Population Dynamics of *Limnoperna fortunei*, an Invasive Fouling Mollusc, in the Lower Paraná River (Argentina)

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Settling and growth of the Asian freshwater mussel *Limnoperna fortunei* on experimental PVC frames in the Paraná de las Palmas river, ca 130 km north of Buenos Aires was monitored at monthly intervals in 1998. Frames were deployed in January. In February and March colonization reached 3800044000 mussels m⁻², with early juveniles (< 2 mm) accounting for over 98% of the population. In April through August the total densities decreased to 9000-2000 individuals m⁻², the populations being dominated by older (> 2 mm) mussels. In September through December densities grew steadily again, with early juveniles (< 2 mm) accounting for over 95% of the mussels recorded. During their first month, animals born in January grew to ca 34 mm in length; in March they reached 7-8 mm, and by mid April 11-12 mm. In late April through July the growth rate decreased to < 2 mm per month, and in August it stopped almost completely, resuming again in late September. During the first year animals born in January reached 20 mm in length; by the end of the second year the estimated length was 30 mm, with a maximum theoretical length of 35 mm being reached after 3 years. The data agree with the reported population dynamics of *L. fortunei* in Hong Kong in that both populations are characterized by extended reproduction periods lasting ca 9 months, and that the spring onset of breeding is triggered by a rise in temperature above approximately 16–17°C. On the other hand, in the Paraná river reproduction was found to be continuous between September and March, and the period of lowest yearly temperatures was characterized by a very strong breeding decline, whereas for the Chinese populations 2-3 yearly spatfalls and breeding pulses roughly coinciding with the lowest and highest water temperatures were described.

Keywords: *Limnoperna fortunei*; biofouling; population dynamics; Argentina; growth

INTRODUCTION

*Limnoperna fortunei* (Dunker), a mytilid bivalve which constitutes a major fouling pest in Hong Kong, Korea, Japan and Taiwan (Ricciardi, 1998), invaded the Paraná-Uruguay drainage basin around 1991 (Pastorino et al., 1993). At present, its confirmed distribution spans from Paraguay (Lopez, personal communication), to Punta Piedras, on the Rio de la Plata estuary (ca 150 km south of Buenos Aires; Darrigran & Pastorino, 1995). Along its entire range *L. fortunei*
has rapidly become a major nuisance for industrial and power plants that use river water. Fouling of water conduits is facilitated by the planktonic larvae (200-300 μm in size) of the mussel, which bysally attach to hard substrata including the inner surfaces of pipes, sieves, heat exchangers and condensers, reaching densities over 120,000 individuals m⁻² (see below) and thus obstructing water flow. Given the characteristics of this species and the rising trend in worldwide shipping traffic, a future North American invasion is highly probable (Ricciardi, 1998).

Despite its high economic impact in Asia, and now in South America, and its potential impact elsewhere, life-history data for this mussel are limited to two surveys in Hong Kong (Morton, 1977; 1982) and one in Japan (Iwasaki & Uryu, 1998). For the Paraná-Uruguay system, Cataldo and Boltovskoy (personal observations) have studied the seasonal occurrence of its planktonic larvae in the water. The present paper presents an analysis of monthly changes in the size-frequency structure of the mussels colonizing experimental frames deployed in the Paraná de las Palmas river. The results differ from those reported for the Asian populations, thus furnishing data for fine-tuning control measures, both locally and elsewhere.

**MATERIAL AND METHODS**

Field work was carried out at the nuclear power plant Atucha I, located on the Paraná de las Palmas river approximately 130 km north of Buenos Aires (33°57.5′S, 59°12.5′W). On 20 January 1998 twelve experimental frames were installed in the channel that diverts the water used by the nuclear plant, next to its junction with the river. The frames were composed of 3 rectangular PVC plates fitted to each other such as to define 3 mutually perpendicular planes, attached to the mooring by two opposite wings (Figure 1). This design ensured (a) that surfaces oriented in all directions were available for colonization, and (b) that all devices were oriented alike, with the base facing downstream. At the time of deployment the bottom depth was 7.3 m, but throughout the period covered it varied between 6 and 8.74 m. Thus, minimum and maximum depths at which the frames were exposed were approximately 2.3 to 6 m. Starting on 17 February 1998, frames were retrieved at monthly intervals; thus, the first frame retrieved had been exposed to colonization by the mussel for ca 1 month, whereas the last one, retrieved on 17 December 1998, for approximately 11 months (Table I). Two frames (retrieved on 20 November 1998 and on 20 January 1999) were extensively covered by loose sediments when pulled out of the water and exhibited very sparse colonization; these data were excluded from the analyses. Upon retrieval, materials adhering to
TABLE I General population data for the experimental frames used

<table>
<thead>
<tr>
<th>Date of retrieval</th>
<th>Davs exposed</th>
<th>Individuals m⁻²</th>
<th>% individuals &lt; 2 mm long</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>17/02/1998</td>
<td>28</td>
<td>37852</td>
<td>98.6</td>
<td>6814</td>
</tr>
<tr>
<td>17/03/1998</td>
<td>56</td>
<td>43962</td>
<td>98.3</td>
<td>7914</td>
</tr>
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<td>91</td>
<td>9188</td>
<td>71.3</td>
<td>2297</td>
</tr>
<tr>
<td>19/05/1998</td>
<td>119</td>
<td>5064</td>
<td>17.8</td>
<td>1266</td>
</tr>
<tr>
<td>19/06/1998</td>
<td>150</td>
<td>3660</td>
<td>46.6</td>
<td>915</td>
</tr>
<tr>
<td>21/07/1998</td>
<td>182</td>
<td>3924</td>
<td>22.4</td>
<td>981</td>
</tr>
<tr>
<td>19/08/1998</td>
<td>211</td>
<td>2248</td>
<td>18.3</td>
<td>562</td>
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<tr>
<td>18/09/1998</td>
<td>241</td>
<td>20956</td>
<td>96.5</td>
<td>262</td>
</tr>
<tr>
<td>23/10/1998</td>
<td>276</td>
<td>85548</td>
<td>98.2</td>
<td>639</td>
</tr>
<tr>
<td>17/12/1998</td>
<td>331</td>
<td>122004</td>
<td>96.5</td>
<td>1248</td>
</tr>
</tbody>
</table>

all surfaces of the frames were removed and screened through a 25 μm mesh gauze in order to eliminate clay and silt particles. All mussels > 2-3 mm in length were picked out from the residue by hand, enumerated, and measured with a digital caliper to the nearest 0.01 mm. The remainder of the wet, sieved sample was subsampled by means of a Folsom plankton sample splitter (McEwen et al., 1954) until a fraction containing at least 150 early juveniles (< 2 mm) was obtained; all mussels in the subsample were subsequently counted and measured with a micrometric eye-piece under a compound microscope.

In a 28-month survey of the population dynamics of L. fortunei in Plover Cove (Hong Kong) reservoir, Morton (1977) concluded that both population densities and individual growth rates are depth-dependent. Depth of deployment was not taken into account in the present survey because, unlike Morton’s (1977) work, which was conducted in a lentic environment with marked vertical stratification, the present study was done in swiftly flowing waters characterized by turbulent flow and no vertical stratification (Bonetto et al., 1998; O’Farrell et al., 1996; 1998). Furthermore, while Morton’s (1977) frames were deployed covering a depth range of ca 14 m, in the present investigation the lowermost frame was only 3.7 m deeper than the uppermost frame.

Also, in Morton’s (1977) experimental design, the same framework was inspected and replaced at monthly intervals, but in the present study different frames were used each month in order to allow for total removal of the organisms, including the earliest juveniles 1-2 mm in size, thus facilitating counting and measurement.

Settlement of larvae occurred preferentially in the crevices defined by the junctions of the mutually perpendicular planes of the experimental frames (Figure 2). On the first frame retrieved mussel densities on the various planes were assessed separately in order to evaluate the settling preferences of L. fortunei. The densities on the variously oriented planes (horizontal facing up and down, and vertical) were different, but no pattern was found, for which reason subsequent counts were performed lumping all planes together.

Population parameters were calculated with the aid of the ELEFAN program (Electronic Length Frequency Analysis; Gayanilo et al., 1995), based on the modal progression analysis of the restructured length-frequency data (FR) (Sparre and Venema, 1991). The growth equation used for estimating population parameters was a seasonally oscillating version of the von Bertalanffy growth formula, the von Bertalanffy Seasonal Growth Formula (VBSGF) (Pauly, 1987)

\[ L_t = L_\infty \left[ 1 - e^{-K(t-t_0)} - (C K / 2\pi) \sin(2\pi(t-WP)) \right] \]

where \( L_t \) is the predicted length at age \( t \), \( L_\infty \) is the asymptotic length, \( K \) is a growth constant, \( C \) is the amplitude of seasonal growth oscillation, which varies between 0 and 1 (0 indicating lack of summer-winter differences in growth), WP is the winter point, which indicates the time of the year (expressed as a decimal fraction) when growth rate is lowest, and \( t_0 \) is the theoretical age of a clam at zero length if it had always grown in the manner predicted by the equation. Longevity was estimated on the basis of the maximum observed length, derived from the relative age-length relationship obtained from the analyses.
February (28 days)

May (119 days)

December (331 days)

FIGURE 2 Examples of colonization of experimental frames after 28, 119 (general view and detail) and 331 (detail only) days exposure.

RESULTS

In 1998, the surface water temperatures at the sampling site varied between 12.9°C (June) and 26.5°C (December) (Figure 3A). The period covered by the survey was characterized by a strong ENSO (El Niño Southern Oscillation) worldwide (Gershunov et al., 1999), for which reason Parana de las Palmas temperatures differed somewhat from the long-term mean. As compared with the 1979-1996 trend, in March-April 1998 values were moderately lower than usual, while in June-December they were higher. However, differences rarely exceeded 1-1.5°C, and were generally within the range for the 1979-1996 period (Figure 3A).

The numbers of individuals recorded on the experimental frames 1 to 11 months after deployment are illustrated in Figure 3B and Table 1. After 28 d exposure the frame retrieved in February hosted ca 38000 mussels m⁻²; a slightly higher density (44000 individuals m⁻²) was recorded the following month, after 56 d exposure. Both periods were characterized by >98% of early juveniles < 2 mm in length (see Figure 3C). In April through August the total densities dropped to 9000-2000 individuals m⁻², and the populations were mostly represented by older (> 2 mm) mussels. In September the total densities showed a 10-fold increase over the previous month, with early juveniles (< 2 mm) again accounting for over 95% of the mussels recorded. From October to December there were further increases in density, chiefly due to the contribution of early juveniles (> 96%).

Figure 4 shows the length-frequency distribution of mussels throughout the period surveyed, along with the growth curve of the cohort born at the beginning of 1998. (Because of their overwhelming numbers, which obscure growth trends, individuals < 2 mm are not included in the graph, and were also excluded from the data for calculating the population parameters assessed). During their first month, mussels born in January grew to ca 3 mm in length; in March they reached 7-8 mm, and by mid April 11-12 mm. In late April through July their growth rates decreased noticeably, to < 2 mm per month. During August growth stopped almost completely, and resumed again in late September. By December,
FIGURE 3  A surface water temperatures at Atucha I during the period of the survey, compared with the long-term mean for 1979–1996 (long-term mean based on daily measurements by Nucleoeléctrica Argentina S A, Atucha I). B densities of L. fortunei larvae in the plankton (line) (from Cataldo and Bolotovskoy, personal observations) and of shells on experimental frames (bars); C proportion of individuals <2 mm in length on the frames during the survey period.

FIGURE 4  Length-frequency distributions of mussels >2 mm in length collected from the experimental frames; line indicates suggested cohort growth trend.
ca 1 year-old individuals were approximately 20 mm in length (Figure 4).

Growth of an average individual from birth to maximum size is illustrated in Figure 5 (data for 2 and 3 year-old individuals are based on values estimated by the growth formula). The growth constant derived from von Bertalanffy seasonally oscillating expression is 1. As indicated by the changes in slope of the curve, summer-to-winter differences in growth rate were very large (C, or seasonal amplitude, equals 1), with the lowest growth around August (winter point = 0.6). As shown above, during the first year animals reached 20 mm in length (Figures 4, 5); by the end of the second year they were 30 mm long, and the asymptotic, or maximum theoretical length (L.), was 35 mm (Figure 5).

**DISCUSSION**

Cohort analysis, such as performed in the present survey, is a powerful technique for the interpretation of population data, although it requires reproduction events to be more or less discrete in time (e.g. Edmondson & Winberg, 1971). Continuous reproduction lacks the pulses whose identification in size-frequency analyses allows the definition of growth parameters. From this point of view, the reproduction mode of *L. fortunei* makes cohort analysis based on mature natural populations marginally suitable for interpretations of its life cycle. Indeed, as shown by the massive presence of its larvae in the plankton between August and April (Cataldo and Boltovskoy, personal observations; see Figure 3B), as well as by the overwhelming proportions of early juveniles on the experimental frames between February and April and from September to December (Figure 3C), the mussel breeds uninterruptedly for 9 months. In such cases, mature natural populations have irregular size-frequency distributions, often punctuated by several modes with little biological meaning (e.g. Villar et al., 1997).

However, sessile species with extended reproduction periods offer an alternative possibility for the analysis of their population parameters by means of cohort analyses, viz. the deployment of experimental substrata. This technique allows elimination of all size classes older than the one coeval with the time of deployment of the substrata. This defines unequivocally a zero age class whose monitoring through time, undistorted by the presence of older individuals, allows description of the growth of the species. This is why, despite the fact that *L. fortunei* has a 9-month reproduction period, the extent to which the growth curve illustrated in Figure 4 fits the corresponding length-frequency data (Rn = 0.251) is roughly similar to the fit obtained for *Corbicula fluminea* (Rn = 0.245), which has two very well circumscribed reproduction pulses per year (Cataldo & Boltovskoy, 1998). Nevertheless, continuous reproduction in *L. fortunei* shows in Figure 4, in so far as the cohort born in late 1997–early 1998 is poorly defined in May and July, and although subsequent cohorts are also suggested (e.g. at 5 mm in May, ca 8 mm in July), the pattern is not clear cut.

The present results, supported by data on larval abundances in the river water (Figure 3B), indicate that the mussel reproduces continuously between August/September and March/April.
In April/May through July/August production of larvae is negligible (Figure 3B), and the proportions of early juveniles on the frames were accordingly low (Figure 3C). The latter period is characterized by surface water temperatures 16–17°C, which seems to be a threshold value for the reproductive activity of *L. fortunei*.

Comparison of the present findings with Morton's (1977) results on the population dynamics of *L. fortunei* in Plover Cove (Hong Kong) reservoir is complicated by the fact that Morton used only one frame for each of 5 depths investigated throughout the entire experimental period. Each frame was retrieved, settled mussels were counted and measured, and the device returned to the medium. Compared with the present methodology, this technique has the advantage of ensuring that the same population is followed throughout the experiment. However, in situ measuring and counting of dense mussel colonies poses problems, which may account for the very low numbers of early juveniles (< 2 mm) in Morton's (1977) study. This information gap however, was subsequently (Morton, 1982) covered by the results of a seasonal survey of gonadal maturation and histologically inferred spawning periods in *L. fortunei*. Data from these two publications agree with the present results in that both populations are concluded to exhibit extended reproduction periods lasting ca 9 months per year, and that the spring onset of breeding is triggered by a rise in temperature above approximately 16–17°C.

However, Paraná de las Palmas populations seem to also show important differences with respect to Hong Kong populations. Morton concluded that in Plover Cove reservoir *L. fortunei* exhibited 2 to 3 spatfalls each year (Morton, 1977), and that breeding pulses roughly coincided with lowest and highest water temperatures (Morton, 1982). The proportions of early juveniles in the present study (Figure 3C), as well as the larval densities in the plankton (Figure 3B), suggest that reproduction is more or less continuous between September and March, and clear-cut pulses are absent. In addition, the present data do not show breeding peaks associated with the highest water temperatures, whereas at the lowest temperatures reproductive activity is clearly discontinued (Figure 3).

Iwasaki and Uryu (1998) studied the life cycle of a natural population of *L. fortunei* in Kyoto, Japan using cohort analysis and gonad size. Their results also point to an extended reproductive period (9 months) centered on the warmest months, although complications arising from the lack of discrete reproductive pulses, as well as the inability to retrieve the earliest recruits below 2 mm in length, obscured some of the populational interpretations offered. The relationships between reproductive activity and temperature were also unclear; the degree of gonad development suggested active breeding at least between 21 and 26°C, but although winter water temperatures at the site sampled drop to as low as 7–9°C, no temperature cutoff values were suggested.

In so far as the reproductive cycle of *L. fortunei* seems to be closely coupled with water temperature, differences between 1998 values and the long-term (1979-1996) mean suggest that during non-El Niño years a slightly different reproductive behavior may take place. Thus, lowest yearly temperatures normally occur between late May/June and August (rather than between mid May and July, as in 1998); this is probably why both cessation and onset of breeding occurred about one month earlier than usual in 1998.

As discussed above and illustrated in Figure 2, settlement of larvae occurred almost exclusively in the crevices defined by the junctions of the mutually perpendicular planes of the experimental frames, which is the result of the highly positive thigmotactic behavior of settling individuals (Morton, 1977; Uryu et al., 1996). This behavior, common in byssally attached bivalves, is thought to be effective in escaping predation and further dislodgement (e.g. Paine and Levin, 1981; Hamilton et al., 1994). In the case of *L. fortunei*, fish predation avoidance may play a major role in this settling pattern. Despite the fact that *L. fortunei*
invaded the Paraná-Río de la Plata basin only 10 years ago, for several fish species (e.g. *Pinelodus albicans*, *Pterodoras granulosus*, *Leporinus obtusidens*, *Hypostomus uruguayensis*, *Paraloricaria cf. vetula*) it already represents an important food item, in some cases accounting for 100% of their gut contents (unpublished data). Furthermore, on hard substrata, such as piers, submerged tree branches, and boulders, the mussel is only present in inaccessible crevices, where it packs densely, and is almost invariably absent on the exposed part of such substrata. On the other hand, at the nuclear power plant Atucha I, concrete walls and other structures located upstream from the grids and sieves designed to rid incoming water from larger objects, including fish, become fully covered with a thick layer of *L. fortunei* a few weeks after cleaning. These observations pose interesting questions regarding the interactions between *L. fortunei* and this newly invaded environment, and also suggest possible new strategies for its control.

Less than a decade after its introduction in the area, industrial and power plants along the lower Parana river and Río de la Plata estuary are experiencing the fouling effects of *L. fortunei*. Mechanical and chemical control measures have been attempted at several plants, yet as far as is known the chemicals used, dosages and exposure times are based on previous experience with other pest mussels, chiefly the North American zebra mussel *Dreissena polymorpha*. However, the modes of reproduction in the two species are quite dissimilar, thus requiring different treatment strategies, especially when the larvae, rather than the adults are targeted. The results of this survey may help in the elucidation of more adequate treatment protocols for minimizing the environmental impact and optimizing costs.

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