Population Dynamics and Growth of *Limnoperna fortunei*

Daisuke Nakano, Takuya Kobayashi and Isamu Sakaguchi

Abstract During its first year of life, *Limnoperna fortunei* grows from ~ 10 to > 30 mm in shell length, primarily depending on water temperature. Two-year-old individuals attain 20–30 mm, and 30 mm is usually the largest size, although specimens up to > 50 mm in size have been reported. The life span is 2–3 years. Water temperature, including the season of each cohort, is the most important factor that determines the growth rate, but other constraints can play important roles too, including calcium concentrations, pollution, food availability and intraspecific competition.

Keywords Estimate methods · Mortality · Growth rate · Cohorts · Size · Biomass

Introduction

Population dynamics and individual growth of *Limnoperna fortunei* are of major importance both in the context of fundamental science (ecology), and for practical applications (biofouling control). The growth rate of *L. fortunei* depends on environmental conditions, and mussel size affects its impacts on the ecosystem through processes such as nutrient cycling, respiration, consumption of organic matter and excretion (see Part 2 in this volume). Growth of mussels on screens, piping and channels of water intake facilities and the size attained by adult individuals are of major importance for gauging and mitigating the damage produced by its fouling (see Chapter "Impacts of *Limnoperna fortunei* on Man-made Structures and Control Strategies: General Overview" in this volume). Understanding the mechanisms that modulate individual growth and population dynamics of *L. fortunei* allows for the definition of suitable methods for implementing antifouling strategies, including the

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time period and frequency of treatment. Several surveys have estimated *L. fortunei* growth by using size distribution data over a given time offset, usually a year. These studies have produced useful results, but limitations associated with low-sampling frequencies have often resulted in gaps and imprecise information that obscure interpretation of the cohorts involved and, hence, conclusions on individual growth. Furthermore, although cohort analysis is a powerful technique for the interpretation of population data, it requires that reproduction events be more or less discrete in time (Edmondson and Winberg 1971; Sparre and Venema 1998). Continuous reproduction modes, as is the case for *L. fortunei* in many tropical and subtropical areas (see Chapter "Reproductive Output and Seasonality of *Limnoperna fortunei*" in this volume), lack the pulses whose identification in size-frequency analyses permits the definition of growth parameters. Sessile species with extended reproduction periods offer an alternative possibility: the deployment of experimental substrata (Boltovskoy and Cataldo 1999; Nakano et al. 2011). This technique allows eliminating all size classes older than the one starting at the time of deployment of the substrata, thus unequivocally pinpointing a zero age class whose monitoring through time allows assessment of the growth of the species. On the other hand, identifying the effects of environmental factors on growth is best achieved through laboratory studies under controlled conditions, an approach which has rarely been used with *L. fortunei*.

This chapter reviews our present understanding of the population dynamics, growth and mortality of *L. fortunei* in Asia and South America, highlighting similarities and differences between these invaded areas.

## Methods Used for Population Dynamics Studies and Growth Estimates

For field estimates of recruitment and growth of *L. fortunei*, the most frequently used method is cohort analysis. This technique consists of the identification of individuals born at approximately the same time (a cohort), and tracking their increase in size through time. Recruitment events are indicated by peaks in the relative abundance of recently settled mussels, usually < 1 mm in shell length, and by peaks in the abundance of veligers in the water column. This method is particularly suitable for populations that have a restricted reproductive period, thus allowing precise separation of generations. In contrast, when reproduction is more or less continuous during extended periods (months), interpretation of successive cohorts is complicated. Furthermore, although at birth (or settlement on a substrate, in the case of byssate mussels) the size of all members of the same cohort is practically identical (Fig. 1, first histogram of upper panel), individual differences in growth increase with time hindering unequivocal identification of the cohort and of its mean size (Fig. 1, last histogram of upper panel). Increasing sampling frequency can alleviate some of these problems, but pinpointing individual cohorts may still pose major difficulties. This is especially complicated when working on samples obtained from natural
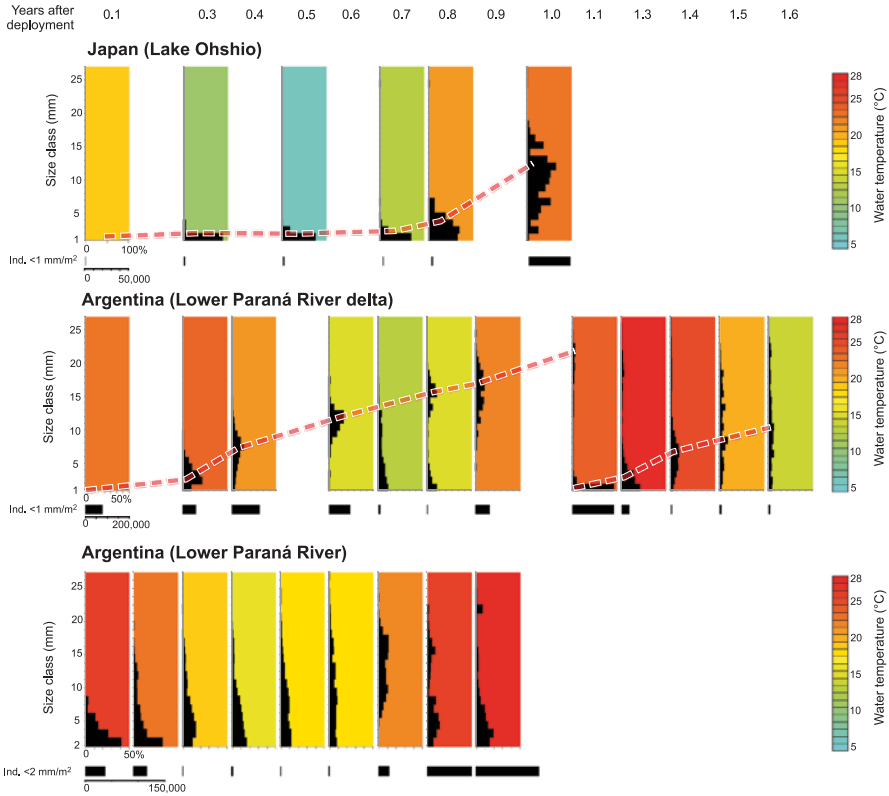
Fig. 1 Changes in the size structure of *L. fortunei* colonizing artificial substrata in Lake Ohshio, Japan (based on data from Nakano et al. 2011), in the delta of the Lower Paraná River, Argentina (based on data from Sylvester et al. 2007) and in the Lower Paraná River (based on data from Boltovskoy and Cataldo 1999). *Dashed red line* suggests evolution of cohorts. Deployment dates were in Japan: 31 August 2008, in Argentina: 6 November 2002 (delta) and 20 January 1998 (Paraná River)

substrata whose time of exposure to colonization is not known (Iwasaki and Uryu 1998; Maroñas et al. 2003).

A widely employed alternative that allows circumventing some of these problems is the use of artificial substrata deployed ad hoc in a water body. This approach allows determining unequivocally a zero age class because all subsequent samples (normally several substrata are deployed, retrieving them one by one at preset intervals) contain no mussels older than the lapse between deployment and retrieval. This facilitates identification of at least one—the first—cohort recruited on the substrata. Nevertheless, when reproduction is continuous, in subsequent samplings this first cohort may be increasingly difficult to separate from subsequent settlement. A variety of artificial substrata have been used by researchers (Fig. 2), all of which offer the mussels hard, colonizable surfaces with different orientation (vertical, horizontal, upper and lower surfaces). Because predation of settled individuals
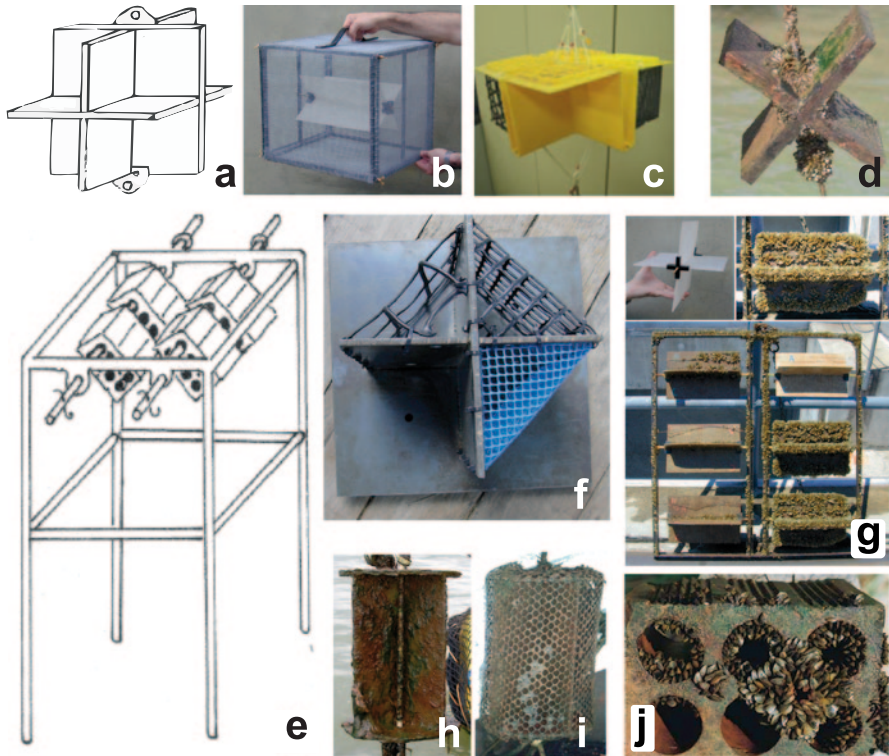
Fig. 2 Various types of artificial substrata and experimental enclosures used for surveys on growth and population dynamics of *L. fortunei*. **a** Morton (1977), **b** courtesy of G. Darrigran, **c** Nakano et al. (2010), **d** Mansur et al. (2009), **e** Santos et al. (2008), **f** Sylvester (2006), **g** Courtesy of G. Darrigran, **h, i** Boltovskoy and Cataldo (2003), **j** Mansur et al. (2003). Notice that some of the designs include surfaces protected from predators by plastic nettings (**b, c, f, i**)

can eliminate over 90 % of the mussels (Sylvester et al. 2007; Nakano et al. 2010), several studies have used unprotected sectors alongside sectors protected by mesh nettings of different sizes in order to exclude predators (Fig. 2c, f, e, h, i).

Protected enclosures (Darrigran et al. 2011; Nakano, unpublished data) and laboratory experiments (Pestana 2006) have also been used for estimating growth of postsettlement individuals (Fig. 2b and 3).

While studies based on artificial substrata have yielded more solid results than those based on natural ones, they still have important limitations. In areas where *L. fortunei* has a single, short, reproductive period per year, as in Korea and Japan (see Chapter "Reproductive Output and Seasonality of *Limnoperna fortunei*" in this volume), identification of cohorts is usually relatively simple. On the other hand, in most of South America, where reproduction can span over 10 months of the year, the first settlers on the substrata can be difficult to separate from subsequent
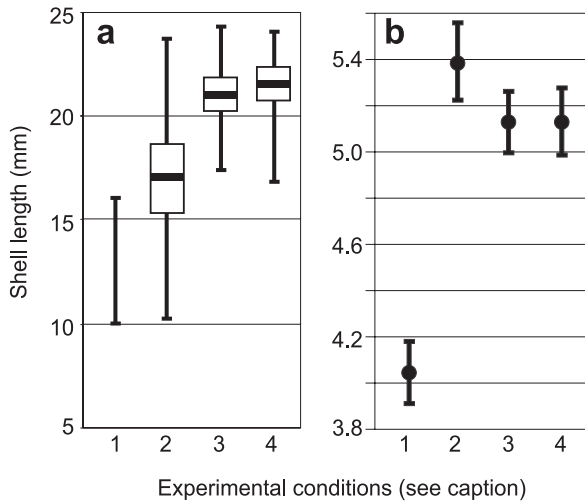
Fig. 3 Contrasting results of the effects of conspecifics on growth of *L. fortunei*. **a** Growth of caged mussels 10–16 mm in length after 104 days in Lake Ohshio, Japan, for a total of 104 days, at water temperatures ranging between 13.6 and 27.7 °C. (*1*) Initial size range of experimental specimens, (*2*) final size of specimens stocked at high densities (140 small mussels per cage), (*3*) final size of specimens stocked at low densities (10 small mussels per cage), (*4*) final size of small specimens (10 ind. per cage) stocked jointly with large specimens (25–32 mm, 10 ind. per cage). Graph shows range of values, the first and third quartiles (*box*) and the median (*band inside the box*). (From Nakano, unpublished.) **b** Size attained by *L. fortunei* specimens 3 months after recruitment on tiles barren of conspecifics (*1*), and on tiles with low (*2*), medium (*3*) and high (*4*) densities of adult conspecifics (800, 4000 and 12,000 mussels/m², respectively), in the delta of the lower Paraná River (Argentina), at water temperatures around 25–26 °C. (Based on data from Sardiña et al. 2009)

recruits. Another major problem is associated with the protective mesh precluding mussel predation. Meshes with large openings allow access to small-sized predators (presumably fish), whereas those with small openings are better at protecting the mussels from predation but eventually clog with the mussels' faeces and pseudo-faeces, and the resulting siltation results in high mussel mortalities (Sylvester et al. 2007).

Population Dynamics and Growth Rates

In general terms, most field studies in subtropical water bodies agree in that *L. fortunei* grows to a size of ~20 mm in its first year of life, attaining ~30 mm during the second year, this being the typical size of large, adult individuals. However, specimens > 50 mm in length have occasionally been recorded (Karatayev et al. 2010). The life span is estimated at 2–3 years. Growth is fastest during warmer months (which is when reproduction is most active; see Chapter "Reproductive Output and

Seasonality of *Limnoperna fortunei*" in this volume), and slows down significantly during the winter. Differences between sites, however, are large, and depend on several factors.

Figure 4 illustrates growth curves for several Asian and South American water bodies, suggesting that growth rates are primarily dependent on temperature and the length of time with high water temperatures. In the Upper Paraná River, where water temperatures are above 20 °C year around, *L. fortunei* can reach over 35 mm in its first year of life (Fig. 4d). Farther south, in the Lower Paraná River, where water temperatures are around 10–28 °C, mussels grow to ~20 mm in 1 year (Fig. 4e, f, h, i). A similar growth rate was also described for Hong Kong (Fig. 4c), where water temperatures vary seasonally from 15 to 31 °C. In Japan, at temperatures ranging from 4 to 26 °C, 1-year-old individuals can attain only 10 mm in length (Fig. 4a; see Table 1).

Slower growth rates at lower temperatures were also found by all field surveys that incorporated seasonality in their estimates, or whose raw data were herein reprocessed taking this variability into account (i.e., the von Bertalanffy seasonal growth formula, VBSGF; Fig. 4a, b, c, f). Slower growth rates have also been documented in laboratory experiments (Fig. 5).

Environmental Drivers of Growth Rates

Growth rates reported in field experiments can vary significantly as a function of the time window employed. Subsequent cohorts may show dissimilar growth rates depending on the time of the year (and, therefore, the water temperature) during the first months after settlement (Fig. 4c, d, g, h, i). Highest growth rates are those of recruits settling in the spring and early summer, whereas slowest rates are characteristic of mussels born in the autumn and winter. Even in tropical and subtropical areas, where temperatures are high year around, seasonal differences in growth are marked. On the basis of data from Bela Vista Reservoir (Upper Paraná River), Belz et al. (2010) concluded that the growth coefficient (k) of the summer (December) cohort (cohort 4 in Fig. 4d) that settled at a temperature around 26 °C, was ca. 50 % higher than that of the winter (July) cohort (cohort 12 in Fig. 4d) that settled at ca. 20 °C ($k=3.2$ and 2.2, respectively). Some surveys have reported the opposite situation, i.e., higher k values for winter than for spring or summer cohorts (e.g., Spaccesi 2013; Fig. 4h, i; Table 1), but the confounding effects of using populations from natural substrata may have obscured identification of the cohorts.

Like most animals, golden mussels grow slower as they age. During their first year of life, they usually reach ~20 mm, but add only ~10 mm during their second year (Fig. 4). The results of Pestana (2006) clearly illustrate the effects of temperature and age on growth rates, showing that small mussels (2.5–8.0 mm) grow proportionally almost 100 times more than large ones (>24 mm) (Fig. 5).

On the basis of data from Lake Ohshio (Japan), Nakano et al. (2011) investigated the effects of water temperature, dissolved oxygen, chlorophyll a concentrations,
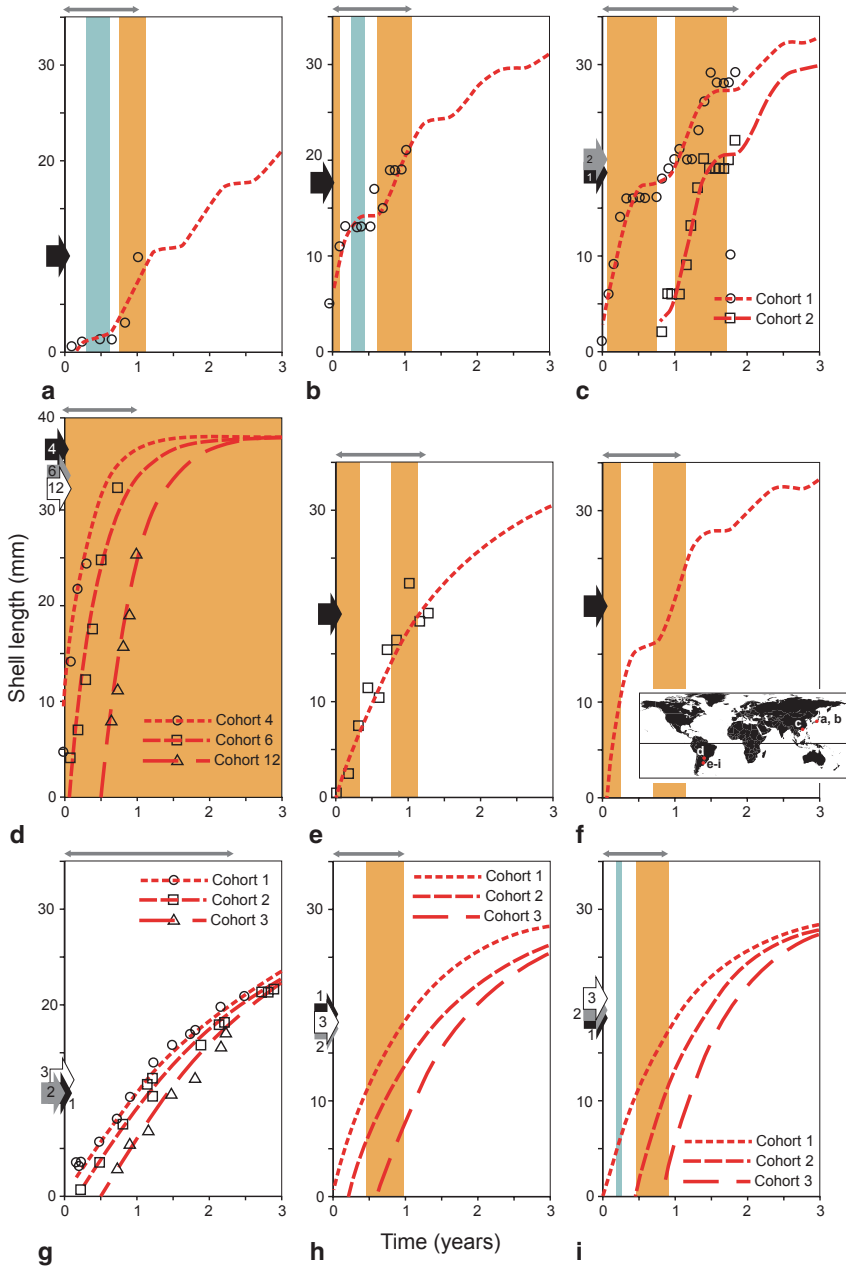
Fig. 4 Growth curves of *Limnoperna fortunei* in various water bodies of Asia and South America. **a** Lake Ohshio, Japan (Nakano et al. 2011), **b** Uji River, Japan (Iwasaki and Uryu 1998), **c** Plover Cove Reservoir, Hong Kong (Morton 1977), **d** Bela Vista Reservoir, Brazil (Belz et al. 2010), **e** Carapachay River (delta of the Lower Paraná River, Argentina; Sylvester et al. 2007), **f** Lower Paraná River, Argentina (Boltovskoy and Cataldo 1999), **g** Bagliardi Beach (1992–1994; middle Río de la Plata estuary, Argentina; Maroñas et al. 2003), **h** Bagliardi Beach (2001–2002; middle

conductivity and turbidity on the growth of *L. fortunei*. They concluded that in this lake only water temperature was positively correlated with the growth of the golden mussel. However, while temperature has an overwhelming influence on the growth of *L. fortunei*, it is not the only variable that can affect growth.

The golden mussel can tolerate very low calcium concentrations (see Chapter "Parallels and Contrasts Between *Limnoperna fortunei* and Species of *Dreissena*" in this volume), but the growth is hindered in Ca-deficient water bodies. Dos Santos et al. (2007) deployed cages with field-collected individuals 7–10 mm in length in three water bodies associated with the Paraguay River (Brazil) with different concentrations of Ca. After 150 days, mussels from the site with highest calcium concentrations (18 mg/L) grew significantly more (0.09 mm/d) than those at the other two sites (4–6 mg Ca/L, 0.02–0.05 mm/d). These results align with those of Hincks and Mackie (1997), showing that Ca concentrations are significantly associated with survival and growth of zebra mussels.

The golden mussel survives in highly polluted waters, but, again, pollution impacts its growth. Bonel et al. (2013) compared population traits of *L. fortunei* in two South American rivers differing in pollution levels (as indicated by dissolved oxygen, pH and conductivity), concluding that growth rates were significantly lower at the more polluted site (Río Santiago River), than in the more pristine one (Coronda River).

Food availability has also been shown to affect growth of byssate freshwater mussels (Schneider 1992; Dorgelo 1993; McMahon 1996), including *L. fortunei*. Bergonci et al. (2012) deployed artificial substrata at two locations in the Jacuí River-Guaíba Lake system (southern Brazil) 4 km apart. After 11 months, substrata were recovered and all mussels were measured and weighed. Organisms from the site with higher concentrations of organic matter had significantly more biomass and were larger than those from the other location, suggesting that differences in food availability were responsible for the dissimilar growth rates observed. The lower particulate organic matter concentrations found in the reservoir Embalse de Río Tercero (central Argentina) compared to those of the Paraná River system were suggested to result in shorter reproductive periods of *L. fortunei* (Boltovskoy et al. 2009).

Effects of Intraspecific Competition on Growth Rates

Life in densely packed clusters of conspecifics, as that of gregarious, sessile mussels, has many advantages but also drawbacks (Bertness and Grosholz 1985; Okamura 1986; Côté and Jelnikar 1999). Among the drawbacks, cannibalism of ready-to-settle larvae and competition for food and space are probably the most important. In order to investigate the effects of neighbouring conspecifics on growth

Río de la Plata estuary, Argentina; Spaccesi 2013), **i** Punta Indio (middle Río de la Plata estuary, Argentina; Spaccesi 2013). *Arrows at top* of each graph denote observational period. *Arrows along y-axis* indicate shell length at 1 year of age for each of the cohorts considered. *Light-blue shading* denotes water temperatures < 10 °C, orange for temperatures > 20 °C. *Inset map* shows the geographic range of growth studies

Table 1 Results of studies of the population dynamics and growth of *Limnoperna fortunei* in various water bodies of Asia and South America. (see Fig. 4 for the corresponding growth curves)

Site	Lake Ohshio (Japan)	Uji River (Japan)	Plover Cove reservoir (Hong Kong)	Bela Vista reservoir (Brazil)	Carapachay River (Argentina)	Lima (Argentina)	Bagliardi beach (Argentina)	Bagliardi beach (Argentina)	Punta Indio (Argentina)
River system	Tone River	Yodo River	Dong River	Paraná River	Paraná River	Paraná River	Río de la Plata estuary	Río de la Plata estuary	Río de la Plata estuary
Latitude	36.22°N	34.93°N	22.28°N	25.40°S	33.38°S	33.95°S	34.87°S	34.92°S	35.27°S
Longitude	138.87°E	135.92°E	144.25°E	54.58°W	58.58°W	59.20°W	57.80°W	57.78°W	57.22°W
k^a	0.3	0.7	0.6–0.7	2.0–3.2	0.7	1.0	0.3–0.4	0.8–1.0	1.0-1.1
Sampling period	2008–2009	1994–1995	1972–1974	2004–2005	2002–2004	1998	1993–1994	2001–2002	2001–2002
Temp. range (°C)	4.2–23.6	7.0–26.0	15.0–29.0	20.0–32.0[c]	13.0–28.0	12.9–26.5	14.0–24.0	10.7–27.9	8.5–28.6
Months > 20°C	4	6	8	12	8	6	ND	6	6
Months < 10°C	4	2	0	0	0	0	ND	0	1
Substrate	Artificial	Natural	Artificial	Natural	Artificial	Artificial	Natural	Natural	Natural
Method[b]	VBSGF	VBSGF	VBSGF	VBGF	VBGF	VBSGF	VBGF	VBGF	VBGF
Reference	Nakano et al. (2011)	Iwasaki and Uryu (1998)	Morton (1977)	Belz et al. (2010)	Sylvester et al. (2007)	Boltovskoy and Cataldo (1999)	Maroñas et al. (2003)	Spaccesi (2013)	Spaccesi (2013)

[a] k, the growth coefficient of the von Bertalanffy growth formula, which reflects how fast the maximum size is reached;

[b] VBGF von Bertalanffy growth formula (growth rate differences between seasons disregarded); VBSGF von Bertalanffy seasonal growth formula (growth rate differences between seasons considered);

[c] based on data from the nearby Itaipu Reservoir

Fig. 5 Growth after 179 days as a function of initial size in mussels held in captivity at 18 and 25 °C. Values are based on 45 individuals for each size class, of which 53–89 % survived through the experimental period. (Based on data from Pestana 2006)
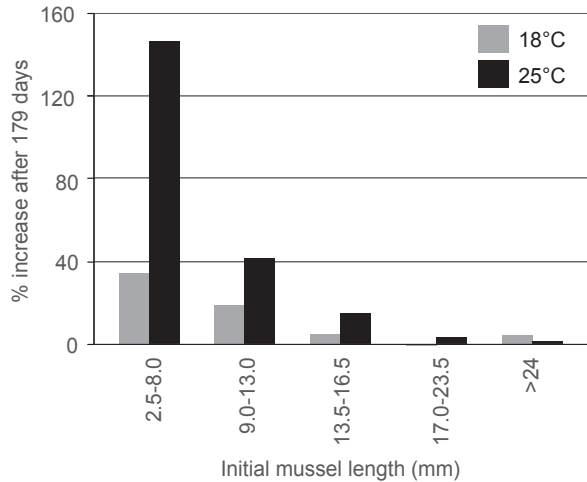
of *L. fortunei*, Nakano (unpublished data) conducted a series of experiments in Lake Ohshio (Japan). Specimens of *L. fortunei* 10–16 mm in length were stocked in cages $10 \times 10 \times 12$ cm in size made of plastic netting with a mesh size of 5 mm. Experimental conditions included low density of small mussels (10 specimens per cage), high density of small mussels (140 mussels per cage), and small (10) + large (25–32 mm, 10) individuals together. Cages were kept in situ at 5 m depth for 104 days. Mortality at the end of the experiment was very low (2.7 %). Comparison of mean shell lengths of 10 small labelled individuals showed that growth in densely populated cages (4.4 ± 1.1 mm) was lower than growth in cages with fewer mussels (7.7 ± 0.8 and 8.1 ± 0.5 mm, in cages with small and small + large mussels, respectively; Fig. 3a). Statistically, end values of low- versus high-stocking densities differed significantly ($P < 0.0001$, t-test), suggesting that intraspecific competition, probably for food and space, may affect growth. However, the impact of adverse conditions associated with high densities seemed to differ widely between individuals, as the range of final lengths in high-density cages was much higher than that in the low density ones (Fig. 3a).

Information on the zebra mussel indicates that there are significant differences between food availability and the quality of the interstitial water at different depths in the colony (Burks et al. 2002; Tuchman et al. 2004). Although in contrast to *D. polymorpha*, *L. fortunei* does not build multilayered mussel beds (see Chapter "*Limnoperna fortunei* Colonies: Structure, Distribution and Dynamics" and Fig. 8 therein), it is conceivable that even in single-layered colonies denser aggregates involve more growth-limiting conditions, especially in stagnant waters (e.g., from higher concentrations of waste products, more oxygen consumption, and lower availability of food).

Despite the fact that high densities may affect mussel growth, the benefits of gregarious behaviour must largely outweigh their drawbacks. Recruitment of golden mussels is significantly higher in areas occupied by older conspecifics than in areas

barren of mussels (Sardiña et al. 2009). Furthermore, growth of recruits was also found to be enhanced by the presence of conspecific adults (Sardiña et al. 2009; Fig. 3b). This disagreement with the data illustrated in Fig. 3a may indicate that relationships between growth and density vary with mussel age, and/or that there are threshold density levels above which the interaction becomes negative.

Mortality

Data on larval mortality of the golden mussel indicate that around 80–90 % of the larvae die before reaching the settling stage, with highest mortalities occurring during the transition from the straight-hinged to the umboned veliger stage (Cataldo et al. 2005; see Chapter "Larval Development of *Limnoperna fortunei*" in this volume). Highest mortalities of settled individuals occur during the earliest stages of growth; comparison of size-frequency distributions indicates that > 93 % of the mussels < 1 mm in size die before reaching 2 mm (Sylvester et al. 2007). These values are roughly comparable to those reported for zebra mussels (up to 99 %; Lewandowski 1982; Sprung 1989). For animals, > 1 mm mortality drops sharply, with ca. 80 % of the mussels 2 mm in length surviving to 20–23 mm (Sylvester et al. 2007). Thus, 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. Mortality rates increase sharply during the winter, with smaller mussels being affected the most (Sylvester et al. 2007).

Size–biomass Relationships

Growth increases both the shell length and the biomass of *L. fortunei*. Relationships between shell length, total wet mass (including the shell), wet tissue weight and dry tissue weight, were estimated by Sylvester (2006) on the basis of organisms collected in the delta of the Lower Paraná River (Fig. 6). Interestingly, at a shell length of about 10–15 mm, there seems to be a break in the size–weight relationship, whereby data below and above these length values are better correlated when analyzed separately than in bulk (Fig. 6a, b, c). These expressions are useful for general purposes, but relationships between size and biomass can vary significantly between water bodies and times of the year, depending strongly on feeding conditions. Pestana (2006), for example, reported that, after ~2 months, the condition index (i.e., the ratio of tissue weight to shell length) of starved *L. fortunei* was about six times lower than that of fed specimens.
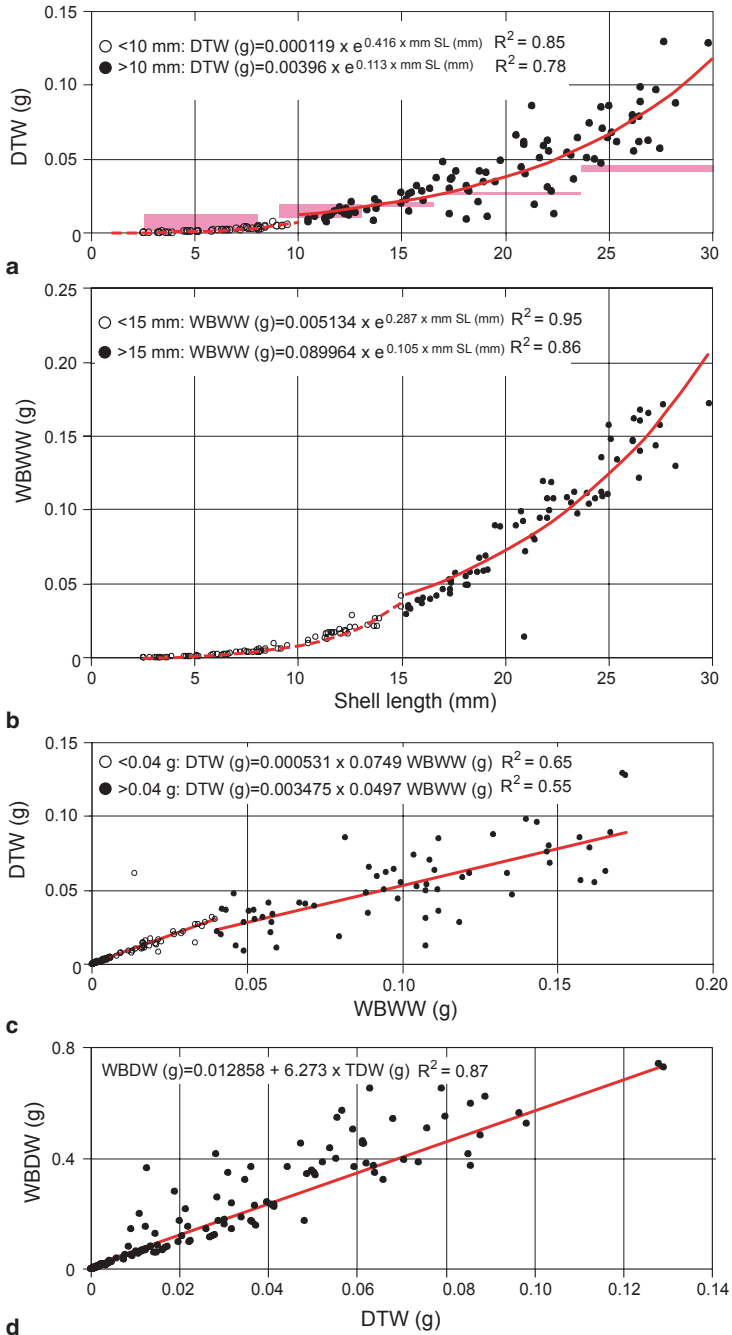
Fig. 6 Relationships between shell length (*SL*), dry tissue weight (*DTW*), whole body dry weight (*WBDW*) and whole body wet weight (*WBWW*) for small and large *L. fortunei* specimens (from Sylvester 2006). *Pink shadings* in panel **a** denote SL vs. DTW ranges reported by Pestana (2006)

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