

Reproductive Output and Seasonality of *Limnoperna fortunei*

Demetrio Boltovskoy, Brian Morton, Nancy Correa, Daniel Cataldo, Cristina Damborenea, Pablo E. Penchaszadeh and Francisco Sylvester

Abstract Young *Limnoperna fortunei* mature sexually from 5–6 to ~15 mm. The species is generally dioecious, with approximately equal numbers of males and females and very small (<0.6%) proportions of hermaphrodites. The gametogenic cycle has been described for both Asian and South American populations, recognizing between four and five reproductive phases. Gonadal cycles based on histological sections yielded somewhat dissimilar results for different areas. In Hong Kong, two yearly peaks in reproductive output were detected. In South America, mature sperm and ova have been recorded year round and several irregularly spaced spawning events have been observed, as well as more or less continuous breeding punctuated by peaks in spring and at the end of the summer. Reproductive studies based on changes in the abundance of larvae in the water column have been carried out in South America and in Japan. In tropical and subtropical South America, larval output is more or less continuous for 6–10 months of the year, often with a major peak in spring–early summer, and a smaller one in the late summer–autumn. In Japan, at considerably lower water temperatures, larval production is limited to 1–2 months centered around summer. Apparent disagreements between results based on histological data and on larval counts stem from the fact that while the latter integrate the reproductive output of extensive mussel beds dispersed over large areas, histological evidence pinpoints with high precision the ripening and spawning of isolated mussel clusters. Aside from water temperature, several other factors (pH, salinity, dissolved oxygen, suspended solids, chlorophyll a, flood–drought cycles) have been proposed as reproductive triggers, but actual associations have not been demonstrated. Peak larval densities can exceed 20,000 ind./m³, but, normally, values range around 6000 ind./m³, showing major fluctuations within short periods, as well as changes as a function of time elapsed post colonization, and availability of substrata suitable for adult occupation. Microcystin-producing cyanobacterial blooms can kill *L. fortunei* larvae.

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Introduction

The reproductive cycle of *Limnoperna fortunei* is probably one of the most intensively studied aspects of the species' biology. This interest is partly due to the fact that reproduction is perceived as one of the main biological traits of organisms in general and, again partly, because being an important fouling nuisance in industrial installations, strategies for its mitigation and control depend largely on the time frame over which such infrastructures are vulnerable to infestation. This occurs through the settlement of its planktonic larvae and therefore coincides with periods when the animal is reproductively active.

Seasonality in the reproduction of *L. fortunei* has been investigated using different approaches: (1) assessment of gonadal maturation, often with the aid of histological thin sections, (2) studies of temporal changes in the density of the species larvae in the plankton, (3) analyses of recruitments onto either natural or artificial substrata, and (4) various combinations of the above (Table 1).

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Table 1 Summary of surveys on reproductive seasonality in *Limnoperna fortunei*

Area	Waterbody	Latitude, Longitude	Months covered (period)	No. of samples or observations	Type of data	Reprod. peaks (months)	Source
Plover Cove (Hong Kong SAR, China)	Reservoir	22.47°N, 114.23°E	29 (Oct 1971 to Feb 1974)	28	R	Jan–Apr, Jun–Jul, Sep	Morton (1977)
Plover Cove (Hong Kong SAR, China)	Reservoir	22.47°N, 114.23°E	29 (Oct 1971 to Feb 1974)	28	G	Jan, Feb, Jun, Jul	Morton (1982)
Uji River (Japan)	River	34.93°N, 135.92°E	Sep 1994 to Oct 1995	12	G R	Jun–Sep	Iwasaki and Uryu (1998)
Lake Ohshio (Japan)	Reservoir	36.22°N, 138.88°E	13 (Aug 2007 to Nov 2008)	49	L	Jul–Sep	Nakano et al. (2010a)
Lake Takenuma (Japan)	Reservoir	36.23°N, 139.02°E	18 (Jun 2007 to Nov 2008)	49	L	Aug–Sep	Nakano et al. (2010a)
Yahagi River (Japan)	River	35.32°N, 137.14°E	22 (May 2007 to Feb 2010)	34	L	Aug	Hamada (2011)
Rio de la Plata (Argentina)	Estuary	34.87°S, 57.81°W	29 (Jul 1992 to Nov 1994)	20	G R	Apr–Jul, Oct	Darrigran et al. (1999)
Paraná de las Palmas (Argentina)	River	33.96°S, 59.21°W	17 (Sep 1997 to Jan 1999)	68	L R	Nov–Dec	Boltovskoy and Cataldo (1999), Cataldo and Boltovskoy (2000)
Rio de la Plata (Argentina)	Estuary	34.56°S, 58.41°W	15 (Oct 1997 to Dec 1998)	63	L	Oct–Feb	Cataldo and Boltovskoy (2000)
Rio de la Plata (Argentina)	Estuary	34.87°S, 57.81°W	13 (Mar 1994 to Mar 1995)	9	R	Mar, May, Jun, Nov	Maroñas et al. (2003)
Rio de la Plata (Argentina)	Estuary	34.87°S, 57.81°W	20 (Aug 1998 to Mar 2000)	16	G R	Jan, Jul, Aug, Nov	Darrigran et al. (2003)
Riacho Santa Fé (Argentina)	River	31.68°S, 60.72°W	24 (Jan 1998 to Dec 1999)	24	L	Nov–Apr	Cepero (2003)

Table 1 (continued)

Area	Waterbody	Latitude, Longitude	Months covered (period)	No. of samples or observations	Type of data	Reprod. peaks (months)	Source
Itaipú (Brazil-Paraguay)	Reservoir	25.41°S, 54.59°W	36 (Mar 2002 to Dec 2004)	34	L	Sep-Jan	Canzi et al. (2005)
Riacho Santa Fé (Argentina)	River	31.63°S, 60.67°W	13 (Dec 1999 to Dec 2000)	11	L	Sep-Mar	Ezcurra de Drago et al. (2006)
Carapachay River (Argentina)	River	33.40°S, 58.60°W	18 (Dec 2002 to Jun 2004)	12	L R	Oct-Apr	Sylvester (2006)
Yacyretá, Paraná River (Argentina-Paraguay)	Reservoir	27.48°S, 56.74°W	26 (Apr 1999 to May 2001)	27	L R	Nov-Feb	Darrigran et al. (2007)
Paraná River (Brazil)	River	34.57°S, 54.59°W	13 (Jan 2005 to Feb 2006)	12	L	Oct-May	Pestana et al. (2008)
Lago Guaíba (Brazil)	Lake	30.21°S, 51.20°W	16 (Sep 2002 to Dec 2003)	24	L R	Oct-Dec	Santos et al. (2008)
Embalse de Río Ter-cero (Argentina)	Reservoir	32.23°S, 64.44°W	13 (Mar 2005 to Mar 2006)	50	L	Dec-Apr	Boltovskoy et al. (2009b)
Itaipú (Brazil-Paraguay)	Reservoir	25.41°S, 54.59°W	13 (Mar 2002 to Apr 2003)	262	L	Nov-Mar	Boltovskoy et al. (2009b)
Colastiné River (Argentina)	River	31.66°S, 60.60°W	12 (Sep 2004 to Sep 2005)	34	L	Oct-Apr	Rojas Molina (2010)
Riacho Santa Fe (Argentina)	River	31.64°S, 60.69°W	12 (Sep 2004 to Sep 2005)	33	L	Oct-Apr	Rojas Molina (2010)
Río Santiago (Argentina)	River	34.85°S, 57.89°W	25 (Mar 2007 to Mar 2009)	14	L R	a	Bonel (2011), Bonel et al. (2013)
Coronda River (Argentina)	River	31.69°S, 60.74°W	22 (Apr 2007 to Feb 2009)	15	L R	a	Bonel (2011), Bonel et al. (2013)
Itaipú (Brazil-Paraguay)	Reservoir	25.41°S, 54.59°W	87 (Mar 2002 to Sep 2009)	87	L R	Oct-Mar	Mata (2011)

Table 1 (continued)

Area	Waterbody	Latitude, Longitude	Months covered (period)	No. of samples or observations	Type of data	Reprod. peaks (months)	Source
Paraguay River (Brazil)	River	19.60°S, 57.43°W	47 (Jan 2004 to Nov 2007)	47	L R	Oct–Feb	Oliveira et al. (2011)
Miranda River (Brazil)	River	19.57°S, 57.25°W	47 (Jan 2004 to Nov 2007)	47	L R	Aug–Sep	Oliveira et al. (2011)
Paraguay River (Brazil)	River	18.98°S, 57.70°W	47 (Jan 2004 to Nov 2007)	47	L R	Nov–Jan	Oliveira et al. (2011)
Salto Grande (Argentina–Uruguay) ^b	Reservoir	31.27°S, 57.94°W	104 (Jun 2004 to Jan 2013)	367	L	Oct–Apr	Boltovskoy et al. (2013)

Type of data, *G* gonadal maturation and/or thin sections, *L* abundance of larvae in the water column, *R* analyses of recruitment

^a Too many gaps in coverage

^b 2010 data only (other years have atypical reproduction trends due to extensive cyanobacterial blooms, see text)

Examination of the literature indicates that larval densities are generally well coupled with recruitment of settled juveniles, but gonadal maturation studies can yield somewhat dissimilar results. This outcome, which may at first seem puzzling, is understandable when one takes into account that the two parameters reflect different aspects of the same reproductive process (see below).

Reproductive Strategy: Evidence from Gonadal Cycles

The reproductive cycle of *L. fortunei* in Asia was described by Morton (1982), augmenting an earlier study (Morton 1977) of recruitment and population dynamics of the species in Plover Cove reservoir in Hong Kong at latitude 22°N. The reservoir was constructed by the damming of a coastal inlet, pumping out the seawater and allowing it to fill from the natural catchment and newly arriving water from China. The species was first recorded from Plover Cove reservoir in 1969, although it had probably arrived in Hong Kong's potable water supply around 1965–1966 (Morton 1977).

Analysis of histological sections of the gonads of *L. fortunei* from Plover Cove reservoir was carried out from October 1971 to February 1974 inclusive (Morton 1982). As with all mytiloids, because the intestine (other than the stomach) does not occur in the visceral mass, this plus the mantle tissues beneath the shell dorsal to their ventral margins (Morton 1973) are occupied wholly by the paired, left and right, maturing gonads (see Chapter “The Biology and Anatomy of *Limnoperna fortunei*, a Significant Freshwater Bio-Invader: Blueprints for Success”, and Figs. 4, 15 therein). *L. fortunei* is dioecious; in Hong Kong, not one hermaphrodite was identified from the ~300 individuals encompassing a range of shell sizes in the 29-month histological study by Morton (1982). Later studies based on South American populations, however, identified low (<0.6%) proportions of simultaneous hermaphroditism (e.g., Darrigran et al. 1998, in the Río de la Plata estuary; Uliana and Callil 2006, in the Paraguay River).

When ripe, male and female gametes are discharged via left and right gonadal apertures situated at the surface of the visceral mass in the supra-branchial chamber of the outer demibranches of the ctenidia. They are then released via the exhalant siphon for external fertilization.

In Hong Kong, *L. fortunei* grows fast, reaching a shell length between 15 and 16 mm in about the first 5 months post recruitment and, by 10 months, individuals are certain to become sexually mature. In South America, sexual maturity was observed to vary seasonally beginning at 5–6 mm in winter–spring, and at 7–10 mm in autumn (Darrigran et al. 1999). In Hong Kong, during the first year of life, individuals are predominantly (>65%) females (Morton 1982), but in South America, a slight predominance of males has been observed (45% males to 40% females, the remainder being represented by sexually undifferentiated individuals; Darrigran et al. 1999).

The gametogenic cycle of *L. fortunei* in Hong Kong was interpreted from histological sections (Morton 1982) and categorized into five phases as follows (Fig. 1):

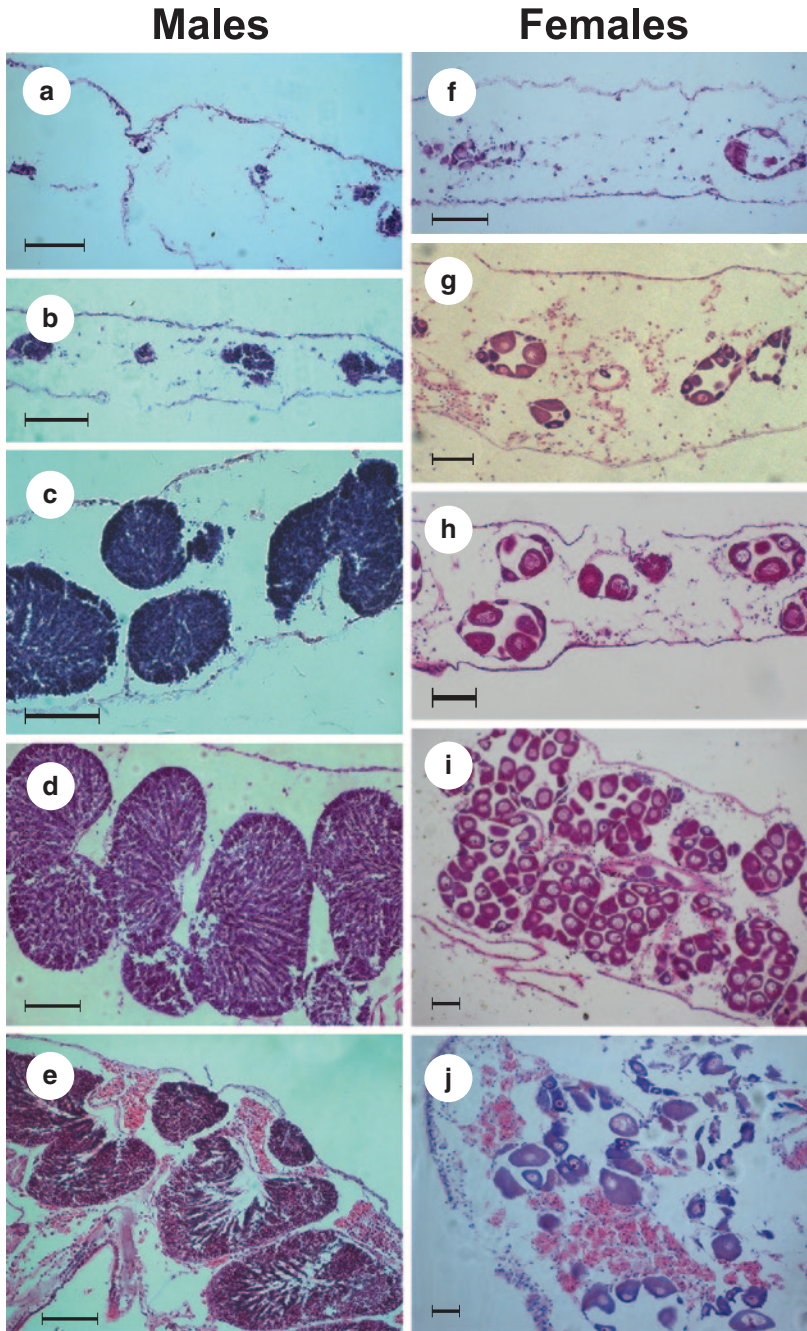


Fig. 1 Photomicrographs of the five stages of gametogenesis in males and females of *Limnoperna fortunei*. **a, f** Primordia; **b, g** developing; **c, h** maturing; **d, i** mature; **e, j** partially spent with resorption of remaining undischarged gametes and simultaneously new growing ova attached to the epithelial wall of the ovarian follicle (**j**). Scale bars: 100 μ m

(1) inactive, (2) developing, (3) maturing, (4) mature, and (5) spent. In a similar study based on Brazilian populations, four gametogenic stages for both sexes were defined (Callil et al. 2012). In Hong Kong, during January–February and July–August, both male and female gonads were inactive and comprised small, primordial, seminiferous tubules and ovarian follicles, respectively (Fig. 1). The tubules comprised a thin germinal epithelium producing round, lightly staining, primary spermatocytes $\sim 5 \mu\text{m}$ in diameter. The follicles are comprised of germinal epithelium from which small oocytes, each with a clear, vesicular nucleus and a distinct nucleolus, were developing. In March and September, the seminiferous tubules had enlarged and comprised primary and more darkly staining secondary spermatocytes $2.5 \mu\text{m}$ in diameter with a few spermatids between 1.5 and $2.0 \mu\text{m}$ in diameter occurring in the follicle lumina (Fig. 1). At this time too, ovarian follicles still possessed narrow lumina, although the epithelial walls of these were producing broadly stalked oogonia with a maximum diameter of $10 \mu\text{m}$ (Fig. 1). By April–May and October, gametogenesis was progressing and the seminiferous tubules and ovarian follicles had increased in size substantially (Fig. 1). In the former, there were considerably more spermatids being produced and a few spermatozoa. In the latter, the oogonia had attained an average diameter of $30 \mu\text{m}$ but were still attached to the epithelial wall by a narrower, more pinched stalk. The testes and ovaries were considered to be mature from May to June and November to December. At these times, the seminiferous tubules comprised many primary and secondary spermatocytes and spermatids, but the central lumina of each tubule was full of slipper-shaped spermatozoa arranged in radial chords and forming lamellae with their heads projecting towards the surrounding and the still active germinal epithelium (Fig. 1). Coincidentally, the follicles were packed with, now detached and rounded, ova some $60 \mu\text{m}$ in diameter and each with a darkly staining nucleus $10 \mu\text{m}$ in diameter (Fig. 1). These mature ova possessed only a little yolk and can thus be classified as oligolecithal. By December–January and July, gonads were spent (Fig. 1). They comprised empty tubules and follicles undergoing a generalized pattern of size reduction and resorption of the remaining gametogenic primordia and un-discharged gametes. Knowing, however, that another cycle of gametogenesis will soon begin in each adult surviving into a new life-cycle phase or maturing juvenile, it is clear that the spent phase lasts but for a short period.

The gonadal cycle exhibited by *L. fortunei* in Hong Kong comprised two phases of reproductive activity each year. During January–February and July–August, the gonads were in a state of regression. These months coincided with the coldest (16 – 17°C , winter) and hottest (27 – 28°C , summer) water temperatures in the reservoir. As temperatures subsequently warmed and cooled, respectively, gametogenesis proceeded, ultimately resulting in gonadal maturity from May to June and November to December. These two phases were followed by gamete release.

In contrast to this pattern, Choi and Shin (1985) estimated that, in South Korea, at a latitude of $\sim 38^\circ\text{N}$, *L. fortunei* showed a unimodal pattern of reproduction over the course of a year with sperm and ova being released in a single event between July and August for a period of only about 15–20 days. This is in contrast to the situation in subtropical Hong Kong where, as identified by Morton (1977, 1982), two cycles of gametogenic activity were recorded each year, although recruitment,

albeit with summer and winter peaks, occurred for 10 months of the year. Also, South American subtropical and tropical populations have been observed to recruit for up to > 10 months of the year (Fig. 2; Boltovskoy et al. 2009b). In tropical Asia, it is possible that *L. fortunei* reproduces year round as well, although this has never been studied.

Working on populations from the Río de la Plata estuary shortly after the species was first discovered in the area, Darrigran et al. (1999) recorded mature sperm year round and five major spawning events between July 1992 and November 1994: in September to October 1992, December 1992 to January 1993, May to July 1993, April to June 1994, and October to November 1994. Subsequent results of Darrigran et al. (2003) and Damborenea and Penchaszadeh (2006) indicated that, in the Río de la Plata estuary, *L. fortunei* produces sperm and oocytes continuously throughout the year, with spawning peaks in spring (September–November) and at the end of summer (February–March).

In Brazil, diverse situations have been described, from uninterrupted breeding throughout the entire year to punctuated breeding with interruptions and more or less extended resting periods (Table 1).

Reproductive Strategy: Evidence from Temporal Series of Larval Densities

Studies of temporal changes in the densities of larvae in the water column spanning at least 1 year have been carried out repeatedly, both in Japan and in South America (Table 1). A few studies extended over more than 1 year, and at least two surveys monitored larval abundances over periods of 7 (Mata 2011) and > 9 years (Boltovskoy et al. 2013; Fig. 2).

In South America, the months of highest larval output vary from site to site and from year to year (Fig. 2), but the most usual pattern involves a spring–early summer peak around November–December, and a second, less pronounced, peak in February–March (Fig. 3), seasonally similar to the situation in Hong Kong. Months barren of larvae are either few or absent. Around 80% of the temporal series performed (Table 1) show that there are at least ten larvae per cubic meter of water for 11–12 months of the year. The remaining 20% of the studies identified larvae in 7–10 months of the year.

In Japan, larval production is also associated with the summer, but the reproductive period is considerably shorter. In the reservoirs and rivers investigated, larvae were absent from the water column for 7–8 months of the year, and peak reproduction was clearly concentrated within 1–2 months (Magara et al. 2001; Nakano et al. 2010a; Hamada 2011; Figs. 2 and 3). In the Uji River (Japan), *L. fortunei* produced recruits during 4 months of the year (June–September; Iwasaki and Uryu 1998).

The highest recorded larval densities of *L. fortunei* are around 100,000 ind./m³ (Darrigran et al. 2007; Nakano et al. 2010a), but such values are exceptional. During months of peak reproduction (November through March in the southern

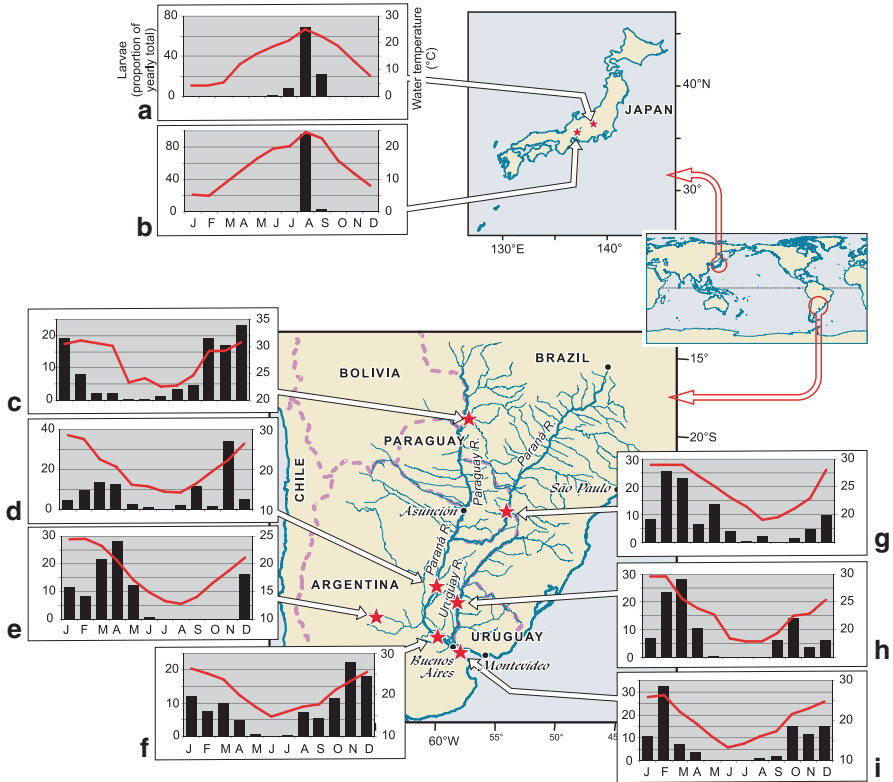
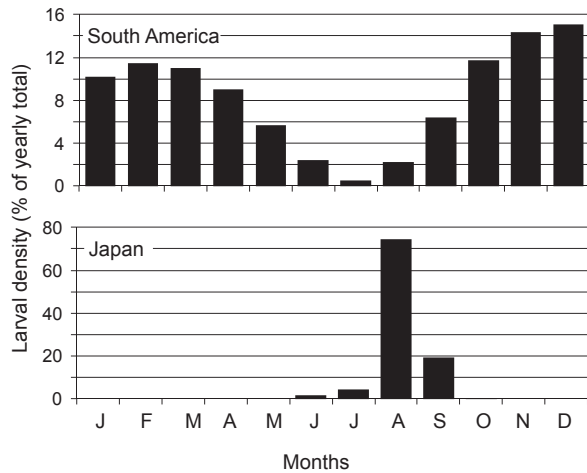


Fig. 2 Reproductive cycles of *Limnoperna fortunei* in different waterbodies, as shown by the seasonal occurrence of its larvae in the plankton. Bars denote proportions of the yearly total recorded each calendar month (January to December, left y-scale; some values are interpolated; overlapping periods for consecutive years are averaged). Red line indicates mean surface water temperature (right y-scale). **a** Yahagi River (35.32°N, 137.14°E), 34 samples collected between May 2007 and February 2010 (based on data from Hamada 2011). **b** Lake Ohshio (36.22°N, 138.88°E), 49 samples collected between August 2007 and November 2008 (based on data from Nakano et al. 2010a, data courtesy of Daisuke Nakano). **c** Paraguay River (19.60°S, 57.43°W), 47 samples collected between January 2004 and November 2007 (based on data from Oliveira et al. 2011). **d** Riacho Santa Fe (tributary of the Middle Paraná River) (31.64°S, 60.68°W), 33 samples collected between September 2004 and September 2005 (based on data from Rojas Molina 2010). **e** Embalse de Río Tercero (32.23°S, 64.44°W), 40 samples collected between March 2005 and March 2006 (based on data from Boltovskoy et al. 2009b). **f** Lower Paraná delta (33.96°S, 59.21°W), 68 samples collected between September 1997 and January 1999 (based on data from Boltovskoy and Cataldo 1999). **g** Itaipú reservoir (Upper Paraná River) (25.41°S, 54.59°W), 12 samples collected between January 2005 and December 2005 (based on data from Mata 2011). **h** Salto Grande reservoir (Uruguay River) (31.27°S, 57.94°W), 37 samples collected between January 2010 and December 2010 (based on data from Boltovskoy et al. 2013). **i** Río de la Plata estuary (34.56°S, 58.41°W), 63 samples collected between October 1997 and December 1998 (based on data from Cataldo and Boltovskoy 2000)

Fig. 3 Seasonal occurrence of *Limnoperna fortunei* larvae in the water column in South America (mean values based on 25 surveys) and in Japan (mean values based on three surveys)



hemisphere), larval densities normally range between 6000 and 7000 ind./m³, whereas in June–September, they decline to <1000 ind./m³. Data are more scarce for Japan, but summer peak larval densities are probably higher than those recorded in South America (e.g., around 20,000–35,000 ind./m³; Magara et al. 2001; Nakano et al. 2010a), but with no larvae for most of the remaining months in the year.

The larval densities described above are considerably lower than the maxima recorded for *Dreissena polymorpha*, which can exceed 500,000 ind./m³ (Garton and Haag 1993; Smit et al. 1993), suggesting that the zebra mussel has a higher instantaneous fecundity. This does not, however, necessarily imply a higher overall fecundity, because the reproductive period of *D. polymorpha* is often considerably shorter (Karatayev et al. 2007; Boltovskoy et al. 2009b; see Chapter “Parallels and Contrasts Between *Limnoperna fortunei* and Species of *Dreissena*” in this volume). Adult population densities, on the other hand, seem either similar or slightly higher for *L. fortunei* (Karatayev et al. 2010).

Differences Between Results: Gonadal Maturation Versus Larval Cycles

Different methods (larval abundance trends vs. gonadal maturation) have produced different results concerning the timing of the periods of highest reproductive output: Larval cycles point to an almost continuous spring-to-autumn reproduction with two more or less conspicuous peaks around December and February–March (in South America), or a single peak in the middle of summer (Japan, Korea; Fig. 3). Gonadal studies, in turn, identify two or more discrete pulses, sometimes even in the middle of winter (Morton 1982; Darrigran et al. 1999, 2003). These differences are most probably due to the fact that the two types of observations reveal different aspects of the same process. That is, larval cycles integrate the reproductive output

of extensive mussel beds dispersed over large areas, whereas gonadal data pinpoint with high precision the ripening and spawning of more or less isolated individuals or spatially restricted clusters.

Larvae of *L. fortunei* collected at any one location are produced by adults dispersed over large areas upstream from the collection site. The time required for a fertilized egg to reach the pediveliger stage, when it is ready to settle, is ca. 20 days at 20°C (Cataldo et al. 2005; see Chapter “Larval Development of *Limnoperna fortunei*” in this volume) and probably longer at lower temperatures (*L. fortunei* reproduces at water temperatures as low as 15–17°C; Morton 1977; Cataldo and Boltovskoy 2000; Brugnoli et al. 2011). At current velocities of ~3–5 km/h, not uncommon in many rivers, larvae caught at any one site could thus have originated from as far as 2000 km upstream. A plankton sample therefore typically integrates the reproductive output of hundreds to millions of *L. fortunei* beds located upstream from the sampling site.

Gonadal maturation, on the other hand, is based on the analysis of a few individuals collected over a small area, usually the same throughout the entire cycle analyzed. As suggested for other bivalves (Garton and Haag 1993), while restricted beds of *L. fortunei* may spawn synchronously, when larger areas are considered, the lack of reproductive synchronicity between populations results in a continuous breeding season and discrete spatfalls are not recognizable in the plankton (Boltovskoy et al. 2009b). As a consequence, both punctuated and continuous reproduction modes have been reported by the same authors when using histological data and larval counts in plankton samples, respectively (Darrigran et al. 1999, 2002).

While inducing *L. fortunei* to spawn using artificial stimuli in laboratory conditions is fairly easy (Cataldo et al. 2005), detecting the timing, frequency, and intensity of spawning events of restricted beds in the field poses serious difficulties and has not been achieved hitherto. With the aid of an experimental device that mimicked natural conditions, Cataldo and Boltovskoy (unpublished) sampled the prefiltered water, bathing a cluster of ca. 2000 adult individuals in order to detect spawning. Although the experiment was carried out at a time of peak reproduction, after a week of uninterrupted filtration, no ova were observed. Admittedly, the observational period was limited, but the result seems to support the notion that reproduction of discrete clusters is not continuous, as suggested by the presence of larvae in the plankton, but punctuated, as deduced from gonadal maturation studies. Given the clear advantages of epidemic over asynchronous spawning (particularly for a species whose distribution encompasses many thousands of kilometers and, due to its requirement for hard substrata, is extremely patchy), it is hard to envision how *L. fortunei* manages to produce such impressive numbers of offspring if it lacks mechanisms for synchronizing the liberation of its gametes. Although epidemic spawning is characteristic of marine invertebrates, and is less common in freshwater organisms (Olive 2002), *L. fortunei* is a member of a typically marine bivalve superfamily (Mytiloidea) and, as such, shares many traits with most of its marine relatives, notably a rather extended free-swimming larval stage.

It is concluded that although both of these methods to identify spawning (gonadal thin sections and larval counts) yield useful data, the information conveyed by them

is dissimilar. Studies based on the assessment of gonadal maturation focus on the reproductive behavior of individuals and, by extension, of the species. They convey precise information on the number and timing of reproductive events in any one breeding season and are, probably, the most promising paths for studies of fecundity. Larval counts, on the other hand, are more meaningful in terms of the overall ecology of *L. fortunei* and of the biota that interacts with it. For fouling control studies, the information conveyed by larval counts is more useful as it better allows the pinpointing of periods when industrial installations are particularly vulnerable to fouling by this species.

Triggers of Reproduction

“What triggers spawning?” is a key question associated with surveys of the reproductive behavior of *L. fortunei*. The variable that has been recurrently observed to covary with reproduction is water temperature (Boltovskoy et al. 2009b; Fig. 2). Several authors have suggested that 15–18 °C is the threshold value below which production of larvae is near zero (Morton 1977; Choi and Shin 1985; Cataldo and Boltovskoy 2000; Nakano et al. 2010a; Brugnoli et al. 2011), but this threshold is obviously not applicable to tropical waterbodies where water temperatures never fall below these values. Even in these locations, however, there usually is a well-defined period of reproductive relaxation, which invariably occurs during the coolest months (Canzi et al. 2005; Boltovskoy et al. 2009b; Mata 2011; Oliveira et al. 2011; Fig. 2c and g). For Salto Grande reservoir (Argentina–Uruguay), where surface water temperatures vary from 14 to 32 °C, densities of *L. fortunei* larvae have been estimated weekly between June 2004 and 2014. Lowest larval densities occurred between ~1 June and 15 August, at temperatures around 14–24 °C (mean: 18 °C). However, of the 87 plankton samples collected between 1 June and 15 August (2004 through 2013), only ten contained no larvae at all (i.e., <0.5 larvae/m³). Boltovskoy et al. (2009b) suggested that, regardless of ambient temperature, *L. fortunei* needs a resting period in order to resume gametogenesis, as has been reported for other invertebrate species (McMahon and Bogan 2001). Interestingly, this behavior differs from that of *D. polymorpha* in artificially heated reservoirs and laboratory conditions at temperatures permanently >12 °C, where the species has been reported to produce larvae year round (Stanczykowska 1977; Lewandowski 1982b; Nichols 1993). Nevertheless, in the temperate and warm waterbodies of southern North America, spawning does not begin until water temperatures rise to >20 °C (Nichols 1996). In southern England, larval settlement of *D. polymorpha* begins at a temperature of ~15 °C (Morton 1969).

While there is little doubt that temperature plays a key role in the reproductive cyclicality of *L. fortunei*, there most probably are other factors that also influence both the timing and the intensity of spawning events. Their association with reproduction, however, is less clear and mostly based on circumstantial evidence (unless they range outside of the normal levels of tolerance of the species, in which

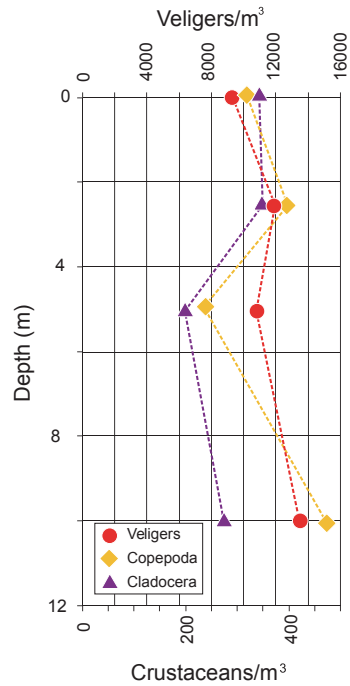
case they affect all vital traits, including reproduction; Nakano et al. 2010a). In his studies of Plover Cove reservoir, Morton (1982) remarked that pH, salinity, and dissolved oxygen may be associated with gametogenesis and spawning. His results suggested that spawning takes place at times of high temperatures and low dissolved oxygen levels in summer and at low temperatures with high dissolved oxygen levels in winter. Oliveira et al. (2011) argued that, in addition to temperature, dissolved oxygen, and calcium levels, pH, water velocity, suspended solids, and chlorophyll *a* concentrations may be instrumental in modulating larval numbers in the upper Paraguay River. Changing conditions associated with flood–drought cycles characteristic of many large South American rivers have also been suggested as important factors involved in the reproduction of *L. fortunei*, particularly in areas where temperatures are high year around (Callil et al. 2012).

The availability of food, which was found to be important in determining the frequency of reproduction in *D. polymorpha* (Gist et al. 1997), may also play a role in the extension of the reproductive period of *L. fortunei*. Boltovskoy et al. (2009b) noted that, in practically all the South American waterbodies surveyed, the winter phase of reproductive relaxation spanned 1.8–3 months, with the exception of the reservoir Embalse de Río Tercero, where larvae were virtually absent from the waterbody for almost half the year (Fig. 2e). Water temperatures in this reservoir were not significantly different from those of other sites, suggesting that this factor is unlikely to account for such a reproductive difference. On the other hand, suspended particulate organic matter in Embalse de Río Tercero (around 0.5–1 mg/L) was much less abundant than in the other waterbodies (around 8 mg/L), which may point to food supply as a significant factor that affects reproductive output.

Vertical Distribution of Larvae

A few studies have investigated the vertical distribution of *L. fortunei* larvae in the water column. In rivers, turbulent flow normally precludes the development of vertical stratification and physical, chemical, and biological properties, including *L. fortunei* larvae and other plankton, are evenly distributed from top to bottom (Fig. 4). In lentic environments, on the other hand, contrasting situations have been described. In Palmar reservoir (Uruguay), Brugnoli et al. (2011) did not identify significant differences in the concentrations of *L. fortunei* veligers at different depths. In contrast, in Lake Ohshio (Japan), veligers were more abundant near the bottom (ca. 18 m) and at mid-depths than in the uppermost 2-m layer (Nakano et al. 2010a). Differential colonization rates at different depths of the same waterbody could also point to differences in preferred larval depth (Morton 1977), but interpretation of these patterns is complicated by possible dissimilarities in the survival of recruits, including the effects of predation (Nakano et al. 2010b). In any case, it would be reasonable to expect that at least older larvae, that is, those nearing the settling stage, are more abundant closer to their final destination—the epibenthos—than elsewhere in the water column (as observed in laboratory conditions, see Chapter “Larval Development of *Limnoperna fortunei*” in this volume).

Fig. 4 Densities of *Limnoperna fortunei* larvae, copepods, and cladocerans at different depths in the Paraná de la Palmas River (Lower Paraná River delta; 34.29°S, 58.56°W) recorded on 3 March 2003 (unpublished authors' data)



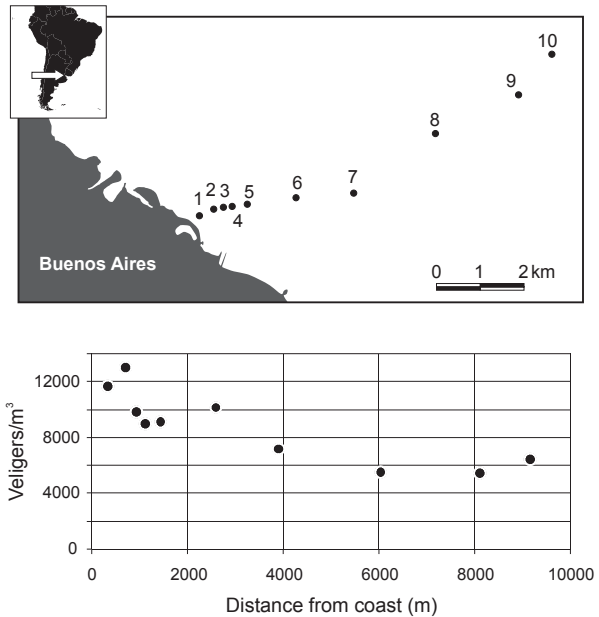
Factors Affecting Larval Densities

In addition to seasonality, several other factors can modulate larval densities in the water column. Some of these have been investigated, including distance from suitable substrata, time after colonization, the effects of cyanobacterial blooms, and sample-to-sample variability.

Distance from Suitable Substrata

Although adult *L. fortunei* can use a variety of substrata for attachment (see Chapter “*Limnoperna fortunei* Colonies: Structure, Distribution and Dynamics” in this volume), hard, immobile surfaces, like stone and wood, are normally favored. Such substrata, especially immobile boulders, are often scarce in natural lotic and lentic systems. In South America, in particular, the main waterbodies colonized by *L. fortunei* are large, lowland, riverine systems, whose streambeds are characterized by fine, unconsolidated sediments, unfit for colonization by *L. fortunei*. Over large river stretches, therefore, the only hard substrata available are man-made structures associated with populated areas, such as piers, groynes, pilings, breakwaters, and revetments. Larval densities may thus be higher in the vicinity of these structures than farther away. Figure 5 shows the results of a transect in the Río de la Plata estuary, off Buenos Aires,

Fig. 5 Larval densities recorded along a transect perpendicular to a coast modified by a concrete coastal revetment densely populated by adult mussels off Buenos Aires, on 11 December 2002. (unpublished authors' data)



roughly perpendicular to a coastal sector modified entirely by a concrete revetment. Larval numbers fell from around 12,000 ind./m³ next to the man-made concrete wall (densely populated by adult individuals) to 6000 ind./m³ at 6–10 km from this substratum (the bottom in this area is silt-mud). While this difference is well within the range of the sample-to-sample variability (Fig. 6), the decreasing trend is consistent, suggesting that distance from the coast plays a significant role in influencing population numbers. This effect is probably of little importance when analyzing seasonal trends in larval abundance at a fixed site, but site-to-site comparisons may be affected significantly.

Time After Colonization

Larval concentrations also depend strongly on the time elapsed after initial colonization of the waterbody. Data from Itaipú reservoir, which was colonized by *L. fortunei* around 2000 (Zanella and Marena 2002), indicate that mean annual larval densities were only 106 ind./m³ in 2002, 512 ind./m³ in 2003, and 2000–2500 ind./m³ in 2004–2005, suggesting that the spread of beds upstream from the sampling site was responsible for this increase (Canzi et al. 2005). In 2006, larval densities fell to ca. 1400 ind./m³ and varied thereafter at around 1000–1500 ind./m³ until 2008 (Mata 2011; Fig. 7). This decline and subsequent plateau could point to stabilization of the adult population densities in the reservoir, although the time elapsed since

Fig. 6 Densities of *Limnoperna fortunei* larvae, copepods, and cladocerans recorded throughout a 24-h period in Honda River (Lower Paraná River delta; 34.32°S, 58.53°W) on 4–5 March 2003 (unpublished authors' data)

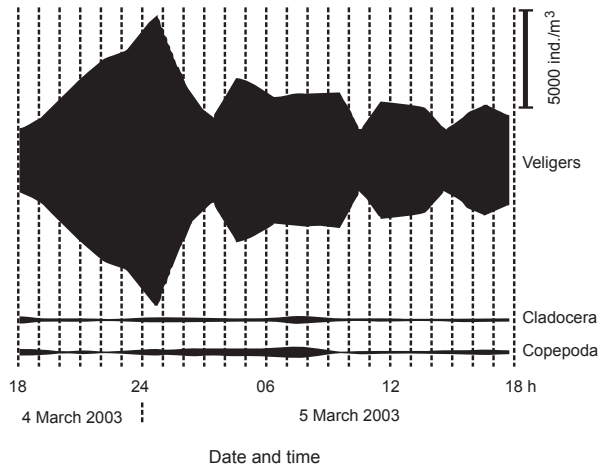
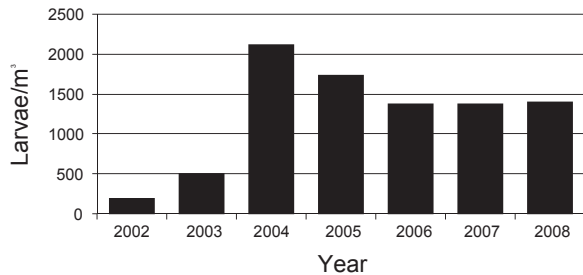


Fig. 7 Mean densities of *Limnoperna fortunei* larvae in Itaipu reservoir between 2002 and 2008 (based on data from Canzi et al. 2005; Pestana et al. 2008; Boltovskoy et al. 2009b; Mata 2011)



initial colonization appears short for this process. Populations of invasive bivalves, including *D. polymorpha*, have been suggested to follow a so-called boom–bust cycle (Stanczykowska 1977), stabilizing at around 7–12 years post introduction (Burlakova et al. 2006; Boltovskoy et al. 2009a, 2009b). Nevertheless, several other population modes have also been described, some of them involving large cyclical or irregular fluctuations (Strayer and Malcom 2006).

Although the scarce evidence available suggests that larval densities increase in response to adult population growth, no direct proof of a significant correlation between the numbers of adults and those of their planktonic larvae has yet been provided. This relationship may not be as trivial as it seems. Several surveys of *D. polymorpha* have failed to establish a clear relationship between adult population size and larval density (Stanczykowska 1977; Garton and Haag 1993; Nalepa et al. 1995), with some authors suggesting that larval numbers in the plankton may be governed by other factors, such as the age structure of the adult population (Lewandowski 1982a) and water levels (Smirnova et al. 1993).

The Effects of Cyanobacterial Blooms

Another factor that has been shown to impact reproductive periods and larval numbers significantly is the development of cyanobacterial blooms. On the basis of 9 years of observational data in Salto Grande reservoir (on the Uruguay River, Argentina–Uruguay), Boltovskoy et al. (2013) showed that reproduction by *L. fortunei* was interrupted during dry summers (January–April), coinciding with periods of peak *Microcystis* spp. growth and low water discharge levels—which favor the buildup of algal biomass. Conversely, wet summers with high discharge rates were characterized by low densities of *Microcystis* spp. and high numbers of *L. fortunei* larvae in the water column (Fig. 8). Laboratory experiments showed that microcystin-LR (produced by toxic strains of several Cyanobacteria) is highly toxic to *L. fortunei* larvae, eliminating 58–100% of individuals in 48 h at 10–20 $\mu\text{g/L}$ (Boltovskoy et al. 2013). Cyanobacterial blooms in this reservoir are particularly strong in late summer–autumn, often suppressing the December/January to April reproductive pulse completely (Fig. 9). While associations between microcystin and larval mortality are beyond doubt, the toxin may also affect other aspects of *L. fortunei* reproduction, such as gamete production and survival, fertilization, and hatching. Suppression of reproduction due to high microcystin concentrations is most likely in subtropical and tropical lakes and reservoirs (Soares et al. 2013), especially when

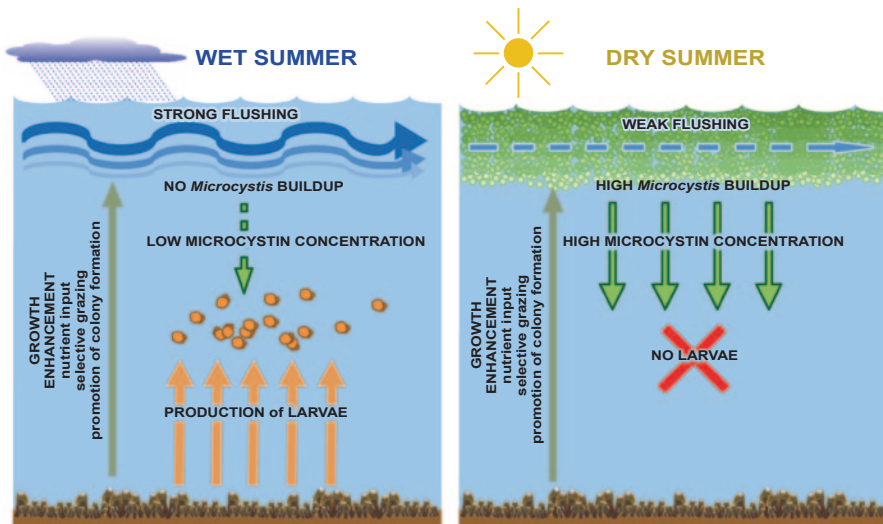


Fig. 8 Schematic diagram of cause–effect relationships between *Microcystis* spp. blooms and *Limnoperma fortunei* reproduction in Salto Grande reservoir (Argentina–Uruguay). During rainy summers, high discharge rates preclude *Microcystis* spp. buildup and microcystin levels are low in the water, allowing for normal production of larvae. During dry summers, weak flushing and strong thermal vertical stratification favor *Microcystis* spp. growth and high microcystin concentrations in the water column, which kill *L. fortunei* larvae precluding reproduction. (Modified after Boltovskoy et al. 2013, with permission from John Wiley & Sons)

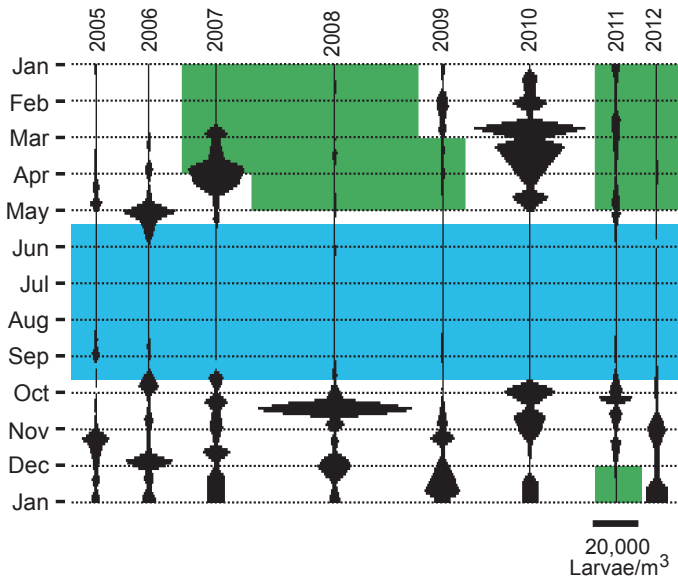


Fig. 9 Densities of *L. fortunei* larvae in Salto Grande reservoir between 2005 and 2012. *Green shading* denotes periods of extensive *Microcystis* spp. blooms (no data for *Microcystis* are available in 2005 and 2006); *light blue shading* denotes water temperatures below 21 °C (mean for 2005–2012; based on data from Boltovskoy et al. 2013)

their drainage areas include agricultural land yielding high nutrient loads. Rivers, on the other hand, rarely host strong blooms, and would thus be less likely to show atypical larval abundance cycles.

In addition to the above, several other factors have been reported to affect the reproductive output of *L. fortunei*. Trematode parasites can inhibit gamete production (Tanaka et al. 2004; see Chapter “Parasites of *Limnoperna fortunei*” in this volume). Stress-inducing factors, like pollution and low dissolved oxygen levels, can impact many of the species’ vital activities and processes, including reproduction (e.g., Morton 1977; Nakano et al. 2010a; Bonel 2011; Oliveira et al. 2011; Bonel et al. 2013).

Sample-to-Sample Variability

Agreement between surveys indicates that the overall trends in the larval abundance profiles of *L. fortunei* do reflect actual density variations throughout the year but, as with most planktonic abundance estimates, variability is high. The profiles shown in Fig. 6 illustrate abundance estimates for veligers, copepods, and cladocerans obtained at hourly intervals on 4 and 5 March 2003 in the Lower Paraná River delta. Numbers of *L. fortunei* larvae varied between ca. 2000 and almost 16,000 ind./m³, or slightly less than one order of magnitude. This variability does not seem to reflect

the result of reproductive pulses from different *L. fortunei* beds distributed upstream from the sampling site, because copepods and cladocerans showed a similar range of variation. All these samples were collected using a submersible centrifugal pump (rather than towed flow-metered net), thus ensuring precise estimates of the volume of water filtered and precluding any possibility of net clogging. Furthermore, all counts were conducted twice in order to minimize methodological bias. These results underscore the need for intensive, densely packed (in space and/or in time) sampling programs when investigating reproductive output trends.

Concluding Remarks

Comparison of annual recruitment cycles from several climatic zones leaves little doubt that temperature has an overwhelming importance on the reproductive process. Remarkably, summer maxima differ moderately between the areas where the reproductive cycles of *L. fortunei* have been investigated, but winter minima are quite dissimilar. Lowest values are those where winter minima are around 0–4 °C (Choi and Shin 1985; Nakano et al. 2010a; Table 2). Here, >90% of the reproductive output is concentrated within 1–2 summer months (July and August); there are no larvae in the water column for the rest of the year. In records from the Uji River (Japan), at somewhat higher water temperatures (ca. 13–26 °C), *L. fortunei* produced recruits during 4 months of the year (June–September) (Iwasaki and Uryu 1998). In the southernmost South American localities investigated (Lower Paraná River delta, Río de la Plata estuary), where lowest water temperatures are ~10 °C, larvae are produced for around 5–7 months of the year, but there often are two more or less well-defined peaks—a major one shortly after the winter trough, in November or December, and a second, usually smaller one, around March. Further north in the Río de la Plata watershed (Upper Paraná River, Paraguay River), winter temperature minima are higher (13–14 °C) and the corresponding reproductive relaxation period is shorter. Finally, in subtropical Asia (Hong Kong), where water temperatures vary seasonally between 15 and 32 °C, gonadal activity is present throughout most of the year and, in addition to the summer peak, there also is a peak in February (northern hemisphere winter; Morton 1977). These differences in reproductive activity are summarized in Fig. 10 and show that reproduction is confined to a single summer peak in the northern temperate zone (Korea, Japan). Most interestingly, however, the data show that in the northern (Hong Kong) and southern (South American) subtropics, there are roughly two reproductive peaks, but both occurring in their respective (and opposite) early spring and late summer seasons.

Contrasts between Korea and Japan, on the one hand, and South America, on the other, are very sharp (Fig. 2), but trends anticipated from the corresponding thermal regimes are not always as clear-cut. For example, water temperatures of the Yahagi River (Japan, 10–26 °C) are similar to those of the Middle Paraná River (Argentina, 10–29 °C), yet larval production is restricted to 1 month in the former, while

Table 2 Temporal concentration of the reproductive activity of *Limnoperna fortunei* in various Asian and South American waterbodies characterized by different water temperatures, as indicated by the number of months needed to account for $\geq 90\%$ of the annual output of larvae when monthly values are sorted in descending order (based on the “production half-time” concept of Berger and Wefer 1990)

Site	Latitude	Lowest water temp. (°C)	Highest water temp. (°C)	Month(s) of the year when % of annual recruitment is $> 20\%$ of the annual total	$\geq 90\%$ of the yearly larval output occurs in (months)	References
Plover Cove reservoir (Hong Kong) ^a	22°N	15	32	Feb, Jul	9	Morton (1977)
Yahagi River (Japan)	35°N	10	26	Aug	1	Hamada (2011)
Lakes Ohshio and Takenuma (Japan)	36°N	4	27.5	Aug	2	Nakano et al. (2010a)
Paldang reservoir (South Korea)	37°N	2	29	Aug	2	Choi and Shin (1985)
Paraguay River (Brazil)	19°S	22.5	31.2	Jan, Nov, Dec	6–9	Oliveira et al. (2011)
Miranda River (Brazil)	19°S	22.5	31.2	Aug, Sep	6	Oliveira et al. (2011)
Upper Paraná River (Brazil–Paraguay)	25°S	18	29	Feb, Mar, Apr, May, Oct, Nov, Dec	4–8	Canzi et al. (2005), Pestana et al. (2008), Boltovskoy et al. (2009b), Mata (2011)
Upper Paraná River, Yacyretá reservoir (Argentina–Paraguay)	27°S	15	32	Feb, Dec	7	Darrigran et al. (2007)
Middle Paraná River (Argentina)	30°S	10	29	Mar, Oct, Nov, Dec	6–8	Cepero (2003), Ezcurra de Drago et al. (2006), Rojas Molina (2010), Bonel (2011)
Guatba Lake (Brazil)	30°S	12	27.5	Oct	8	Santos et al. (2008)
Uruguay River, Salto Grande reservoir (Argentina–Uruguay) ^b	31°S	18	30	Feb, Mar	7	Boltovskoy et al. (2013)

Table 2 (continued)

Site	Latitude	Lowest water temp. (°C)	Highest water temp. (°C)	Month(s) of the year when % of annual recruitment is >20% of the annual total	≥90% of the yearly larval output occurs in (months)	References
Embalse de Río Tercero reservoir (Argentina)	32°S	12.8	24.5	Mar, Apr	5	Boltovskoy et al. (2009b)
Río Negro River, Palmar reservoir (Uruguay)	33°S	12.5	27	Apr	8	Brugnoli et al. (2011)
Lower Paraná River delta (Argentina)	34°S	13.3	26.4	Nov, Dec	8	Boltovskoy and Cataldo (1999), Sylvestre (2006)
Río de la Plata estuary (Argentina)	34°S	13.3	27.6	Feb	6–8	Cataldo and Boltovskoy (2000), Bonel (2011)

^a Estimated recruitment values

^b 2010 data only (other years have atypical reproduction trends due to extensive cyanobacterial blooms, see text)

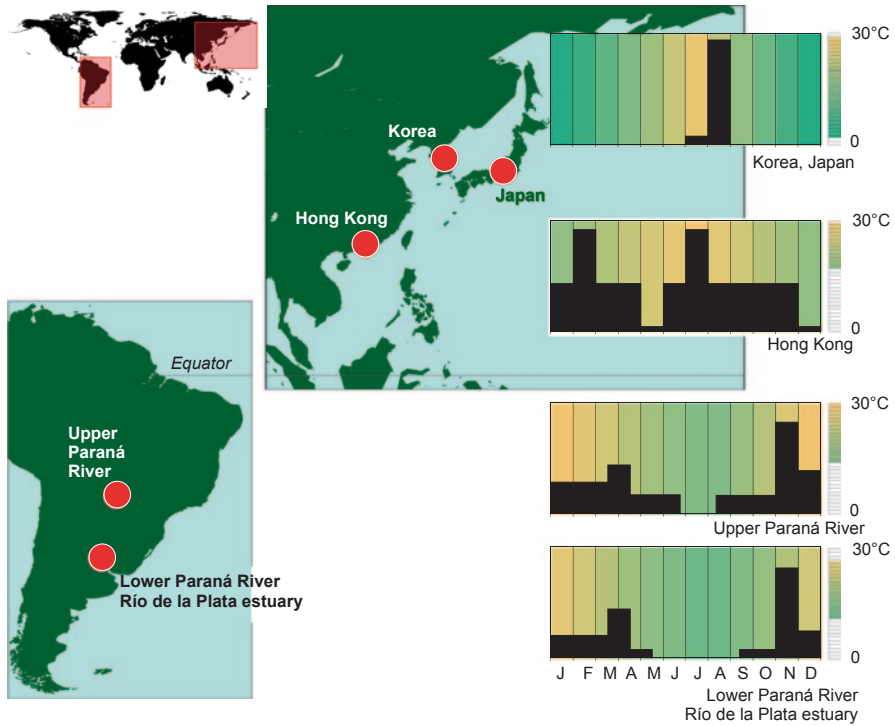


Fig. 10 Proposed relationship between latitude, water temperature, and reproductive activity of *Limnoperna fortunei*. Histograms indicate relative strength of recruitment throughout the year. Bars next to histogram denote water temperature (see text for explanation)

it extends more than 6–8 months in the latter (Table 2). At similar thermal regimes (around 13–26°C), larvae are present during only 4 months in the Uji River (Japan; Iwasaki and Uryu 1998), and up to 8 months in the Río de la Plata estuary (Table 2). Departures from this temperature-dependent reproduction mode are also evident when comparing several South American sites. For example, in the reservoir Embalse de Río Tercero (Argentina), the reproductively active period is at least 3–4 months shorter than expected from its water temperature span (Table 2). Boltovskoy et al. (2009b) suggested that a lower food supply is possibly responsible for the shorter reproductive period at this waterbody. In the Miranda River (tributary of the Paraguay River), where water temperatures are always above 20°C, larvae are absent for half of the year (Table 5.1.2), which may be a response to extended anoxic events and/or low calcium concentrations (Oliveira et al. 2011). In Salto Grande reservoir (Uruguay River, Argentina–Uruguay), extensive blooms of toxic cyanobacteria can suppress reproduction almost entirely, regardless of water temperature (Boltovskoy et al. 2013; Figs. 8 and 9).

These results suggest that, in addition to temperature, many factors can play key roles in shaping the reproductive cycle of *L. fortunei*. Ultimately, however, the reproductive cycle, in coordination with aspects of its overall physiological

tolerances, determines the success of the species not only in its native environment but also in its introduced ranges. In particular, the short life span of *L. fortunei*, rapid sexual maturity, and fast growth designate it as an *r*-selected species in contrast to the more long-lived, slow-growing, and similarly freshwater representatives of the Unionidae, which follow *K*-selected life history strategies (Morton 1991).

The heteromyarian, triangular, basally flattened, body form associated with byssal attachment has allowed *L. fortunei* to exploit the epibenthic niche of both lentic and lotic waters—previously unoccupied by representatives of the Bivalvia. These freshwater habitats were similarly invaded by species of Dreissenidae, notably *D. polymorpha*, and thus provide us a remarkable example of convergent evolution. In both mytiloid and dreissenid cases, however, it is their similar reproductive strategies of fast growth, rapid maturity, high fecundity, broadcast spawning, external fertilization, brief larval lives, and recruitment to established colonies (probably mediated by parental pheromones: Sardiña et al. 2009) that are undoubtedly responsible for the success of them both.

At present, the natural and introduced ranges of both *L. fortunei* and *D. polymorpha* do not overlap and although we can but hope that they never do, they most likely inevitably will. In that scenario, it will be fascinating to research the outcome (see Chapter “Parallels and Contrasts Between *Limnoperna fortunei* and species of *Dreissena*” in this volume). In the modern world, increasingly, it is the opportunists who are coming to dominate our global ecosystems, and nowhere else is this more obvious than in freshwaters.

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