

Appendix: Ecological performance and possible origin of a ubiquitous but under-studied gastropod

Table 1: List of published and unpublished accounts of *Batillaria australis* (hereafter *Batillaria*) and its parasites in the Swan River estuary (SR). There are only a few published accounts of *Batillaria* from Western Australia outside the Perth metropolitan area; a museum record from Albany (Cotton, 1959), which is believed to be a misidentification or a subfossil (Appleton, 1980; Kirke, 1984; Huisman et al., 2008) and a recent record from the Dampier Archipelago, which is under verification (Slack-Smith and Bryce, 2004). Note that *Batillaria* is not included in the Australian Marine Pest database on marine invaders (NIMPIS; <http://www.marinepests.gov.au/>, accessed 10 February 2010).

A: Studies emphasizing lack of <i>Batillaria</i> (or its parasites) from early surveys and geological fossil records	
Early gastropod surveys (Hedley, 1916; Reath, 1925; Thiele, 1930; Thomson, 1946).	No <i>Batillaria</i> recorded.
Fossil surveys (e.g. Kendrick, 1960; Kendrick, 1976; Kendrick, 1977).	No <i>Batillaria</i> recorded, but virtually all other native present-day gastropods in the SR have been found fossilized.
Parasites in bird (Goss, 1940)	Cormorants not infected by trematode parasite <i>Strictodora laria</i> (a common parasite in <i>Batillaria</i>)
B. Studies documenting presence of <i>Batillaria</i> in Swan River estuary and adjacent oceanic waters	
Early published record (Serventy, 1955, no data presented;	State that <i>Batillaria</i> is ‘common’ in the SR.

Kendrick, 1960, no data presented).	
Qualitative collections (Ewers, 1967c; Ewers, 1967a; Ewers, 1967b)	In depth studies from eastern Australia of fossils and parasitological and ecological aspects of <i>Batillaria</i> with emphasis on morphological differences (white bands vs. no bands on shells). Ewers include a few collections from SR and note the highly disjunct distribution but does not discuss if a possible introduction event could have happened.
Qualitative collections (Blackwell, 1969).	Qualitative collections of macrofauna from 17 sites in the SR – only found <i>Batillaria</i> at Peppermint Grove.
First report in WA from outside SR (Hodgkin, 1971)	First collections of <i>Batillaria</i> from Woodmans point, northern part of Cockburn Sound, ca. 10 km south of the SR oceanic entrance. Also include collections from SR. Hodgkin suggest a larval period of 2 week. Report densities of 2-250 ind m ⁻² amongst rocks and weeds.
Distribution map in SR (qualitative, Hughes, 1973).	<i>Batillaria</i> apparently absent from the southern part of the middle estuary (but not clear how many sites were visited and how much effort was allocated).
Qualitative observations (Chalmer et al., 1976).	State that <i>Batillaria</i> is ‘common’ in the lower SR, middle SR, and present at a single zone in the upper SR.
Quantitative survey from Pelican Rocks in SR (Wallace, 1977)	Report densities <50 ind. m ⁻² amongst below 3 m but no snails from deeper waters

<p>Quantitative surveys and parasite biology (Appleton, 1980).</p>	<p>State that <i>Batillaria</i> was found for the first time in 1954 in the SR (and WA) in a shell collection from Melville Waters – and that it did not appear regularly in shell collections until the early 1960s. Note that that parasite <i>Strictodora laria</i> is common in cormorants (were absent from cormorants in early studies, Goss 1940). Quantified <i>Batillaria</i> densities in (a) <i>Halophila</i> beds = 98.8 ind m⁻² (± 3.0 from 9 sites in middle and lower SR, total n=201), (b) deeper waters >2 m depth and below the main <i>Halophila</i> zone = 34.4 ind m⁻² (± 21.3, from 2 sites; n=14), and (c) narrow sandy intertidal zone = 7.4 ind m⁻² (± 2.6; 6 sites; n=29).</p>
<p>Parasites biology (Appleton, 1983b; Appleton, 1983a)</p>	<p>Document parasites diversity and prevalence in <i>Batillaria</i> in relation to collection sites, snail density, depth, and salinity and temperature levels. A low SR parasite diversity compared to East Australian <i>Batillaria</i> hosts was discussed in relation to low bird diversity in SR (i.e. not in relation to a possible introduction event, see Appleton, 1989).</p>
<p>Qualitative survey and genetic analysis (Kirke, 1984; Kirke et al., 1987).</p>	<p><i>Batillaria</i> found alive at 24 sites, as dead shells at 7 sites, and it was absent from 9 sites (all sites in middle and upper SR). Kirke also measured molecular diversity; all populations in the SR and Woodman point were genetically similar.</p>
<p>First published case for a human introduction (Appleton, 1989)</p>	<p>Provide a review of existing evidence for a possible introduction. Include much of the material listed in the supplementary table 3 (see below). A low parasite diversity in <i>Batillaria</i> is argued to be related to an invasion event. Appleton conclude ‘there is little doubt that <i>V. australis</i> (= <i>Batillaria</i>) was inadvertently</p>

	introduced into the Swan River estuary through human agency around 1950'. Ironically, although the purpose of the communication was to 'draw attention' to this introduction event, no other published papers or books have subsequently stated that <i>Batillaria</i> in SR is introduced with similar certainty.
Taxonomic keys (Wells and Bryce, 1986; Edgar, 2000; Wells and Bryce, 2000)	These references note the disjunct distribution (common in eastern Australia, but only from the SR and Woodman Point in WA, and state that <i>Batillaria</i> 'may' be introduced in WA.
Quantitative surveys (Kanandjembo et al., 2001; Pennifold and Davis, 2001).	Kanandjembo et al., (2001) collected grab samples from 9 sites <1 m and 9 sites >2 m, from the upper reaches of the SR (Canning and Swan river arms); 42 invertebrate species collected; <i>Batillaria</i> was ranked 21 and 23 (151 and 18 individuals counted, 0.1% and <<0.1% of assemblage) respectively. Pennifold and Davies (2001) collected cores from summer and winter at Pelican Point (middle SR). <i>Batillaria</i> was fifth most abundant species in winter but not amongst 10 most abundant species in summer. There is no mention of <i>Batillaria</i> potentially being an invader.
Review of SR ecology (Brearley, 2005)	State that <i>Batillaria</i> is common in SR, but list it as a native species.
Qualitative review of introduced species in Western Australia (Huisman et al., 2008)	List <i>Batillaria</i> as introduced, but with the caveat that 'the record as an introduced species is tentatively accepted here'.

Table 2: Evidence for the status of *Batillaria australis* (hereafter *Batillaria*) as a NIS in the Swan River estuary (SR) based on Chapman and Carlton's (1991) criteria (adapted from Freshwater et al. 2006) with addition of points 11-14.

1. <i>Appearance in local regions where not found previously.</i>	Collected for the first time in the SR and WA in 1954 (Appleton, 1980; Appleton, 1989).
2. <i>Initial expansion of local range after introduction.</i>	Observed at increasing number of sites with increasing densities, over 60 years (cf. supplementary Table 1 and the main research paper).
3. <i>Association with human mechanisms of dispersal.</i>	Sibling species known from aquaculture (Byers, 1999; Byers, 2005); a free-swimming pelagic larva (MacIntyre, 1961) can be pumped into ballast water tanks.
4. <i>Association with, or dependency on, other NIS.</i>	Sibling species associated with oysters (Byers, 1999; Byers, 2005) – and oysters have been transplanted between regions and countries for centuries (Nell, 2001; Ruesink et al., 2005).
5. <i>Prevalence on new/artificial environments.</i>	Found in multiple habitats, e.g. man-made piers, intertidal rocks, seaweed habitats, and seagrass beds (pers. obs.).
6. <i>Restricted distribution compared to native species.</i>	Native species from the SR found at other sites in WA (Chalmer et al., 1976; Kendrick, 1977; Appleton, 1980; Wells and Bryce, 2000). <i>Batillaria</i> is only found in the SR and its adjacent surroundings.
7. <i>Disjunct populations in isolated oceans.</i>	Abundant in estuaries in east-southeastern Australia (Ewers, 1967a; Ewers, 1967b). The SR population separated by >3,000 km from living or fossil populations (See maps in Ewers, 1967a;

	Ewers, 1967b; Appleton, 1989).
<i>8. Insufficient active dispersal mechanisms to account for observed distribution.</i>	Produce veliger larvae (MacIntyre, 1961), pelagic for ca. 2 weeks (Appleton, 1980); insufficient for long distance drift.
<i>9. Insufficient passive dispersal mechanisms that could account for the observed distribution.</i>	South and east flowing Leewin Current provides barrier for drift and floating debris (e.g. rafting) (Pearce, 1991).
<i>10. Exotic evolutionary origin.</i>	Endemic to Australia from Whitsunday Islands, Queensland to Victoria and Tasmania, (http://seashellsofsw.org.au/Batillariidae/) (Ewers, 1967a). Died out in South Australia in Pleistocene where fossils are encountered (Ludbrook, 1984).
<i>11. Not present in fossil record at study site.</i>	Molluscs are generally abundant in fossil deposits in the SR and WA. <i>Batillaria</i> is not found in WA deposits but is an abundant fossil in other regions where it exist today (southeast-east Australia) or where it is extinct (South Australia).
<i>12. Low molecular diversity.</i>	Low genetic diversity in the SR and Woodman Point populations. Kirke expected high variability due to the presence of strong salinity gradients as observed for other molluscs in other estuaries (Kirke, 1984; Kirke et al., 1987). Kirke interpreted the low variability as a result of high larval dispersal within SR. However, an alternative explanation is a recent arrival of a small population with a low intraspecific molecular diversity (founder effects). It should be emphasized that no comparative data exist from the east coast populations and hence the term ‘low diversity’ remain ‘relative’.

<p><i>13. Low parasite diversity.</i></p>	<p>Only 3 trematode parasites exist in SR <i>Batillaria</i> populations, compared to 8 in <i>Batillaria</i> from New South Wales (Appleton, 1983a; Appleton, 1989). Similar lowered parasite diversity has been observed in numerous introduced species and has been proposed to facilitate invasions (enemy release hypothesis, Torchin et al., 2003).</p>
<p><i>14. Sudden appearance of invader-associated diseases and parasites.</i></p>	<p>Cormorants were not infected by <i>Stictodora lari</i> parasites and humans did not develop schistosome dermatitis skin diseases (associated with avian blood-fluke <i>Austrobilharzia terrigalensis</i>) prior to the first observation of <i>Batillaria</i> in SR (both parasites are common in <i>Batillaria</i>) (Appleton and Lethbridge, 1979; Appleton, 1980; Appleton, 1989).</p>

Table 3. Calculations of possible ecosystem impacts of *Batillaria australis* in the Swan River estuary (SR); up-scaled from gastropod densities (Fig. 2), and the existence of ca. 600 ha of *Halophila* beds and 1200 ha of sand flats <2 m in the middle and lower Swan River (Hillman et al., 1995).

<i>Batillaria</i> Impact in SR	Unit size	Unit	Total SR	Unit	Formula
Shell Length	2.400	cm	87614976	m	Measured
Shell Width	1.252	cm	45716764	m	Length vs. Width
Shell Volume regression	0.689	ml	2513915	l	WW vs. Volume
Shell Surface area	4.719	cm ²	1722608	m ²	Cone: Sideline \times r \times π
Shell WW	1.240	G	4528366	Kg	Length vs. WW
Shell DW	0.980	G	3576875	Kg	WW vs. DW
Shell AFDW	0.852	G	3111243	Kg	AFDW vs. DW
Shell DW tissue	0.128	G	465632	Kg	DW – AFDW
Shell circle - drill area (see note)	1.231	cm ²	449421	m ²	Circle: $\pi \times r^2$
Drilling moving sediment	123.108	cm ³ /d	449421	m ³ /d	Observations & calculation (100 cm movement per day per snail)
Snails with <i>Stictodora lari</i>	18.8	%	3650623987	Ind	Table I: (Appleton, 1983a); infection prevalence rate of 18.5%
Snails with <i>Philopthalmus</i>	4.7	%	675365438	Ind	Table I: (Appleton, 1983a); infection prevalence rate of 4.7%

<i>burrili</i>					
Snails with <i>Austroilharzia terrigalensis</i>	1.8	%	171579327	Ind	Table I: (Appleton, 1983a); infection prevalence rate of 4.7%
Faeces production	0.00638	g/d	23282	kg/d	Fig. 3: (Kamimura and Tsuchiya, 2006); 50 mg faeces/day/g DW snail tissue
Nitrogen production in faeces	1.275E ⁻⁵	g/d	2.33	kg/d	Fig. 3: (Kamimura and Tsuchiya, 2006); 0.1 mg N/day/g DW faeces
Water clearance	892.84	ml/d	3259421663	l/d	Table 1: (Kamimura and Tsuchiya, 2006); 7 l/d/gDW snail tissue

Note: Shell length (mmL) was measured on a random sample to calculate average snail size. Snail length (mmL), width (at the widest part, mmW), wet weight (gWW), wet volume (mlWV), dry weight (gDW), and ash free dry weight (ADW) were measured on a sample covering a range of snail sizes, to provide conversions formulas between size-metrics. The average length of *B. australis* was 24.02 mm (± 0.02 , n = 689). Strong correlations were observed between all morphometrics; (1) length vs. width: $\text{mmW} = 0.408 \times \text{mmL} + 0.2731$, $R^2 = 0.844$, n = 98; (2) length vs. weight wet: $\text{gWW} = 0.0002 \times \text{mmL}^{2.7478}$, $R^2 = 0.962$, n = 100; (3) wet vs. dry weight; $\text{gDW} = 0.8027 \times \text{gWW} - 0.0159$, $R^2 = 0.9651$, n = 98; (4) wet weight vs. wet volume: $\text{mlWV} = 0.5828 \times \text{gWW} - 0.0343$, $R^2 = 0.9552$, n = 26; and (5) dry weight v. ash-free dry weight: $\text{gAFDW} = 0.844 \times \text{gDW} + 0.0253$, $R^2 = 0.9656$, n = 31. The ‘drilling’ replacement of sediment was calculated based for a single snail as its average traveled distance per day (in m, based on simple tagging data) multiplied with its moving frontal surface area (in m²). This volume provides a rough estimate of sediments that has to be displaced in the crawling/burying moving process. We finally add this displaced sediment volume by the estimated total snail population size in SR.

References

- Appleton, C.C., 1980. Studies on the ecology of *Austroilharzia trigonatus*. Phd thesis Murdoch University, Western Australia, Perth, Australia, 185 pp.
- Appleton, C.C. 1983a. Studies on *Austroilharzia terrigalensis* (Trematoda: Schistosomatidae) in the Swan Estuary, Western Australia: frequency of infection in the intermediate host population. *International Journal of Parasitology* 13, 51–60.
- Appleton, C.C. 1983b. Studies on *Austroilharzia terrigalensis* (Trematoda: Schistosomatidae) in the Swan Estuary, Western Australia: observations on the biology of the cercariae. *International Journal of Parasitology* 13, 239–247.
- Appleton, C.C. 1989. Translocation of an estuarine whelk and its trematode parasites in Australia. *Environmental Conservation* 16, 172-174.
- Appleton, C.C., Lethbridge, R.C. 1979. Schistosome dermatitis in the Swan Estuary, Western Australia. *Medical Journal of Australia* 10, 141-145.
- Blackwell, J., 1969. A study of macrofauna of the Swan River estuary. MSc. Thesis, University of Western Australia, Perth, Australia.
- Brearley, A., 2005. Ernest Hodgkin's Swanland. Estuaries and coastal lagoons in South Western Australia. University of Western Australia Press, Perth, Australia, 550 pp.
- Byers, J., 2005. Quantifying geographic variation in physiological performance to address the absence of invading species. *Ecoscience* 12, 358-365.
- Byers, J.E., 1999. The distribution of an introduced mollusc and its role in the long-term demise of a native confamilial species. *Biological Invasions* 1, 339-352.
- Chalmer, P.N., Hodgkin, E.P., Kendrick, G.W. 1976. Benthic faunal changes in a seasonal estuary of south western Australia. *Records of the Western Australian Museum* 4, 383-410.
- Chapman, J.W., Carlton, J.T. 1991. A test of criteria for introduced species: the global invasion by the isopod *Synidotea laevidorsalis* (Miers, 1881). *Journal of Crustacean Biology* 11, 386-400.
- Cotton, B.C., 1959. South Australian Mollusca I: Archaeogastropa. Government Printer, Adelaide, Australia

- Edgar, G.J., 2000. Australian marine life - the plants and animals of temperate waters. New Holland Publishers. 544 pp.
- Ewers, W.H., 1967a. The distribution of *Velacumantus australis* (Gastropoda: Potamididae). Australian Journal of Zoology 15, 581-591.
- Ewers, W.H., 1967b. Geographic variation in the snail *Velacumantus australis* (Gastropoda: Potamididae). Australian Journal of Zoology 15, 1163-1171.
- Ewers, W.H. 1967c. Selection pressures and polymorphism in *Velacumantus australis* (Quoy & Gaimard). Australian Journal of Zoology 15, 727-738.
- Freshwater, D.W., Montgomery, F., Greene, J.K., Hamner, R.M., Williams, M., Whitfield, P.E., 2006. Distribution and identification of an invasive *Gracilaria* species that is hampering commercial fishing operations in southeastern North Carolina, USA. Biological Invasions 8, 631-637.
- Goss, O.M., 1940. Platyhelminth and acanthocephalan parasites of local shags. Journal and Proceedings of the Royal Society of Western Australia 26, 1-13.
- Hedley, C., 1916. A preliminary index of the mollusca of Western Australia. Journal Royal Society of Western Australia 1, 152-233.
- Hillman, K., McComb, A.J., Walker, D.I., 1995. The distribution, biomass and primary production of the seagrass *Halophila ovalis* in the Swan/Canning estuary. Aquatic Botany 51, 1-54.
- Hodgkin, E.P., 1971. Report on investigations into populations of *Velacumantus australis* in the Swan estuary (1969-1970). Department of Zoology, University of Western Australia, Australia, 8 pp.
- Hughes, J., 1973. The response of two estuarine molluscs (*Velacumantus australis* and *Notospisula trigonella*) to seasonal hydrological change. Honors Thesis, Zoology Department, the University of Western Australia, Australia, 74 pp.
- Huisman, J.M., Jones, D.S., Wells, F.E., Burton, T., 2008. Introduced marine biota in Western Australian waters. Records of the Western Australian Museum 25, 1-44.

- Kamimura, S., Tsuchiya, M. 2006. Effects of opportunistic feeding by the intertidal gastropod *Batillaria zonalis* and *B. flectosiphonata* on material flux on a tidal flat. *Marine Ecology Progress Series* 318, 203-211.
- Kanandjembo, A.N., Platell, M.E., Potter, I.C., 2001. The benthic macroinvertebrate community of the upper reaches of an Australian estuary that undergoes marked seasonal changes in hydrology. *Hydrological Processes* 15, 2481-2501.
- Kendrick, G.W., 1960. The fossil mollusca of the Peppermint Grove limestone, Swan River district of Western Australia. *Western Australia Naturalist* 7, 53-66.
- Kendrick, G.W., 1976. The Avon: Faunal and other notes on a dying river in south-western Australia. *Western Australian Naturalist* 13, 97-114.
- Kendrick, G.W., 1977. Middle Holocene marine molluscs from near Guildford, Western Australia, and evidence for climatic change. *Journal of Royal Society of Western Australia* 59, 97-104.
- Kirke, A.B., 1984. Population genetic structure of *Velacumantus australis* in a seasonal estuary. B.Sc. Hon. thesis. University of Western Australia, Perth, Australia: 77 pp.
- Kirke, A.B., Knott, B., Burke, C., 1987. A population genetic study of a gastropod from the Swan river in relation to seasonal environmental variation. *The Swan River estuary, Ecology and Management*, Curtin University, Environmental Studies Group Report No. 1, 127-140.
- Ludbrook NH (1984) Quaternary molluscs of South Australia. Handbook 9. Department of Mines and Energy, South Australia: Adelaide
- MacIntyre, R.J., 1961. Larval development of *Velacumantus australis*. *Proceedings Linnaean Society of New South Wales* 86, 183-184.
- Nell, J.A., 2001. The history of oyster farming in Australia. *Marine Fisheries Review* 63, 14-25.
- Pearce, A.F., 1991. Eastern boundary currents of the southern hemisphere. *Journal of the Royal Society of Western Australia* 74, 35-45.
- Penniford, M., Davis, J. 2001. Macrofauna and nutrient cycling in the Swan River Estuary, Western Australia: experimental results. *Hydrological Processes* 15, 2537-2553.
- Reath, J.L., 1925. The mollusca from the sub-recent shell beds of the lower Swan River. *Journal Royal Society of Western Australia* 11, 31-41.

- Ruesink, J., Lenihan, H.S., Trimble, A., Heiman, K., Micheli, F., Byers, J., Kay, M.C., 2005. Introduction of non-native oysters: ecosystem effects and restoration implications. *Annual Review of Ecology, Evolution, and Systematics* 36, 643-689.
- Serventy, D.L., 1955. The fauna of the Swan river estuary. Chapter 10. In Swan River Reference Committee: Report on pollution of the Swan River. Perth: Government Print 70-77.
- Slack-Smith, M.S., Bryce, C.W., 2004. A survey of the benthic molluscs of the Dampier Archipelago, Western Australia. *Records of the Western Australian Museum Supplement* 66, 221–245.
- Thiele, J., 1930. Die Fauna Sudwest-Australiens. Bd. 5, lief. 8. Gastropoda und Bivalvia.
- Thomson, J.M., 1946. The fauna of the algal zone of the Swan River estuary. A preliminary survey of Freshwater Bay with notes on chief species. *Journal of Proceedings of Royal Society of Western Australia* 30, 55-73.
- Torchin, M.E., Lafferty, K.D., Dobson, A., McKenzie, V., Kuris, A., 2003. Introduced species and their missing parasites. *Nature* 421, 628-630.
- Wallace, J., 1977. The macrobenthic invertebrate fauna of Pelican Rocks. Report to the Department of Conservation and Environment and Public Works Department, Perth, Australia.
- Wells, F.E., Bryce, C.W., 1986. *Seashells of Western Australia*. Western Australia Museum, Perth, Australia, 207 pp.
- Wells, F.E., Bryce, C.W., 2000. *Seashells of Western Australia*. 2nd edition, Western Australia Museum, Perth, Australia, 208 pp.