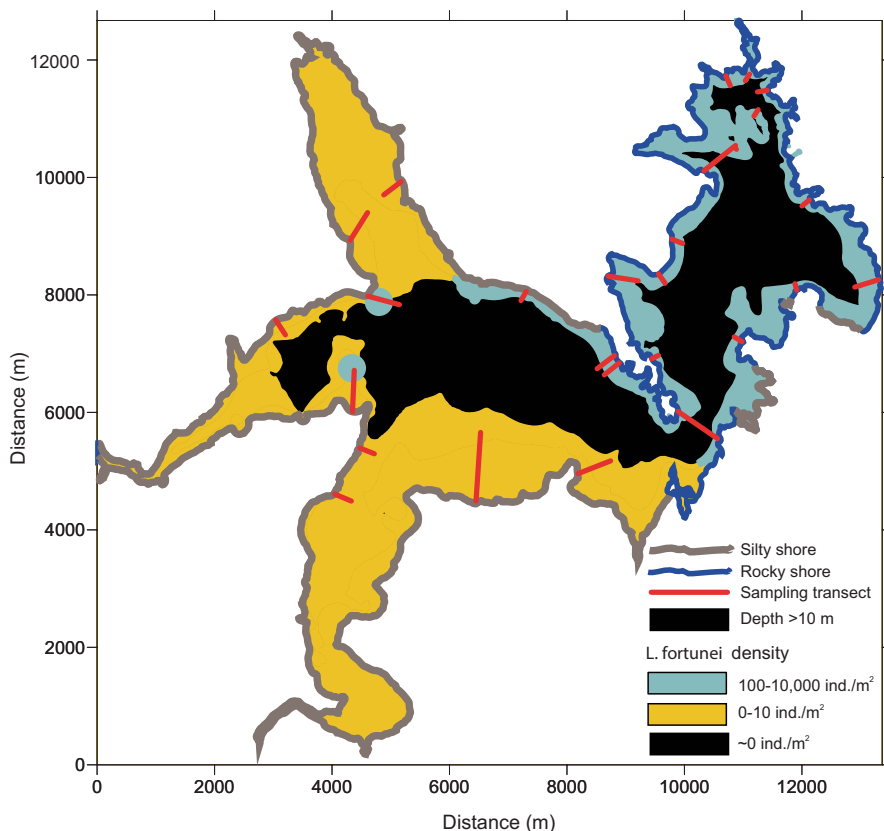
Fig. 11 Distribution of *Limnoperna fortunei* beds in Embalse Río Tercero reservoir. (Based on data from Boltovskoy et al. 2009a)

of the ecological importance of the bivalve is very limited. Indeed, practically all these figures refer to abundances over very restricted areas, usually less than 1 m^2 in size, and the sites in question are not selected at random, but because they are densely covered by mussels. Assessment of average densities over large areas is complicated by the fact that beds of *L. fortunei* have an extremely patchy distribution (Fig. 6). This seems to be associated not only with the uneven distribution of available substrate, but also with some other less obvious traits (see above).

The only work that attempted to produce density estimates over a large area (an entire water body) is that of Boltovskoy et al. (2009a), in a 47 km^2 reservoir (Embalse de Río Tercero, Argentina). Densities were assessed on the basis of diver-collected samples along 25 transects perpendicular to the coast. According to this survey, the reservoir hosted 4.5×10^{10} mussels, over 98 % of them along the coastal fringe between depths of ~1 and 10 m (Figs. 11 and 12). Deeper areas were invariably covered by a thick (up to over 23 m) layer of silt with practically no mussels. Mussel presence was closely associated with bottom type, where rocks yielded the highest mean values, and silt the lowest (Figs. 12 and 13). The mean density for the entire reservoir was 959 ind./m^2, or around 0.1 ind. per liter of reservoir water.

Fig. 12 *Limnoperna fortunei* densities on different substrata as a function of water depth in Embalse Río Tercero reservoir. The highest value (12,096 ind./m² on silty bottom) was recorded on an isolated hard object lying on the mud. (From Boltovskoy et al. 2009a)
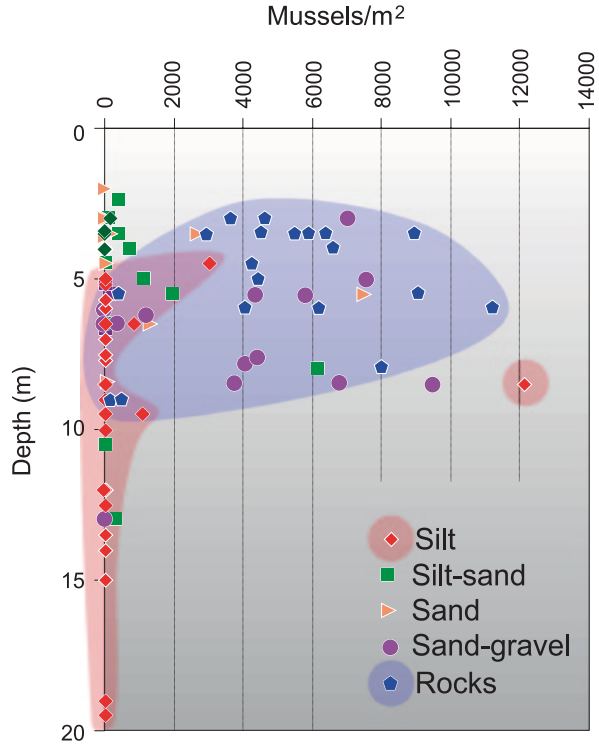
In lakes and rivers, removal and resettlement of sediment particles decreases with depth (Bloesch 2004); this process is responsible for the fact that the deepest areas are usually covered by fine-grained sediments (clay and silt), whereas exposed rock, boulders and pebbles are restricted to shallower areas, normally along the coasts. Thus, the type of distribution of *L. fortunei* found in Embalse de Río Tercero reservoir, where colonization is restricted to the coastal fringe down to depths < 10 m, is probably characteristic of many other reservoirs, lakes and rivers. This constraint imposes a severe cost on the bivalve, especially in waterbodies where water-level fluctuations are large exposing extensive *L. fortunei* beds for periods long enough to produce massive kills. Such events have been observed in

Fig. 13 Mean densities and variabilities of *L. fortunei* recorded on different substrate types (standard errors and coefficients of variation) in Embalse Río Tercero reservoir. (Modified after Boltovskoy et al. 2009a)
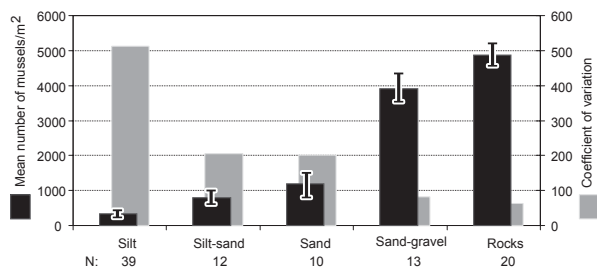
Fig. 14 Empty *Limnoperna fortunei* shells along Salto Grande Reservoir resulting from a massive mortality event due to extended exposure of coastal mussel beds during a period of low water levels. (From Boltovskoy et al. 2006)

several Argentine reservoirs, including Embalse de Río Tercero and Salto Grande (Figs. 5 and 14).

With the exception of the Uruguay River, where coastal stretches with rock outcrops and large boulders are common, the margins of most other rivers of the Río de la Plata basin are largely dominated by loose sediments, ranging from clay to sand (the main river channels are invariably soft bottom throughout). Hard substrata are therefore scant in most of the area colonized by the mussel, which may suggest that sessile populations are few, small and scattered. However, indirect evidence does not support this conclusion. According to data collected in 2005–2006, the mean annual density of *L. fortunei* planktonic larvae in Embalse de Río Tercero is 4168 ind./L, which are produced by a total population of 4.5×10^{10} animals spread over 47 km^2, or 959 mussels/m^2 (Boltovskoy et al. 2009a). Mean annual larval densities in the Paraná and Río de la Plata are around 6000–7000 larvae/m^3, (Boltovskoy et al. 2009b); assuming that the mussel's fertility is roughly similar in these water bodies (fertility is probably somewhat lower in Embalse de Río Tercero; Boltovskoy et al. 2009b), adult densities needed to produce the larval output recorded in the Paraná and Río de la Plata must be at least comparable to those of Embalse de Río Tercero. Thus, the significance of alternative substrata, in particular biological substrata (reed roots, emergent, submerged and floating plants, tree branches and trunks, Fig. 3), must be more important than the impression conveyed by a visual assessment of these environments.

In areas subject to tidal and/or wind-induced changes in water level, mussels have some tolerance to air exposure (see Chapter "Control of *Limnoperna fortunei* Fouling by Desiccation" in this volume), but densities drop sharply away from the permanently submerged sectors. Mudrock substrata along the coasts of the Río de la Plata estuary host extensive *L. fortunei* beds (Fig. 6); the tidal span in these areas is about 1–1.5 m, but the effects of wind can increase these values to over 5 m. Analysis of *L. fortunei* densities along transects perpendicular to the coastline shows that an increase in air exposure from 5% (of the overall time) to 25% results in a fourfold density drop (from ca. 8000–2000 ind./m^2, Fig. 7).

L. fortunei is clearly a ubiquitous species with very broad environmental tolerance. Most of the limiting factors that are important for *D. polymorpha*, including temperature, pollution, pH, nutrients and dissolved calcium (Ramcharan et al. 1992b, 1992a) seem to be well within the tolerance ranges of the golden mussel (Karatayev et al. 2007; Xu et al. 2013a). However, in some areas, such as the Pantanal wetlands associated with the Paraguay River, extreme conditions (e.g. very low calcium concentrations and carbonate mineral undersaturation, extensive anoxic events) may limit the distribution of *L. fortunei* or produce important seasonal die-offs (Oliveira et al. 2010a, 2010b, 2010c, 2011). Pollution is tolerated by the mussel (Contardo-Jara et al. 2009; Young et al. 2014), but at a cost: contaminated areas host lower densities and individuals have a lower length:width ratio, probably reflecting a slower growth rate (Bonel et al. 2013).

Depth-Related Colonization Trends

Some studies have noticed differences in the density and/or size structure of mussel beds in association with water depth. These variations have been tentatively ascribed to vertical gradients in the abundance of larvae (probably in response to environmental parameters, including light penetration, turbidity, food availability, temperature, dissolved oxygen), to behavioural responses of the recruits (Uryu et al. 1996), and/or to differences in predation pressure.

On artificial substrata deployed in Plover Cove Reservoir (Hong Kong) at five depths between 0 and 12 m, the highest densities of recruits were found between 6 and 9 m (Morton 1977). Brugnoli et al. (2011) also recorded higher densities of recruits at 10 m depth than at 0.5 m (Palmar Reservoir, Uruguay). In a study using artificial substrata deployed at 6, 12 and 18 m, Nakano et al. (2010) concluded that, after 105 days at 18 m densities of recruits were higher, but their sizes were lower than higher up in the water column.

In a series of laboratory experiments, Iwasaki (1997) noticed that mussels kept in a fish tank tend to climb up the glass walls, nearly 40% of them attaching just beneath the water surface (see Chapter "Behavior and Taxis of Young and Adult *Limnoperna fortunei*" in this volume). A similar behaviour was also attributed to populations in aqueducts. He speculated that such behaviour may respond to several factors, including avoidance of deeper, brackish water in estuaries, avoidance of siltation, of deoxygenated water layers, and of benthic predators. Our own (unpublished) observations confirm that many mussels of variable size climb up the walls of the fish tank and re-attach next to the air–water interface, but the advantages of this behaviour are still unclear because most of these animals die when the water level in the tank drops from evaporation (as would presumably happen in nature).

While there is little doubt that recruits favour precolonized areas and crevices over open surfaces, it is not yet clear whether variations in mussel beds associated with depth are due to differences in the preferred living depth of the larvae, in their settling depths, or to postsettling effects associated with differential survival and predation.

Multiannual Changes in Adult Densities

The difficulties described above concerning estimates of adult densities that are unbiased by the patchy distribution of mussel beds are also responsible for the lack of reliable information on the evolution of *L. fortunei* populations over multiannual periods. Surveys aimed at investigating reproduction and population dynamics, both on natural substrata (Iwasaki and Uryu 1998; Belz et al. 2010; Spaccesi and Rodrigues Capitulo 2012) and on artificial ones (Morton 1977; Boltovskoy and Cataldo 1999; Pestana 2006; Sylvester 2006; Santos et al. 2008; Nakano et al. 2010, 2011; Bonel 2011; Brugnoli et al. 2011), yielding precise abundance estimates (albeit on small areas), are normally restricted to a single annual cycle.

Darrigran et al. (2003) reported densities of settled individuals at Bagliardi Beach (Río de la Plata estuary) between October 1991 and October 2001. However, interpretation of these data is difficult since only one or two monthly values were available for most years, and studies were not carried out in 1996, 1997, 1999 and 2000. Mata (2011) produced a similar series for Itaipú Reservoir between 2001 and 2010, based on 6–12 data points per year. A potential problem of comparing these abundance estimates is that they were performed collecting and counting all mussels from a known surface, which was obviously different on each new sampling date. Thus, the resulting series reflects two sources of variation (time and site), rather than time only. Despite these shortcomings, both studies concluded that *L. fortunei* reached peak densities 3–5 years after invading the corresponding water body, and decreased thereafter.

The longest multiannual record for the golden mussel is a 9-year series (2004–2013) of the abundance of its larvae in the reservoir Embalse de Salto Grande, based on weekly plankton samples (Boltovskoy et al. 2009b, 2013). *Limnoperna fortunei* was first detected in this reservoir around 2000, and by 2013 larval densities did not show signs of decreasing (Boltovskoy et al. 2013). It should be noted, however, that recruitment of the mussel in this water body is strongly affected by recurrent cyanobacterial blooms that kill *L. fortunei* larvae (Boltovskoy et al. 2013), and this may account for a unique long-term trend in these populations (see Chapter "Reproductive Output and Seasonality of *Limnoperna fortunei*" in this volume).

The fact that *L. fortunei*, as any other introduced species, needs some time to build up its population numbers after invading is obvious and has been observed repeatedly (Boltovskoy et al. 2009a, 2009b). On the other hand, subsequent density declines or significant interannual variations, like those described for *D. polymorpha* (Stanczykowska 1977; Ramcharan et al. 1992b; Burlakova et al. 2006; Strayer and Malcom 2006) have not yet been unequivocally demonstrated, although there are some hints that support the notion that populations of the golden mussel in South America have been waning in recent years. Observations in the lower delta of the Paraná River and Río de la Plata estuary seem to indicate that mussel beds are less dense and occur more sparsely than 10 years ago. This impression is confirmed by comments from local residents, who agree that mussel presence has decreased in recent years. Evidence from other water-

bodies, such as the Embalse de Río Tercero reservoir, also point in the same direction. In particularly dry years, the water level in this reservoir can drop over 10 m exposing colonized areas. One such event occurred in November 2005, exposing hard substrata very densely covered by mussel growth. Eight years later the same substrata were exposed again by another strong drawdown, showing a dramatic decrease in *L. fortunei* densities (Fig. 5). Although none of this has been evaluated and quantified objectively, it agrees with the notion of a cycle characteristic of many invasive species, whereby the initial explosive population growth, shortly after introduction, is followed by a decline and subsequent stabilization (e.g. Stanczykowska 1977). Limitations in the carrying capacity, including availability of food and substrate, could explain a stabilization of population densities (although food shortage is unlikely, at least in the Paraná watershed; Sylvester et al. 2005), but not a decline. On the other hand, an increase in predation pressure by organisms that consume *L. fortunei*, due to growth of predators favoured by the availability of more high quality food, could account for lower survival rates. In the Great Lakes, *Dreissena* species have been observed to decline steadily after an initial density peak due to increasing predation pressure by several water fowl attracted to the area by the availability of mussels (Petrie and Knapton 1999). Many fish species have been reported to feed actively on both adults and larvae of the golden mussel (see Chapters "Trophic Relationships of *Limnoperna fortunei* with Larval Fishes" and "Trophic relationships of *Limnoperna fortunei* with adult fishes" in this volume); several of these take years to reach maturity (e.g. Sverlij et al. 1993), which could account for the lag between the mussel's peak population densities and their subsequent decline as predator populations increase.

Size Structure in Mussel Colonies

The size-frequency distribution in mussel beds depends chiefly on the time of year. During the reproductive season (typically between spring and autumn; see Chapter "Reproductive Output and Seasonality of *Limnoperna fortunei*" in this volume), tiny recruits 0.5–2 mm in length account for over 90 % of the population. In winter, their proportion is the lowest (5–20 %), but they rarely drop to zero, suggesting that reproduction never stops altogether (Fig. 15; Cataldo and Boltovskoy 2000). Sylvester et al. (2007) noticed that highest mortalities occur immediately after settlement, at sizes below 1 mm, when over 93 % of the juveniles are lost. For animals > 1 mm, mortality between successive size classes drops sharply, oscillating around 20 % for the interval between 2 and 20–23 mm. These data indicate that approximately 2 % of the animals that reach the settling stage survive until first reproduction (at about 7 mm, cf. Darrigran et al. 1999), and only 0.5 % survive the first year of life (approximately 20 mm, cf. Boltovskoy and Cataldo 1999). Overall densities decrease sharply during the winter, chiefly due to reduced recruitment and, probably, to enhanced mortality.

Fig. 15 Changes in the
size–frequency distribution
of *Limnoperna fortunei* shells
a during the reproductive
season (February) and **b** dur-
ing the period of reproductive
relaxation (October). (Based
on data from Sylvester 2006)
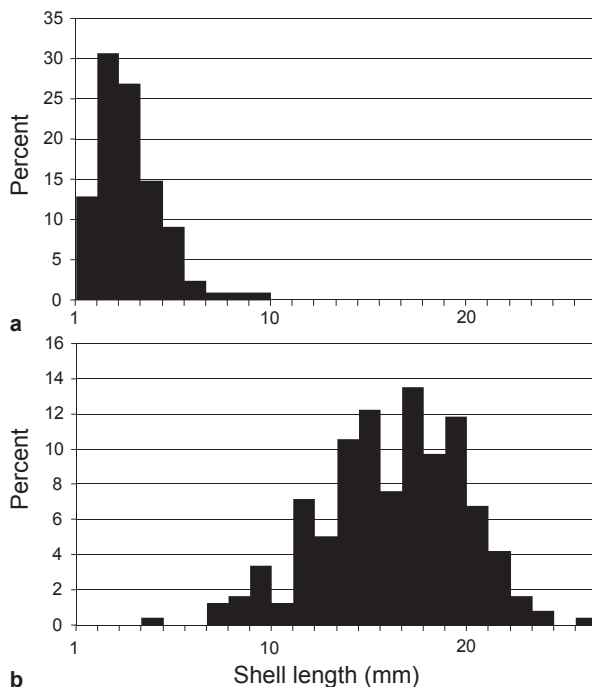
Biomass

The biomass of mussels is closely associated with their size; the function that best
describes the relationship between length and dry tissue weight is a power func-
tion (see Chapter "Population Dynamics and Growth of *Limnoperna fortunei*"
and Fig. 6 in this volume). The strength of this association, however, changes
with mussel size, with cutoff values at 10–15 mm (Sylvester 2006). While both
size and weight increase with age, weight obviously increases faster, and growth
from 2.5 to 30 mm in length involves a 12-fold length increase in size, but a
427-fold increase in tissue dry weight. Although this contrast may seem obvi-
ous, it underscores limitations of data reporting mussel densities alone, without
information on the size structure of the population involved (Fig. 16; Young et al.
1996; Burlakova et al. 2006).

Fig. 16 Seasonal changes in
Limnoperna fortunei density
and biomass on artificial sub-
strata deployed in the lower
delta of the Paraná River
between 6 November 2002
and 15 June 2004. (Based on
data from Sylvester 2006)
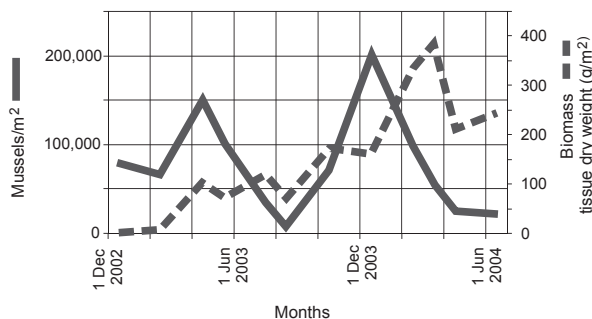
The valve accounts for approximately 80 % of the overall (dry) weight of the mussel. This proportion changes little throughout the life of the animal. Water represents around 93–94 % of the weight of the mussel's tissue (excluding the shell), with slightly higher values in older specimens (Sylvester 2006).

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