

Effect of lowered salinity on the survival, condition and reburial of *Soletellina alba* (Lamarck, 1818) (Bivalvia: Psammobiidae)

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Abstract Mass mortalities of fauna are known to occur in estuarine environments during flood events. Specific factors associated with these mortalities have rarely been examined. Therefore, the effect of exposing, to lowered salinities, an infaunal bivalve that is susceptible to mass mortalities during winter flooding in a southern Australian estuary was tested in the present study. In a laboratory experiment, low salinities (≤ 6 parts per thousand [ppt]), which mimicked those expected during flood events in the Hopkins River estuary, were shown to affect *Soletellina alba*, both lethally and sublethally. All bivalves died at 1 ppt, while those at 6 ppt took longer to burrow and exhibited a poorer condition than those at 14 and 27 ppt. The limited salinity tolerance of *S. alba* suggests that lowered salinities are a likely cause of mass mortality for this species during winter flooding.

Key words: bivalve burrowing, estuarine infauna, intermittent estuary, mass mortality, salinity tolerance.

INTRODUCTION

Dynamic salinity regimes are a characteristic feature of estuarine environments, particularly those intermittently open estuaries common to the southern coasts of Africa and Australia. Rainfall, and hence discharge patterns, can be extremely erratic in the southern hemisphere (de Villiers *et al.* 1999; Kench 1999), and flows in southern Australia are typically characterized by the alternation of summer baseline flows with winter peak flows that can cause flooding. Baseline and peak flows can differ by four orders of magnitude, which is unique to Australia and southern Africa (Kench 1999). Changes to the salinity regime are often reflected in these changes in flow. Insufficient baseline flows often promote the accumulation of sand at the estuary mouth, which can lead to extended periods of mouth closure and elevated salinities, including hypersalinity in some estuaries (Wells & Threlfall 1982; Owen & Forbes 1997a,b; Schumann & Pearce 1997; Hodgkin & Hesp 1998; de Villiers *et al.* 1999; Schumann *et al.* 1999). In contrast, peak flows or winter flooding can cause salinities to fall below 1 ppt for extended periods, depending on flow duration and magnitude (Sherwood & Rouse 1997; Matthews 2001).

Flooding has been shown to cause mass mortalities of estuarine fauna (Goodbody 1961; Stone & Reish 1965; Thomas & White 1969; McLachlan & Grindley 1974; Boesch *et al.* 1976; Stephenson *et al.* 1977; Tettelbach *et al.* 1985; Hakenom 1989; Owen &

Forbes 1997a,b). Factors such as increased turbidity or sedimentation and changes in temperature may be responsible for these mortalities, although a rapid decrease in salinity is often regarded as the most important factor. Direct tests of these hypotheses in the field have proven difficult and hence tolerance tests performed in the laboratory have been the most widely used method to infer the likely cause of mass mortality (McLachlan & Grindley 1974; Tettelbach *et al.* 1985; Hakenom 1989; Whitfield & Paterson 1995).

Mass mortalities of *Soletellina alba* (Lamarck 1818) in the Hopkins River estuary, western Victoria, Australia (140°30'S, 38°12'E) were observed during winter flooding in 1995 and 1996 (Matthews 2001). The potential causes of these mass mortality events have not been investigated. Therefore, the purpose of the present study was to examine both the lethal (as indicated by mortality) and sublethal (as indicated by the commencement of burrowing and body condition) effects of exposing *S. alba* to a range of salinity concentrations.

METHODS

Salinity profiles were measured from seven stations situated on the Hopkins Point Road bridge (approximately 500 m upstream of the estuary mouth, Matthews 2001) to illustrate how river discharge affected salinities during the flood and non-flood periods of 1996. Data for 1996 rather than later years are presented here, as there was no winter flooding during the drought of 1996–1999 (Matthews 2001).

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Measurements were taken with a Yeokal Intelligent Water Quality Analyser (model 611) at three depths corresponding to depths of water 0.14 m above, and 0.36 and 0.86 m below the Australian Height Datum (AHD). The average water height in the Hopkins River estuary recorded from 124 observations between 4 April 1996 and 13 April 1999 was 0.64 m above AHD.

Small *S. alba* (<1 mm) have been shown to exhibit a greater ability to survive during winter flooding than individuals greater than 1 mm (Matthews 2001). It was hypothesized that the small individuals had a greater tolerance to changes in the physico-chemical environment (particularly salinity) than their larger counterparts (Matthews 2001). Unfortunately, it was not possible to test this hypothesis directly during the present study because there were insufficient numbers of small bivalves available in the estuary at the time (Matthews 2001). Nonetheless, the salinity tolerance of *S. alba* of any size was yet to be investigated, so a laboratory experiment was conducted between October and November 1998 using larger bivalves with a shell length ranging from 21 to 30 mm. A description of *S. alba* found in the Hopkins River estuary is provided by Matthews (2001).

Four salinity concentrations were used during the experiment: 1, 6, 14 and 27 ppt. A salinity of 27 ppt was used as the control, as this was the salinity near the mouth of the estuary at the time when bivalves were collected for the experiment. This salinity was used to acclimate bivalves at the beginning of the experiment. During the flood years of 1995 and 1996, mass mortalities were observed in the estuary when salinities fell below 1 ppt (Rouse 1998; Matthews 2001). Therefore, the 1 ppt salinity was expected to be lethal to *S. alba*. During the non-flood years of 1997 and 1998, salinities had not fallen below 4 ppt and mortalities in the estuary were not observed during this time (Matthews 2001). Therefore, we chose two intermediate salinities greater than 4 ppt (6 and 14 ppt) for comparison, where significant lethal effects were not expected, but significant sublethal effects were possible.

All bivalves and sand used during the experiment were collected from an area of unvegetated sediment near the mouth of the Hopkins River estuary (at 0.1 m below AHD, approximately 100 m downstream of Site 1 in Matthews 2001). The experiment was conducted in a laboratory maintained at a constant temperature (12°C), under fluorescent lighting, which was set (13:11 h day : night cycle) to mimic conditions expected in the estuary during winter flooding. Jars used in the experiment were randomly arranged and moved to different positions every second day to reduce any effect of position on the experimental outcome.

Ten replicate 1-L jars were used for each salinity treatment ($n = 40$ jars, height of jar = 100 mm). One bivalve was added to each jar, which was half filled with

sand so that the bivalve had the opportunity to burrow. The remainder of the jar was filled with estuarine water and continuously aerated. For the three more saline conditions, water consisted of a mixture of water taken from the Hopkins estuary and rainwater taken from a large outdoor concrete tank. The same rainwater was used for the lowest salinity treatment (1 ppt). Each jar was sealed with a lid with a small hole to allow an air hose to pass into the jar. The lids minimized evaporation and kept salinities, measured each day with an optical refractometer (Iwaki 508-IIW), constant for the duration of the experiment.

The experiment ran for 21 days between 13 October 1998 and 3 November 1998. For the first 9 days, all 40 bivalves were held individually in jars at 27 ppt to acclimate to test conditions. At the end of this 9-day period (21 October 1998), each bivalve was forced to the top of the sand by gently swirling the jar. Mortality was recorded if bivalves were not moving and had a flaccid foot protruding from the shell. The time taken for each live bivalve to commence burrowing (as indicated by the penetration of the foot into the sand and upright positioning of the bivalve) was then recorded for each jar. Reburial time is a convenient and useful indicator of stress in bivalve molluscs (Chícharo *et al.* 2003). Once all bivalves had burrowed beneath the sand, the water was gently decanted from each jar and then replaced with the adjusted salinity treatments. Ten of the 40 jars were randomly allocated to each of the four salinity treatments. The number of dead individuals and burrowing commencement times were again recorded at 8 days (28 October 1998) and 14 days (3 November 98) after exposure to these adjusted salinity treatments. At the end of the experiment (3 November 1998), measurements of length (mm) and mass (g) for both living and dead bivalves were also recorded. These measurements were used to provide an indication of the condition of individuals (as indicated by total mass per length³). Valve measurements (mm) of entire bivalves were made between the anterior and posterior margins of the valve using digital vernier callipers (Mitutoyo, CD-8 \leq C). A digital balance (OHAUS, GT410) was used to measure the total mass (shell + tissue) of bivalves that had been dried in an oven at 60°C for 3 days.

The hypotheses for this experiment were as follows:

1. The number of mortalities for bivalves (M_n) exposed to the 1 ppt treatment would be significantly greater than for those exposed to the 6, 14 and 27 ppt treatments, but mortalities would not differ between the latter three treatments; that is, $M_n(1 \text{ ppt}) > M_n(6 \text{ ppt}) = M_n(14 \text{ ppt}) = M_n(27 \text{ ppt})$.
2. The burrowing commencement time (B_t) for bivalves exposed to the 1 ppt treatment would be significantly greater than for bivalves exposed to the 6, 14 and 27 ppt treatments, but burrowing times would not differ between the latter three

treatments unless there were sublethal effects; that is, $B_t(1 \text{ ppt}) > B_t(6 \text{ ppt}) = B_t(14 \text{ ppt}) = B_t(27 \text{ ppt})$.

3. The condition (C , as indicated by total mass per length³) of bivalves exposed to the 1 ppt treatment would be significantly poorer than that of the bivalves exposed to the 6, 14 and 27 ppt treatments, but the condition of bivalves would not differ between the latter three treatments unless there were sublethal effects; that is, $C(1 \text{ ppt}) < C(6 \text{ ppt}) = C(14 \text{ ppt}) = C(27 \text{ ppt})$.

Data analysis

Frequencies of mortality of the 10 bivalves held at each salinity were compared across treatments using a χ^2 contingency table. The burrowing commencement times were analysed using an unevenly spaced, repeated-measures ANOVA with a single grouping factor, salinity. Burrowing commencement times were recorded 9 days after they were acclimated at 27 ppt (Time 1), and then 8 days (Time 2) and 14 days (Time 3, end of experiment) after exposure to the

adjusted salinity treatments. There was 100% mortality of bivalves in the 1 ppt salinity treatment by Time 2, so the factor 'salinity' consisted of only three levels (6, 14 and 27 ppt). The factor 'salinity' was considered fixed. Tests for sphericity (F -max test) and compound symmetry (comparison of Huynh and Feldt P -values with the P -value of the F -statistic) followed Quinn and Keough (2002) and were non-significant and all data were log-transformed [$\log_{10}(x)$] to meet the normality and homogeneity of variance assumptions of ANOVA (as determined by inspecting residuals).

Measurements of bivalve condition (measured at the end of Time 3 only) were compared using a one-way ANCOVA. The factor 'salinity' consisted of four levels (1, 6, 14 and 27 ppt) and both biomass and length data were log-transformed [$\log_{10}(x)$] to meet the assumptions of ANCOVA. The log-transformed lengths were used as the covariate. All statistical analyses were conducted using version 7 of the SYSTAT software package.

RESULTS

Salinities in the estuary

Salinity profiles near the mouth of the estuary in relation to periods of high (flooding) and low (non-flooding) river discharge during 1996 are shown in Figure 1. During periods of winter flooding, river discharge was sufficient to cause salinities to fall below 2 ppt at water depths as great as 1 m, whereas sub-surface salinity approached values of seawater during periods of low flow when there was capacity for vertical stratification of the water column (Fig. 1).

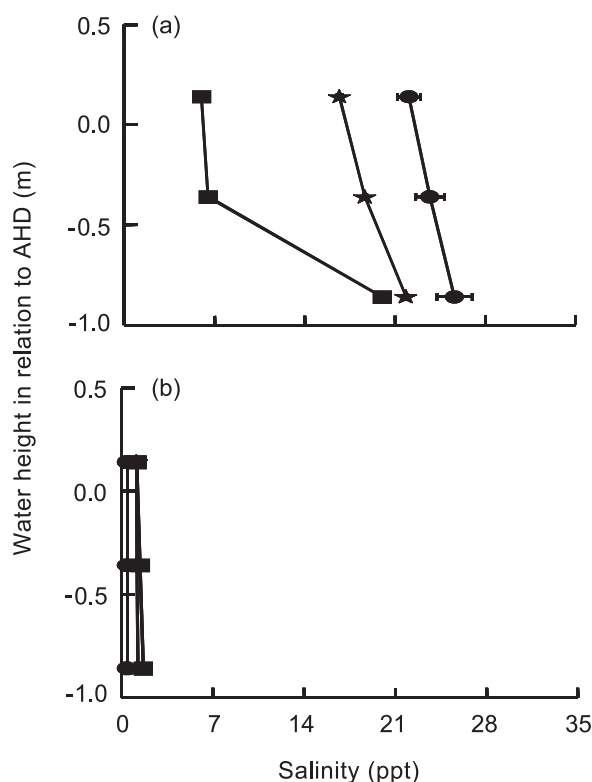


Fig. 1. Salinity profiles measured at three different times of (a) non-flood discharges (5 June 1996 (★), 29 June 1996 (●), 12 June 1996 (■)) and (b) flood discharges (18 September 1996 (★), 9 August 1996 (●), 18 September 1996 (■)) in the Hopkins River estuary. Water depths measured were 0.14 m above and 0.36 and 0.86 m below the Australian Height Datum (AHD). n ranged from 6 to 14; error bars show standard errors.

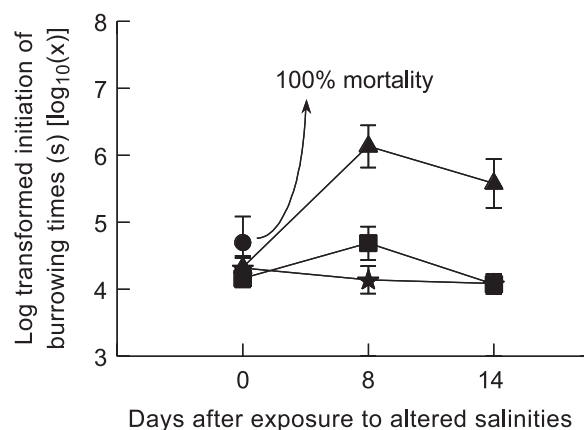


Fig. 2. Mean burrowing times for bivalves exposed to different salinities. Error bars represent \pm standard error; $n = 10$ except for the 6 ppt treatments at 8 and 14 days of exposure, where $n = 6$ (because not all animals managed to burrow). (★), 27 ppt; (■), 14 ppt; (▲), 6 ppt; (●), 1 ppt.

Lethal effects

All 10 bivalves in the 1 ppt treatment had died before the end of the first 8 days of exposure (at Time 2). In contrast, there were no mortalities observed among the 30 bivalves in the three remaining salinity treatments – a difference in frequencies that is highly significant by contingency table analysis ($\chi^2 = 40.0$, degrees of freedom (d.f.) = 3, $P < 0.01$).

Sublethal effects

The burrowing commencement times at the end of the 9-day acclimatization period (all bivalves held at 27 ppt to Time 1) were very similar for all but one of the 40 bivalves (Fig. 2). This slowest burrowing individual (an outlier as detected by SYSTAT in terms of its residual being >3 SD from the fitted values) required 2302 s to burrow, which differed greatly from the mean commencement time of the remaining 39 bivalves (mean = 80.5, SE = 7.4, range = 40–266 s). Commencement times did not differ significantly (tested via one-way ANOVA) across the four treatments at Time 1 after the 9-day acclimatization period either with ($F_{3,36} = 1.055$, $P = 0.380$) or without (d.f. = 3, $F_{3,35} = 0.701$, $P = 0.558$) the inclusion of this outlier.

After exposure to the adjusted salinities, the health and reburial of *S. alba* changed significantly at the lowest salinity treatment included in the analysis, 6 ppt (Fig. 2; Table 1). Although all bivalves survived in the 6 ppt treatment, not all managed to burrow after either 8 or 14 days (Times 2 and 3, respectively). Those that

did manage to burrow responded to the salinity treatments differently depending on the duration of the experiment (i.e. a significant time–salinity interaction; Table 1) and changes in burrowing commencement over time were best described by a curvilinear rather than a linear trend (highly significant ‘time’ and ‘time’ \times ‘salinity’ factors for the second order polynomial; Table 1). A formal multiple comparison of each treatment mean was not possible because of the unbalanced nature of these data (a result of an uneven

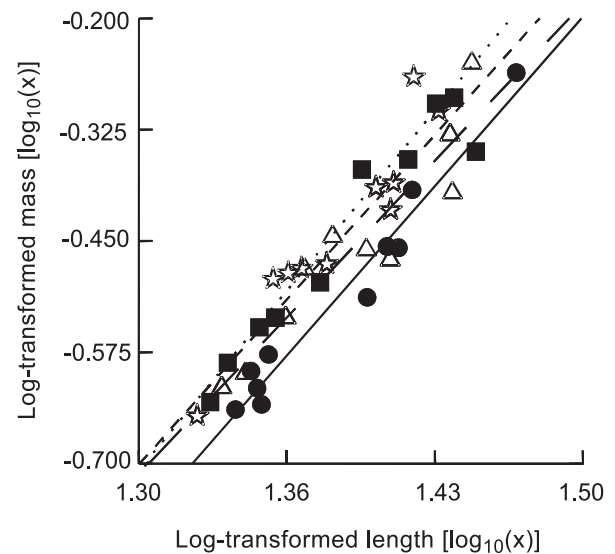


Fig. 3. Log-transformed mass (g) [$\log_{10}(x)$] plotted against log-transformed length (mm) [$\log_{10}(x)$] for bivalves measured at the end of the experiment. $n = 10$ for each treatment. (■), 27 ppt; (☆), 14 ppt; (△), 6 ppt; (●), 1 ppt.

Table 1. Repeated-measures ANOVA with one grouping factor comparing the log-transformed [$\log_{10}(x)$] commencement times of burrowing when exposed to 6, 14 and 27 parts per thousand (ppt; 1 ppt treatment excluded because of 100% mortality)[†]

Source of variation	d.f.	MS*	F	P	G-G [‡]	H-F [§]
Univariate and multivariate repeated-measures analysis						
Between subjects						
Salinity	2	1.508	19.7	0.000		
Error	23	0.076				
Within subjects						
Time	2	0.653	9.7	0.000	0.001	0.000
Time \times salinity	4	0.411	6.1	0.000	0.001	0.001
Error	46	0.067				
Single d.f. polynomial contrasts						
Polynomial test of order 1 (linear)						
Time	1	0.167	3.6	0.069		
Time \times salinity	2	0.371	8.1	0.002		
Error	23	0.046				
Polynomial test of order 2 (quadratic)						
Time	1	1.139	12.8	0.002		
Time \times salinity	2	0.451	5.1	0.015		
Error	23	0.089				

[†] $n = 10$ except for the 6 ppt treatments at 8 and 14 days of exposure, where $n = 6$ (because not all animals managed to burrow); *MS, mean square [‡]G-G epsilon = 0.7992; [§]H-F epsilon = 0.9242. d.f., degrees of freedom; G-G, Greenhouse-Geisser adjustment; H-F, Huynh and Feldt adjustment.

ability to burrow), so explanations for the significant time-salinity interaction have been interpreted from Figure 2 only. Commencement times of burrowing for all treatments were the same at Time 0, but bivalves took significantly longer to start burrowing in the 6 ppt treatment at 8 and 14 days after exposure to the adjusted salinities. These differences in the 6 ppt treatment are likely to be responsible for the significant time-salinity interaction.

The final mass of bivalves measured at the end of the experiment was related to the covariate length (Fig. 3). The condition (as indicated by total mass per length³) of *S. alba* was significantly influenced by salinity (Tables 2,3). As expected, the bivalves exposed to 1 ppt, all of which had died, showed the poorest condition. The condition of bivalves exposed to the 1 and 6 ppt treatments were significantly different from each other and from the remaining two treatments (Tables 2,3). As expected, bivalve condition was similar and greatest for the 14 and 27 ppt treatments.

DISCUSSION

Generally, the health, condition and reburial of *S. alba* changed with lowered salinity. As expected, mortalities were evident at very low salinities (1 ppt), but not at salinities ≥ 6 ppt. However, the sublethal responses of bivalves held at 6 ppt were unexpected. There were no mortalities over the experimental period at this salinity, but individuals exhibited poorer condition and those that did manage to burrow took longer to commence burrowing than those held at 14 and 27 ppt.

The reduced burrowing ability of *S. alba* at low salinities (i.e. 6 ppt) is potentially significant in terms of their ability to survive prior to being directly killed by lower salinities. For example, reduced burrowing ability might increase their susceptibility to predators, such as the teleost *Acanthopagrus butcheri* (pers. obs.), if they become exposed to the overlying water column. There

are at least three potential ways for *S. alba* to become exposed at the surface of overlying sediments during flooding: (1) by way of severe sediment scouring during floods (McLachlan & Erasmus 1974); (2) by crawling to the surface; or (3) by disturbance by bait collectors (pers. obs.). The overlying sediment has been shown to buffer infauna against physico-chemical changes that occur in the overlying water column (Sanders *et al.* 1965). Unfortunately, the salinity of interstitial waters in the Hopkins River estuary during flooding have not been measured. However, buffering from interstitial sediments is likely to be of limited importance for bivalves that filter water from the overlying water column to acquire food and/or oxygen. Dead and moribund *S. alba* have been sampled deep in the sediments during flooding (Matthews 2001), which suggests that they are probably not capable of escaping low salinities (or other flood-induced physico-chemical fluctuations) by living at increased sediment depths.

Soletellina alba might have exhibited greater tolerance to lower salinities if two alterations had been made to the experimental design. First, salinity changes used in the present study were possibly more acute and sudden than those encountered in the estuary. *Soletellina alba* might have tolerated lower salinities if salinities had been altered gradually, rather than abruptly. Salinities within the Hopkins River estuary during flooding can change by 26 ppt in 5 h (unpubl. data), although hourly samples have never been recorded during a flood, so even more sudden changes are possible. Second, many of the bivalves examined by Castagna and Chanley (1973) exhibited an increased tolerance to lower salinities if they were acclimated at intermediate salinities. Therefore, *S. alba* might have tolerated lower salinities if they had been acclimated at 14 ppt rather than in 27 ppt.

Bivalves living at shallow water depths in the Hopkins River estuary can be exposed to salinities of less than 2 ppt during flooding for extended periods much

Table 2. One-way ANCOVA comparing the log-transformed mass (g) [$\log_{10}(x)$] at the end of the salinity tolerance experiment[†]

Source of variation	d.f.	MS*	F-ratio	P
Length	1	0.460	402.2	0.000
Salinity	3	0.011	9.8	0.000
Error	35	0.001		

[†]Log-transformed length (mm) [$\log_{10}(x)$] was used as the covariate. d.f., degrees of freedom; *MS, mean square

Table 3. Grouping of least-square adjusted means of salinity treatments ranked in decreasing order of mass (g) [$\log_{10}(x)$] (Peritz multiple comparison procedure)

Salinity (ppt)	14	27		6		1
Mean	-0.430*	-0.446*	>	-0.470	>	-0.507

*Means are not significantly different; ppt, parts per thousand.

greater than the 14 days used in the present experiment. For example, salinities measured 0.14 m above AHD in the Hopkins River estuary were less than 2 ppt on eight consecutive occasions between 8 August 1996 and 25 September 1996 (approximately weekly samples; e.g. see Fig. 1). Salinities during that period were not measured daily, but the high river-discharge values (from 1100 to 13 872 ML/day) measured during this time suggest that salinities were not likely to have changed greatly within that period.

The salinity tolerance of several bivalve species from both estuarine and marine habitats in Australia and overseas are summarized in Table 4. The most extensive study of bivalve salinity tolerances, including both lethal and sublethal effects, appears to be that by Castagna and Chanley (1973). They exposed 36 species to varying salinities, so only the infaunal, estuarine bivalves used in their study are included in Table 4. Several members of the superfamily Tellino-

idea (which includes *S. alba*) – that is, *Macoma balthica*, *Macoma mitchelli*, *Macoma litoralis* and *Tagelus plebeius* – exhibited a high tolerance to low salinities (Table 4). Other than these members of the Tellinoidea, most estuarine bivalves examined thus far have a higher salinity tolerance limit (i.e. ≥ 7.5 ppt; Table 4). Five estuarine species (*Amygdalum papyria*, *Mulinia lateralis*, *Ensis directus*, *Barnea truncata* and *Cyrtopleura costata*) and one salt marsh species (*Modiolus demissus granosissimus*) that commonly occur in environments of similar or greater ranges of salinity than those in the Hopkins River estuary exhibited a higher salinity tolerance limit than *S. alba* (Table 4). *Soletellina alba* is notable in that it can tolerate lower salinities than many other related species (Table 4), but mass mortalities result because the Hopkins estuary experiences even lower salinities during floods (Fig. 1).

Shell morphology can be important for the survival of bivalves during large fluctuations in salinity. Wells

Table 4. LST limits for species from Australia versus species from overseas[†]

Species	LST (ppt)	Habitat	Country	Reference
<i>Soletellina alba</i>	6.0	Estuarine	Australia	Present study
<i>Xenostrobus securis</i>	1.5	Estuarine	Australia	Wilson (1968)
<i>Mytilus edulis planulatus</i>	15.0	Marine/estuarine	Australia	Nell and Gibbs (1986)
<i>Anadara trapezia</i>	15.0	Marine/estuarine	Australia	Nell and Gibbs (1986)
<i>Plebidonax deltooides</i>	20.0	Marine	Australia	Nell and Gibbs (1986)
<i>Ostrea angasi</i>	20.0	Marine/estuarine	Australia	Nell and Gibbs (1986)
<i>Katelysia rhytiphora</i>	20.0	Estuarine	Australia	Nell and Paterson (1997)
<i>Tapes dorsatus</i>	20.0	Estuarine	Australia	Nell and Paterson (1997)
<i>Katelysia scalarina</i>	25.0	Estuarine	Australia	Bellchambers (1998)
<i>Pecten fumatus</i>	25.0	Marine/estuarine	Australia	Nell and Gibbs (1986)
<i>Rangia cuneata</i>	0.0	Brackish/estuarine	USA	Castagna and Chanley (1973)
<i>Macoma balthica</i>	0.0–2.5	Estuarine	USA	Castagna and Chanley (1973)
<i>Macoma mitchelli</i>	0.0–2.5	Brackish/estuarine	USA	Castagna and Chanley (1973)
<i>Tagelus plebeius</i>	2.5	Estuarine	USA	Castagna and Chanley (1973)
<i>Amygdalum papyria</i>	2.5–5.0	Estuarine	USA	Castagna and Chanley (1973)
<i>Mulinia lateralis</i>	2.5–5.0	Estuarine	USA	Castagna and Chanley (1973)
<i>Cyrtopleura costata</i>	2.5–5.0	Estuarine	USA	Castagna and Chanley (1973)
<i>Modiolus demissus granosissimus</i>	3.0	Salt marsh	USA	Pierce (1970)
<i>Barnea truncata</i>	5.0–10.0	Estuarine	USA	Castagna and Chanley (1973)
<i>Macoma litoralis</i>	7.0	Estuarine	South Africa	McLachlan and Erasmus (1974)
<i>Lucina multilineata</i>	7.5	Estuarine	USA	Castagna and Chanley (1973)
<i>Laevicardium mortoni</i>	7.5	Estuarine	USA	Castagna and Chanley (1973)
<i>Gemma gemma</i>	7.5	Estuarine	USA	Castagna and Chanley (1973)
<i>Anadara transversa</i>	7.5	Estuarine	USA	Castagna and Chanley (1973)
<i>Lyonsia hyalina</i>	7.5–10.0	Estuarine	USA	Castagna and Chanley (1973)
<i>Petricola pholadiformis</i>	7.5–10.0	Estuarine	USA	Castagna and Chanley (1973)
<i>Modiolus demissus demissus</i>	8.0	Salt marsh	USA	Pierce (1970)
<i>Anadara ovalis</i>	12.5	Estuarine	USA	Castagna and Chanley (1973)
<i>Noetia ponderosa</i>	12.5	Estuarine	USA	Castagna and Chanley (1973)
<i>Ensis directus</i>	12.5	Estuarine	USA	Castagna and Chanley (1973)
<i>Solemya velum</i>	12.5	Estuarine	USA	Castagna and Chanley (1973)
<i>Solen corneus</i>	13.0	Estuarine	South Africa	McLachlan and Erasmus (1974)
<i>Solen capensis</i>	13.0	Estuarine	South Africa	McLachlan and Erasmus (1974)
<i>Dosinia hepatica</i>	14.0	Estuarine	South Africa	McLachlan and Erasmus (1974)
<i>Modiolus squamosus</i>	22.0	Marine	USA	Pierce (1970)

[†]Only data for infaunal species are presented from studies conducted outside Australia. LST, lower salinity tolerance; ppt, parts per thousand.

and Threlfall (1982) showed that the burrowing activity of *Arthritica semen* ceased at 15 ppt, whereas *S. alba* continued to rebury at 6 ppt. In contrast to *S. alba*, *A. semen* is a minute bivalve (<4 mm) with a non-gaping shell. The cessation of burrowing by *A. semen*, and hence prolonged shell closure, might enable this species to isolate its body tissue from the external environment, thereby increasing its chance of survival. For example, *Arthritica helmsi*, which is closely related and possibly conspecific (Wells 1984) to *A. semen*, exhibited a greater ability to survive than *S. alba* during flooding in the Hopkins River estuary in 1995 (Matthews 2001). Prolonged shell closure and extended periods of survival at low salinities are also exhibited by the epifaunal bivalve *Xenostrobus securis* (Wilson 1968). In addition, McLachlan and Erasmus (1974) found that bivalves with a thick, non-gaping shell exhibited a greater ability to insulate themselves against salinity and temperature changes than those with a gaping shell. The thin shell of *S. alba* gapes at both the anterior and the posterior ends. Despite this, *S. alba* exhibited a greater tolerance to low salinities than many of both the gaping and the non-gaping bivalves examined by McLachlan and Erasmus (1974) (Table 4).

Although salinity has been shown in the present study to have a significant effect on the health, condition and reburial of *S. alba*, mass mortalities of this species in the field could be exacerbated by any interaction between salinity and other factors causing stress, such as increased turbidity and river velocity. For instance, increased silt and sedimentation can smother certain bivalve species (Peterson 1985) and interfere with feeding and respiring apparatus of other invertebrate fauna (Posey 1986). *Soletellina alba* is presumably a deposit feeder (Willan 1998), and therefore, may be better able to cope with sedimentation than a filter-feeding bivalve. Similarly, increased water velocities can impede bivalve feeding (Wildish & Saulnier 1993). Unfortunately, tests of such interactions have proven difficult thus far, particularly those conducted in the field, and as a consequence remain scant in published ecological reports.

There are few ecological studies of intermittent estuaries, and hence we know very little about how organisms persist in these highly dynamic environments. To our knowledge, only three other studies have examined the salinity tolerance of bivalves in intermittent estuaries – two looked at only lethal effects of lowered salinities (Wilson 1968; McLachlan & Erasmus 1974) and the other examined only sublethal effects (Wells & Threlfall 1982). The present study contributes to our limited understanding of these highly dynamic ecosystems, especially in regard to the threat posed to bivalve populations by seasonal flooding from rains in the catchment.

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