



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

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ABSTRACT

Invasions by non-indigenous species (NIS) have been suggested to alter local, regional and global biota on unprecedented scales. To manage NIS, it is pivotal to identify whether a species is introduced or native, but even today the geographical origin of thousands of species worldwide remain uncertain. Most of these 'cryptogenic species' are inconspicuous and rare, but in a few instances, they can also be abundant and conspicuous species, with large impacts on community structure. The identification of cryptogenic species, and summarizing information on their most likely origin, is an important task in invasion biology, and can highlight the need for research and management. Here, we document that the gastropod *Batillaria australis* in the Swan River estuary (Perth, Western Australia) is a conspicuous species of uncertain origin. A literature review combined with new survey data revealed that all evidence point to a recent human-mediated transfer; for example, it is absent from the fossil record, was first collected in 1954, has a low parasite diversity, has increased its population size dramatically in recent times, is separated by >3000 km from conspecifics, has no long-distance dispersal mechanisms, and existing ocean currents run against a natural range extension. Surprisingly, despite political and scientific focus on NIS hardly any ecological data have been published on this species from Western Australia. We show that *B. australis* is highly abundant in both seagrass beds (424 ± 29 ind m^{-2}) and on unvegetated sand flats (92 ± 22 ind m^{-2}) being orders of magnitudes more abundant than any native gastropod in the Swan River. Experiments showed that high resistance to predation and environmental stress potentially explains its success. From our survey data, we calculated that >3.6 billion invasive snails today occupy the Swan River. This large snail populations support other organisms; for example, almost 1 billion macroalgae are found attached to living *B. australis* and >100 million hermit crabs occupy its empty shells. Given *Battilaria's* high abundance, wide distribution, large size, persistent shells that support other organisms and bioturbating behavior, it seems inescapable that this potential invader has impacted the ecosystem functioning of the Swan River. We argue that the search for abundant species of uncertain origin should continue, and that these species generally should be treated with the same interest as high status invaders to mitigate impacts in already invaded systems and to avoid secondary spread into neighboring ecosystems.

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1. Introduction

Invasions by non-indigenous species (NIS) are considered a serious global conservation problem, as successful NIS may compete with and consume native species, alter local biotic

communities and ecosystem properties, and homogenize regional and global biotas (Parker et al., 1999). To understand, manage and mitigate effects of NIS invasions, it is of fundamental importance to first identify whether species are introduced or native. However, this is not always a straightforward task because humans transported organisms within and between the world's major biogeographical regions long before taxonomic surveys and monitoring programs became everyday practices. In addition, a large number of species are difficult to identify and have ambiguous taxonomies. Currently, thousands of such 'cryptogenic' species, i.e. species of

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uncertain geographical origin, exist in terrestrial, freshwater and marine ecosystems (Carlton, 1996). A comprehensive understanding of basic questions about vector ecology, and what characterizes system invasibility and superior invasion traits, requires recognition of both the well-known and cryptogenic invaders. For example, if many cryptogenic species indeed are NIS, then the total impact of NIS in structuring natural ecosystems may be vastly under-estimated. Moreover, from a conservation perspective, recognition of cryptogenic species as likely NIS can help managers to mitigate impacts of early-stage invasions and stimulate programs to reduce secondary dispersal to non-invaded neighboring ecosystems, i.e. promote pro-active management.

Most cryptogenic species are inconspicuous and rare, and are typically not detected in standard sampling programs (Carlton, 1996; Hewitt et al., 2004). However, occasionally species of uncertain origin can be conspicuous, abundant, and control community structure and ecosystem functioning. There are two primary reasons why the cryptogenic status of conspicuous species may remain unresolved: (1) the species was introduced centuries ago, prior to scientific recording and species descriptions; or (2) the species has invaded a region where a morphologically similar species exists, making recognition as a novel species in the region challenging. Examples of the first reason include the common periwinkle snail (*Littorina littorea*) and the soft shell clam (*Mya arenaria*) both species were likely introduced to North America and Europe, respectively, by early transatlantic voyagers (Blakeslee et al., 2008; Chapman et al., 2008; Thomsen et al., 2008). Examples of the second reason include the common reed (*Phragmites australis*) (intraspecific genotype, Saltonstall, 2002), green crabs (*Carcinus* spp.) (Geller et al., 2003), the common carp (*Cyprinus carpio*) (Mabuchi et al., 2008), and Japanese Gracilaria seaweed (*Gracilaria vermiculophylla*) (Thomsen et al., 2006) – all of which, for some time, were mistakenly classified as their morphologically similar native congeners. In contrast, with the political and scientific focus on invasive species, we would not expect that recent introductions of conspicuous invaders that do not resemble native species, into intensively researched ecosystems, could go unnoticed and unstudied. Nevertheless, in the present paper, we provide such an example.

Australia is a continent where scientific, political, public and management interest in NIS and cryptogenic species have existed for decades (Groves and Burdon, 1986). This awareness is partly a reflection of a long biogeographical isolation (susceptible to invasions), high degree of endemism (importance of preservation) and known record of invaders that has transformed landscapes (Groves and Burdon, 1986; Low, 2001). The capital of Western Australia, Perth, is located on the Swan River estuary (hereafter the Swan River). European colonization of Perth, and subsequently Western Australia, originated from this estuary less than 200 years ago. Today, it is the most utilized and intensively managed estuary in the state (Brearley, 2005). The location of four universities, the Commonwealth Scientific and Industrial Research Organization (CSIRO), the Department of Conservation, and several environmental consultancies in close proximity to the Swan River, has resulted in a wealth of scientific publications and technical reports about the natural history of the estuary (reviewed in Brearley, 2005).

Huisman et al. (2008) recently listed >30 NIS in the Swan River and adjacent oceanic waters, but in spite of species invasions being a highly ranked research and management priority, only three published accounts exist that address the invasion ecology in the Swan River: two brief descriptions on the rare Asian date mussel *Musculista senhousia* (Slack-Smith and Brearley, 1987; McDonald and Wells, in press) and a short communication on the mudsnail *Batillaria australis* Quoy (former *Velacumantis australis*, hereafter *Batillaria*) (Appleton, 1989). Even though Appleton advocated convincingly for a human-mediated introduction, his conclusion

has not been embraced by contemporary scientists and managers. For example, a comprehensive review of the natural history of the Swan River described *Batillaria* as a native species (Brearley, 2005) and publications on the invasion ecology of a sibling species (*Batillaria attramentosa*), makes no references to the Swan River case (e.g. Byers, 2000; Byers, 2005; Wonham et al., 2005). Similarly, although *Batillaria* studies from the Australian east coast, and parasite studies from the Swan River, recognized an isolated population in Perth, these papers did not discuss this distribution anomaly in an invasion context (Ewers, 1964, 1966, 1967a,b,c; Ewers and Rose, 1966; Appleton, 1983a,b). Finally, taxonomic keys and reviews specifically emphasize that *Batillaria* has an uncertain (not definitive) origin stating that *Batillaria* 'may be' or is only 'tentatively' included as a NIS (Wells and Bryce, 1986, 2000; Edgar, 2000; Huisman et al., 2008). In summary, despite Appleton's publication two decades ago, there appear to be limited, if any, consensus that *Batillaria* is an important invasive NIS in the Swan River. In eastern Australia, *Batillaria* is reported to be a dominant gastropod in saline lakes and estuaries, particularly in seagrass beds, and with a wide tolerance to salinity and temperature fluctuations (e.g. Ewers, 1965, 1966, 1967a,b,c; Ewers and Rose, 1966), but no detailed ecological data has been published on this species from Western Australia (but see Appleton, 1983a,b, 1989 for details on parasite infestations).

Here we combine a review of published and unpublished sources with surveys, experiments, and estimations of possible ecosystem impacts, to address research gaps on the Swan River *Batillaria* populations. Based on preliminary observations from casual dives in the Swan River, and established distribution records of living and fossil records of this species, we hypothesize that *Batillaria* (a) is most likely an introduced species from eastern Australia, (b) has increased its population size in recent times, (c) is today the most abundant snail in the Swan River, and (d) is resistant to environmental stress and native predators.

2. Methods

2.1. Past and present day abundances

Peer-reviewed biological and geological literature, unpublished management reports and environmental assessment reports, student theses, and various types of early accounts of gastropod distributions, were located and reviewed to evaluate the possible origin and past distribution and abundance of *Batillaria* in Western Australia. One unpublished study reported mean *Batillaria* densities from nine *Halophila* seagrass beds in the lower and middle Swan River (Appleton, 1980), and these data were extracted for statistical comparison to a contemporary survey. We conducted a snail survey (1) to quantify present day abundances in both seagrass beds and on interspersed sand flats, (2) to test if *Batillaria* is more abundant than native snails, (3) to compare with the older *Halophila* survey data, and (4) to upscale snail specific impact-traits to possible Swan River ecosystem impacts. We selected 10 sites at 0.5–2 m depth covering the middle and lower Swan River estuary, thereby being representative for the ca. 30 km² main and lower estuary (our sites were generally similar to Appleton's, although he only reported broad sample locations, Fig. 1; Robson et al., 2008). Sites were systematically spread out in the main portions of the estuary where seagrasses exist to represent possible environmental gradients along north-south and east-west axes (upper river arms were excluded since snails and seagrasses are absent due to high turbidity and low salinity). At each site, 8 samples were collected haphazardly, 4 from sand flats and 4 from *Halophila* seagrass beds (the boat was anchored haphazardly, and divers swam 10–20 m with eyes closed before putting down the sampling device). All

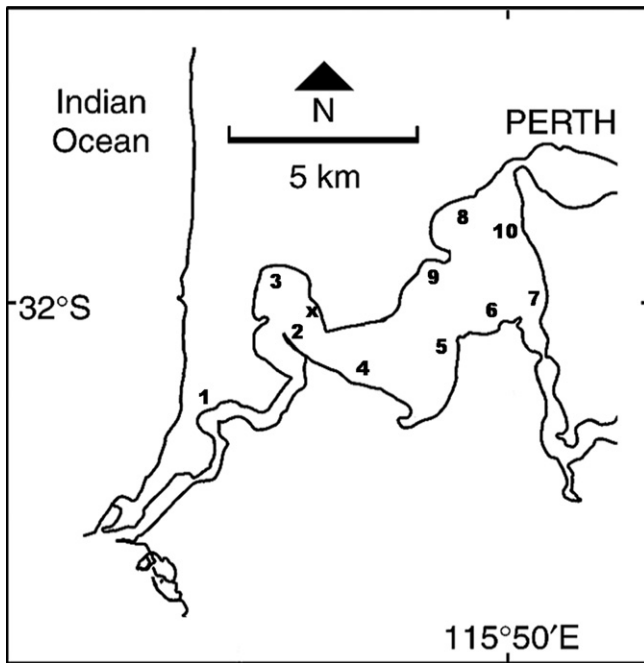


Fig. 1. Macroscopic gastropod survey sites in the Swan River Estuary, Perth, Western Australia. 1 = Rocky Bay, 2 = Armstrong Spit, 3 = Freshwater Bay, 4 = Attadale, 5 = Lucky Bay, 6 = Heathcote, 7 = Como south, 8 = Matilda Bay, 9 = Pelican Point, 10 = Como North, x = Point Resolution (*Batillaria australis* predation experiments).

macroscopic gastropods (>2–3 mm) were identified and counted *in situ*. In the seagrass beds, where preliminary observations had indicated higher snail densities than adjacent sand flats, snails were counted within a 33 cm inner diameter circular frame (0.085 m²), whereas less dense sand flats were surveyed using 2.5 m × 0.5 m belt transect (1.25 m²). Snails were collected by carefully filtering through the top 5 cm sediment/seagrass bed by hand and returned unharmed after counting. We also counted the number of empty shells, their occupancy by hermit crabs, and dead and live snail shells with two size groups of visible macroalgae attached (shells with single holdfast and 2–10 mm fragments vs. shells with dense aggregations of holdfast with larger fronds >10 mm).

2.2. Ecological performance

Several experiments were conducted to quantify the susceptibility of *Batillaria* to predation and environmental stress, and quantify links between attached macroalgae (mainly *Gracilaria comosa*) attached to snails and the production of unattached algal fragments. First, a tethering experiment was conducted to quantify field predation rates. A 50 cm tether of fishing line was tied around the shell of individual adult *Batillaria* and attached to a peg. Pegs were added to both sand flats ($n = 20$) and seagrass patches ($n = 20$). The experiment was set up at Point Resolution (Fig. 1) twice (25 April 2007 and 4 January 2008) and run for 30 and 14 days, respectively.

Second, short-term field predation experiments were conducted to test if the ubiquitous and voracious blowfish (*Torquigener pleurogramma*) could prey on *Batillaria*. Experiments were again conducted at Point Resolution twice (8 May 2007 and 17 January 2008) in the morning and repeated at mid-day. Each time, 10 *Batillaria* (2–4 cm total length) and 10 *Soletellina biradiata* (a common native bivalve, also 2–4 cm total length) were collected. The sediment was stirred to attract fish (there was always a minimum of 15 blowfish in close proximity to the experimenter)

and molluscs released one by one 50 cm above the sediment surface. The fate of each mollusc was followed until it was either eaten or the fish stopped biting it (typically <30 s, the fate of each mollusc was easily classified as either completely consumed or entirely unharmed).

Third, a laboratory experiment tested if the common oyster drill (*Bediva paivae*) could prey on *Batillaria*. One oyster drill and two *Batillaria* were added to 250 mL plastic containers ($n = 8$, and 8 controls containing only *Batillaria*). Snails and water was collected from Point Resolution, and were kept in 12:12 LD and at 19 °C. The experiment was initiated on 12 June 2007 and run for 10 days. Water was exchanged every two days.

Fourth, a laboratory experiment tested the resistance of *Batillaria* to salinity stress, using three constant salinity levels (9, 18 and 36 psu, oceanic seawater was diluted with freshwater), using similar plastic containers and laboratory conditions as outlined above (but only 1 snail per container and 16 containers per treatment). The experiment was initiated on 13 June 2007 and run for 14 days.

Finally, an outdoor experiment (conducted under shade) examined if *Batillaria* can survive fluctuations in salinity and temperature and also quantified links between the macroalgae *G. comosa* attached to snails and the production of unattached algal fragments. The experimental design and snail containers were generally similar to the previous experiment, except only salinities 18 and 36 psu were tested (as we noted only little snail activity at 9 psu in experiment four). For this experiment, snails were selected that either had a high (>10 holdfasts) or low (<5 holdfasts) density of attached *Gracilaria*. We pruned the high density algae down to 25 mm length and the low density algae to 5 mm to provide contrasting, but standardized characteristics of attached algae, representing a high vs. low 'abundance' (corresponding roughly to the algal size classes distinguished in the survey). The experiment was initiated on 9 May 2007 and run for 47 days, where fragment production (unattached algal fragments >2 mm) was quantified from 9 to 19 July. Water was exchanged weekly to allow salinity to rise due to evaporation. A 30% reduction in water volume per week was observed, corresponding to a 30% increase in salinity. Water temperature fluctuated diurnally from 10 °C on cold nights to 30 °C during hot days. It should be noted that, in this experiment, we lacked control over salinity and temperature conditions and that the stress factors co-vary, but we argue that these fluctuating environmental conditions are realistic, and that surviving snails and attached seaweeds provide testimonies to their stress resistance.

For each of the experiments, the response variable was snail survival that was verified by inspecting the snail carefully to observe foot movements. For the last experiment we also calculated seaweed fragmentation rates, i.e. how many new fragments were produced in the four treatment combinations (2 salinity levels × 2 attached seaweed densities) over 10 days.

2.3. Statistical analysis and impact calculations

We used ANOVA on site-specific mean *Batillaria* densities, to test if present day abundances were different from abundances reported by Appleton (1980). ANOVA was also used to test if more seaweed fragments were produced on snails with high *G. comosa* densities compared to low densities, and if fragmentation depended on salinity levels. We did not test if *Batillaria* is more abundant than native snails because these results were self-evident (*Batillaria* was orders of magnitude more abundant than any native snails). Similarly, we did not apply χ^2 tests to survival rates from performance experiments because all snails survived in all experiments.

Parker et al.'s (1999) invasion impact formula was used to provide ball-park estimations on possible ecosystem impacts from *Batillaria* in the Swan River. This formula assume that the total

ecosystem impact is proportional to the average invader density (ind m⁻²), its range (total area in the Swan River where *Batillaria* exist), and its specific *per capita* effect (what do a single invader do over a given period of time). We combined survey data with morphological measurements and literature values of metabolic rates measured on congeneric sibling species to obtain the necessary data. These calculations were done to estimate the possible range and magnitude of effects of *Batillaria* in the lower and middle reaches of the Swan River where it (and *Halophila* seagrass) is abundant. These estimates should only be interpreted as explorative and hypothesis-generating. Several morphological snail traits were quantified. First, the shell length was measured on a random subset of snails collected in the survey to calculate average snail size ($n = 689$). Second, snail length ($n = 100$), width (at the widest axis, $n = 98$), wet weight ($n = 100$), wet volume ($n = 26$), dry weight ($n = 99$), and ash free dry weight ($n = 31$) were measured on a sample covering a range of snail sizes to provide conversion formulas between size-metrics. The surface area for an averaged sized *Batillaria* snail was calculated from length and width data applied to the geometric formula for a cone. We calculated an average frontal 'drill-area' (the area a snail touch when it moves through a perpendicular plane) using half the maximum shell width (=radius) applied to the formula for a circle. This drill-area was combined with preliminary tagging observations suggesting that snails can move 100 cm in 24 h, to calculate the volume of sediment that is touched, encountered and possibly also displaced during crawling and burying by an average snail.

We estimated the total standing populations of live and dead (empty shells) *Batillaria*, with and without attached seaweed, and hermit crabs (living in *Batillaria* shells) by multiplying the survey data with the total seagrass and sand flat areas existing in the middle and lower Swan River (ca. 600 ha seagrass bed and 1200 ha sand flats shallower than 2 m, Hilman, 1987). A system wide daily summer seaweed fragmentation (associated with live *Batillaria*), was calculated by multiplying the standing stock of snails with attached *G. comosa* times the fraction containing large and dense seaweed aggregations times the fragmentation rates (obtained from the outdoor performance experiment, assuming a linear production = 0.87 fragments produced per snail per day in the high-density treatment). The total standing stock of snails infested with individual parasite species were calculated based on known prevalence infection rates (Appleton, 1983a). We finally calculated system wide snail-associated fecal production, nitrogen production in feces and water clearance rates, by multiplying metabolic rates measured on morphologically similar sibling species, *Batillaria zonalis* and *Batillaria flectosiphonata*, from Japan (50 mg feces/day/g DW snail tissue; 0.1 mg N/day/g DW feces; 7 l/d/g DW snail tissue, see also Appendix, Table 3) times the estimated total dry weight of snails in the Swan River.

3. Results

3.1. Past and present day abundances

Early gastropod surveys from Western Australia did not report a presence of *Batillaria* and it has never been found in fossil deposits (Appendix, Table 1), even though it builds erosion-resistant shells and is very common in fossil shell deposits from sites in east Australia where it is also abundant today (Ewers, 1966, 1967b,c). The first observation in the Swan River was apparently in 1954 (Appleton, 1989) and the first record published one year later stated *Batillaria* to be 'common' (Appendix, Table 1). Appleton (1989) also noted that *Batillaria* did not appear regularly in shell collections until the early 1960s. Today, the only other observations in Western Australia, outside the Perth metropolitan area (i.e. including

Woodmans point, northern part of Cockburn Sound, ca. 10 km south of the entrance to Swan River), is a single museum record from Albany, a coastal distance of ca. 700 km to the south and east, later determined to be a subfossil (Huisman et al., 2008), and a recent record from the Dampier Archipelago >1300 km to the north, which needs to be verified (Slack-Smith and Bryce, 2004). In the late 1970s, high densities were typically found in *Halophila* seagrass beds in the Swan River, intermediate to low densities in deeper waters below the main *Halophila* zone, and low densities in a narrow sandy intertidal zone (Appendix, Table 1).

In our 2006 survey, only four species accounted for >99% of all gastropods recorded; *Batillaria*, *Nassarius pauperatus* and *Nassarius burchardi* (hereafter combined to *Nassarius* spp.) and *B. paivae*. *Batillaria* and *B. paivae* are of similar size, whereas *Nassarius* spp. are much smaller (<10 mm). *Batillaria* was found in all 80 samples, and was orders of magnitude more abundant than *Nassarius* spp. and *B. paivae* in both sand flats and seagrass patches (Fig. 2), with mean densities of 92 ind m⁻² (range 0.8–605) and 424 ind m⁻² (93.6–865.6), respectively. Densities in seagrass beds in 2006 were >4 times greater and significantly different from 1978 densities (mean density 1978 ± SE = 98.8 ± 3.0; $p < 0.001$, $F_{1,17} = 34.705$, Levin's p for test of variance homogeneity = 0.297, Appendix, Table 1). We found many more live *Batillaria* than 'dead' (empty or hermit crab occupied *Batillaria* shells) in both seagrass patches and on sand flats (Fig. 2). Most empty shells were intact, but some (<20%) had holes and showed signs of drilling, crushing or clipping predators. Hermit crabs were found in 49% of the dead *Batillaria* shells on seagrass patches and 16% on sand flats. Attached macroalgae (both size classes combined) were found on 32% and 26% of live and dead *Batillaria* shells, respectively, in the seagrass patches, and on 24% and 14%, respectively, on the sand flats. Finally, 5.6% of live *Batillaria* with attached *G. comosa* were classified as 'large and dense' seaweed aggregations (i.e. with many *G. comosa* holdfasts and fronds being > 10 mm).

3.2. Ecological performance

No *Batillaria* snail died in any of the predation experiments, as verified by snail movements after termination of the experiments

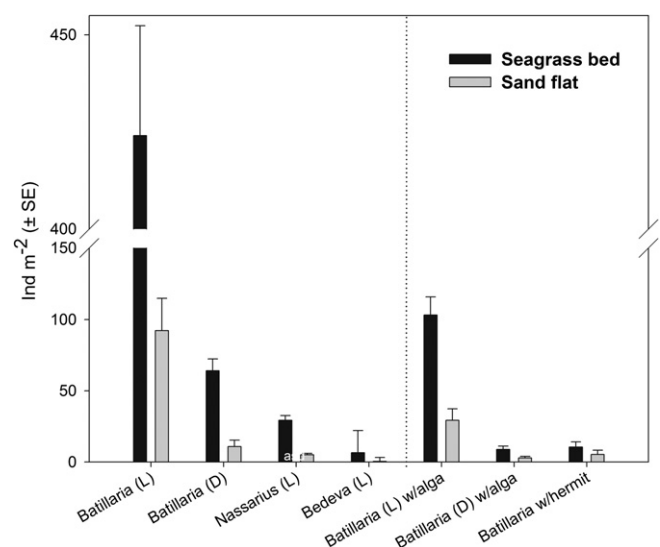


Fig. 2. The most abundant macroscopic gastropods in the Swan River Estuary. *Batillaria* = *B. australis*, *Nassarius* = *Nassarius pauperatus* and *N. burchardi* combined, *Bedeva* = *B. paivae*. L = live snails, D = dead (empty shell), with macroalgae attached to shells (w/algae) and with hermit crabs occupying empty shells (w/hermits). The data shown in the right panel is a subset of the data shown in the left panel.

and all, but one tether, were recovered with live snails attached. The missing tether was most likely buried by sediments or lost due to storms, boating or windsurfing activities. Blowfish did not consume any of the 40 *Batillaria* snails; a few bites were observed, but with no impact on the snail (each snail was carefully examined). In contrast, every single bivalve was immediately attacked and consumed before it reached the sediment surface. In several cases we observed *B. paivae* sitting on *Batillaria*, but we did not find any visible boring marks after 10 days of experiment and all *Batillaria* survived.

No *Batillaria* snails died in any of the stress experiments. We noticed that at low salinities snails often had closed operculum, were frequently found buried deeper in the sediment and the surface sediment had only few visible snail-tracks (indicating an inactivity escape response to avoid stressful conditions). We found a significant effect of algal abundance attached to snails on the number of fragments produced ($F_{1,31} = 30.70$, $p < 0.001$) irrespective of salinity ($F_{1,31} = 0.38$, $p = 0.550$, abundance \times salinity, $F_{1,31} = 1.08$, $p = 0.308$). Thus, ca. 10 times more fragments were produced from snails with high densities of attached *G. comosa* compared to snails with low *G. comosa* densities (8.68 fragments per snail over 10 days \pm 5.49 SD, $n = 16$ vs. 0.67 ± 0.62 , $n = 15$).

3.3. Impact calculations

Based on snail densities in our surveys and the areal extent of seagrass beds and sand flats (Hillman, 1987; Hillman et al., 1995), we calculated a current standing population of 3,650,623,987 snails in the Swan River, weighing a total of 4528 tons wet weight and occupying 1.72 km² of hard substratum (ca. 5% of the entire area of Swan River, see also Appendix, Table 3). These ca. 3.6 billion snails may, via their movements, encounter ca. 449,421 m³ sediment per day. 126,611,306 hermit crabs live in empty *Batillaria* shells and 966,000,000 erect macroalgal fronds are attached to live *Batillaria* (the vast majority of fronds being *G. comosa*), where 54,096,000 have multiple holdfasts and fronds >10 mm. Given snail densities, frequencies of attached algae and fragmentation rates, we estimate that 47,063,520 seaweed fragments can be produced in a single summer day in the Swan River. We also calculate that ca. 675, 171 and 65 million *Batillaria* snails are infested with *Stictodora lari*, *Philophthalmus burrilli*, and *Austrobilharzia terrigalensis* trematode parasites, respectively. Finally, by combining the total standing snail population with literature values for various life processes of *Batillaria*, we estimate the production of feces to be 23,282 kg DW snail tissue day⁻¹, representing a nitrogen input of 2.33 kg N day⁻¹. At the same time, the clearance rate from snails was calculated to be 3,259,421,663 L d⁻¹.

4. Discussion

We argue that the conspicuous gastropod *B. australis* in the Swan River, despite an uncertain origin, has remained unnoticed and unstudied by researchers and managers in Australia. More specifically, we document that *Batillaria* is the single most abundant snail in the Swan River, being common in seagrass beds and sand flats, and we argue that it has had ecosystem-wide impacts due to a high abundance, shell-production and bioturbating behavior.

Many lines of evidence suggest that *Batillaria* in the Swan River is a recent introduction from the east coast of Australia (Appleton, 1989; Chapman and Carlton, 1991; see Appendix, Table 2 for details). Most importantly: (1) it is not described in the old geological or biological literature from the region and it is not present in fossil record; (2) it was collected for the first time in Swan River in 1954 and has increased in population size dramatically in recent decades; (3) it has a disjunct distribution, with thousands of kilometers to the nearest living or fossil conspecifics;

(4) it lacks capacity for long-range dispersal (possibly up to 2 weeks pelagic larval stage) and would have to go against the direction of the main oceanographic flow, the Leeuwin Current to reach the Swan River naturally; (5) sibling species are known to be associated with anthropogenic dispersal vectors such as oyster transplants and ballast water; (6) it has a reduced parasite diversity compared to *Batillaria* populations from eastern Australia (3 vs. 8 trematode species) and *Batillaria* associated parasites and diseases are today common in birds and humans.

The alternative explanation – that *Batillaria* in the Swan River represents a single surviving relict population with a past continuous distribution from Perth to Queensland – seems unlikely, particularly because high abundances of fossilized *Batillaria* are found in known native locations (Ewers, 1966, 1967b,c) and given that other native snails in the Swan River are common in local fossil records (Kendrick, 1960, 1976, 1977). Clearly, molecular analyses comparing the Swan River population and its parasites, with native populations from southeastern Australia are needed. However, genetic data do not automatically provide unequivocal evidence of place of origin. For example, conflicting DNA studies and decades of controversy exist over the origin of *L. littorea* in North America (Warres et al., 2002; Blakeslee and Byers, 2008; Blakeslee et al., 2008; Chapman et al., 2008). In short, many lines of evidence, combining multiple molecular methods and evaluated in the context of the presented circumstantial evidence, will be needed to resolve the invasion status of *Batillaria*.

We argue that *Batillaria* was introduced from southeastern Australia via larval transport in ballast water or via oyster transplants. *Batillaria* may have a pelagic larval phase of ca. 2 weeks (Appendix, Table 2), which would be sufficient to survive in ballast tanks during shipping transport from the eastern states. In addition, the pacific oyster *Crassostrea gigas* has been transported between Australian regions for decades (Nell, 2001). Importantly, Appleton (1980:90) describes that oysters were (unsuccessfully) introduced from the eastern states on a trial basis to supply Perth restaurants with fresh oysters and were kept alive in the Swan River until required. A sibling species (*Batillaria attramentaria*) was introduced to USA as juvenile snails, or egg strings attached to the oyster shells, and it is now displacing native *Cerithid* species (Byers, 1999, 2002). Interestingly, Ewers (1967a) have quantified the geographical distribution of 'polymorphic white-bandedness' (white lines on *Batillaria* shells) and found a latitudinal cline in both living and fossil *Batillaria* showing high prevalence of banding in northern and low prevalence in southern populations. The Swan River population was similar to populations from northern New South Wales to Harvey Bay in Queensland. It is therefore possible that the Swan River population originate from this region (Ewers interpreted the banding in a latitudinal context only, and did not discuss a possible introduction event).

Our survey showed that *Batillaria* is by far the most conspicuous and dominant gastropod in the Swan River. Similar dominance is reported from many east Australian estuaries and saline lakes (Ewers, 1964, 1965, 1967a,b). Dominance of sibling species has also been reported from New Zealand (Fredensborg et al., 2005; Jones and Marsden, 2005), Japan (Kamimura and Tsuchiya, 2004, 2006) and in invaded estuaries on the US west coast (Byers, 1999, 2005; Wonham et al., 2005).

Invasive species are typically characterized by 'super-traits' to match the invaded habitat conditions (Mack, 1996). For *Batillaria* species in general, and *B. australis* in particular, this can be summed up by high resistance to predation and environmental stress; traits of general importance to succeed in estuaries. Our experiments did not show any evidence of top-down control, although it is possible that past higher densities of the blue crab (*Portunus pelagicus*), could have exerted some predation pressure (e.g. in the US, small

Callinectes sapidus prey heavily on *Bittium varium*, Wright et al., 1996, a species morphologically similar to *Batillaria*). In contrast to Ewers (1967c), who estimated that 50–60% of empty shells showed signs of predation in east Australian saline lakes, we observed relatively few empty shells with obvious predation marks. Also, sibling species have been documented to be abundant surface dwellers on exposed intertidal flats (Fredensborg et al., 2005; Jones and Marsden, 2005), and do not appear to be preyed upon by either birds or terrestrial organisms (pers. obs.). In short, predation on *Batillaria* is low in the Swan River.

In addition, a high stress-tolerance to environmental fluctuations is also paramount; in particular, temperature and salinity fluctuations. We showed that *Batillaria* can survive a wide range and fluctuations in these parameters and several unpublished studies have documented similar high stress-tolerances (Appendix, Table 1). Specifically, inactivity has been reported below 10–15 psu, suggesting the snail survive adverse environmental fluctuations by closing the operculum for long periods of time (weeks/months) (this study, Appleton, 1980; Kirke et al., 1987). Still, more experiments are needed to test for long-term interactive effects of multiple estuarine stress factors – including desiccation, salinity, temperatures, hypoxia, and substratum conditions – to better understand the species traits, and to be able to predict what habitats can be invaded. For example, it is likely that *B. australis*, like its sibling *B. attramentaria* (Byers, 2000), also is resistant to low oxygen levels, another common stress in eutrophic estuaries.

There are several approaches to quantify impacts of NIS and cryptogenic species; Before-After/Control-Impact tests, experimental manipulations or application of formulas (Parker et al., 1999). Without before-invasion community data BA/CI tests cannot be performed and experimental manipulations are typically limited in space and time, and will only test what happens in an already invaded system which may be irreversibly altered by the invader (Thomsen et al., 2009). Parkers et al.'s (1999) impact formulas provide an alternative to calculate ecosystem effects. Specifically, Parker et al. suggest that impact is proportional to the abundance, range, and the *per capita* effect of the NIS, but also assume that structures and processes of the native community otherwise have been un-affected. Despite these assumptions, we used this formula to provide ball-park estimates on possible ecosystem impacts of *Batillaria* in the Swan River.

Based on current *Batillaria* densities we estimated a standing population of ca. 3.6 billion snails. The true population is probably larger, as *Batillaria* can be abundant in deeper waters (pers. obs.) not included in our calculations. Thus, the impact question was restated to 'what do 3.6 billion snails do? Most importantly, *Batillaria* produce hard substratum within the estuarine 'sea of soft sediments'. Thus, ca. 1.7 km² of *Batillaria* substratum move around on a daily basis in the Swan River. These moving "mini-reefs" provide a habitat resource (attachment space) for sessile species, such as macroalgae, that often are substratum limited in soft sediment estuaries (Thomsen et al., 2007a). For example, up to 1 billion *G. comosa* macroalgae are attached to live *Batillaria* snails (and this does not include other erect taxa or crustose forms). Even though a large proportion of the fronds were small, this spatially fixed and potentially stable algal population may provide a significant feeder-linkage to more ephemeral drift algae communities (Thomsen et al., 2007b) that co-exist in the Swan River (Astill and Lavery, 2004). Such a possible linkage was supported by our experiment that showed a high production of fragments when algal fronds are densely attached to shells. Thus, ca. 45 million small seaweed fragments may be produced (=vegetative reproduction), from living *Batillaria* shells, in a single summer day in the Swan River. Fragment production from snail substrates is thereby likely to provide an enormous propagule supply for vegetative re-growth,

dispersal, and additional fragmentation and accumulations in low-energy environments. In addition to attached *G. comosa*, we also observed attached *Chaetomorpha linum* and *Laurencia* spp., and tube-building polychaetes, bryozoa, encrusting algae, and sea anemones (not quantified here) and similar biotic communities have been documented on *B. attramentaria* in the US (Wonham et al., 2005). Interestingly, we have also observed crustaceans, polychaetes, gastropods and macroalgal epiphytes associated with *G. comosa* fronds attached to *Batillaria* (unpubl. data). Thus, *Batillaria* may, via this 'habitat-cascading' mechanism (i.e. *Batillaria* create habitat for *G. comosa* which create habitat for seaweed-associated epibiota) have indirect positive effects on seaweed-associated epibiota communities in the Swan River (Altieri et al., 2007).

Empty *Batillaria* shells are also an important resource, particular for hermit crabs that use these shells for protective housing. We calculated that ca. 125 millions hermit crabs occupy these relatively new but massive housing constructs in the Swan River. We found only few hermit crabs associated with native gastropod shells (e.g. *Nassarius* spp. shells are too small) and it is therefore most likely that the hermit crab population have increased dramatically in response to the appearance of *Batillaria*. Although a few hermit crabs were found in shells of the much less common *B. paivai* shells (unpubl. data), this predatory snail is unlikely to ever have reached similarly high densities. For example, in our survey, we found no evidence of any abundant native recently fossilized snails (potentially out-competed) that could have provided hermit crabs with a similarly abundant housing material prior to the arrival of *Batillaria*. Given an average *Batillaria* life expectancy of ca. 2.5–3 years (Appleton, 1980), and assuming a present day relatively stable population size, more than a billion new shells are produced every year. Thus, *Batillaria* provides a large renewable amount of hard substratum and habitat for hermit crabs and sessile species. The ultimate fate of these erosion-resistant shells is likely sediment burial, subtidal surface accumulations where hydrodynamics allow so, or beach deposits (Fig. 3), and may thereby also affect deep in-faunal- as well as semi-terrestrial communities. *Batillaria* may potentially also indirectly affect ecological performance of fish, birds and mammals, as the intermediate host for trematode parasites. For example, millions of invasive snails are infested with *A. terrigalensis* and *S. lari*, parasites known to cause human skin diseases and/or infection of seagulls and other birds (Appleton, 1983a,b). Clearly, such less obvious indirect effects should be explicitly tested for in future impact experiments.

Batillaria is an active snail that moves around on the sediment surface or just below (unpubl. tagging experiments) and up to 450,000 m³ sediments may be in physical contact, and thus potentially moved, with the snail daily in the Swan River due to its movement patterns. An unknown proportion of this sediment will be ingested and oxygenated, and diatoms, bacteria, organic material and invertebrate eggs and larvae possible consumed (Kamimura and Tsuchiya, 2004, 2006). Thus, *Batillaria* could potentially impact sediment microflora and fauna via bioturbation and ingestion of sediments, as observed for other sediment feeding gastropods (Brenchley and Carlton, 1983; Hunt et al., 1987; Kelaher et al., 2003). Similarly, *Batillaria* can affect sediment properties via fecal production and re-mineralization of nitrogen, e.g. >to 2 kg nitrogen may be released daily in the Swan River by this single snail. Re-mineralization of the nutrients in the feces may enhance growth of the attached seaweed populations, thereby providing both mechanical and physiological facilitation to this group of organisms (Thomsen and McGlathery, 2007).

Finally, it has been documented from laboratory experiments that the sibling species *B. zonalis* and *B. flectosiphonata* from Japan are dual feeders that, in addition to deposit feeding on sediments

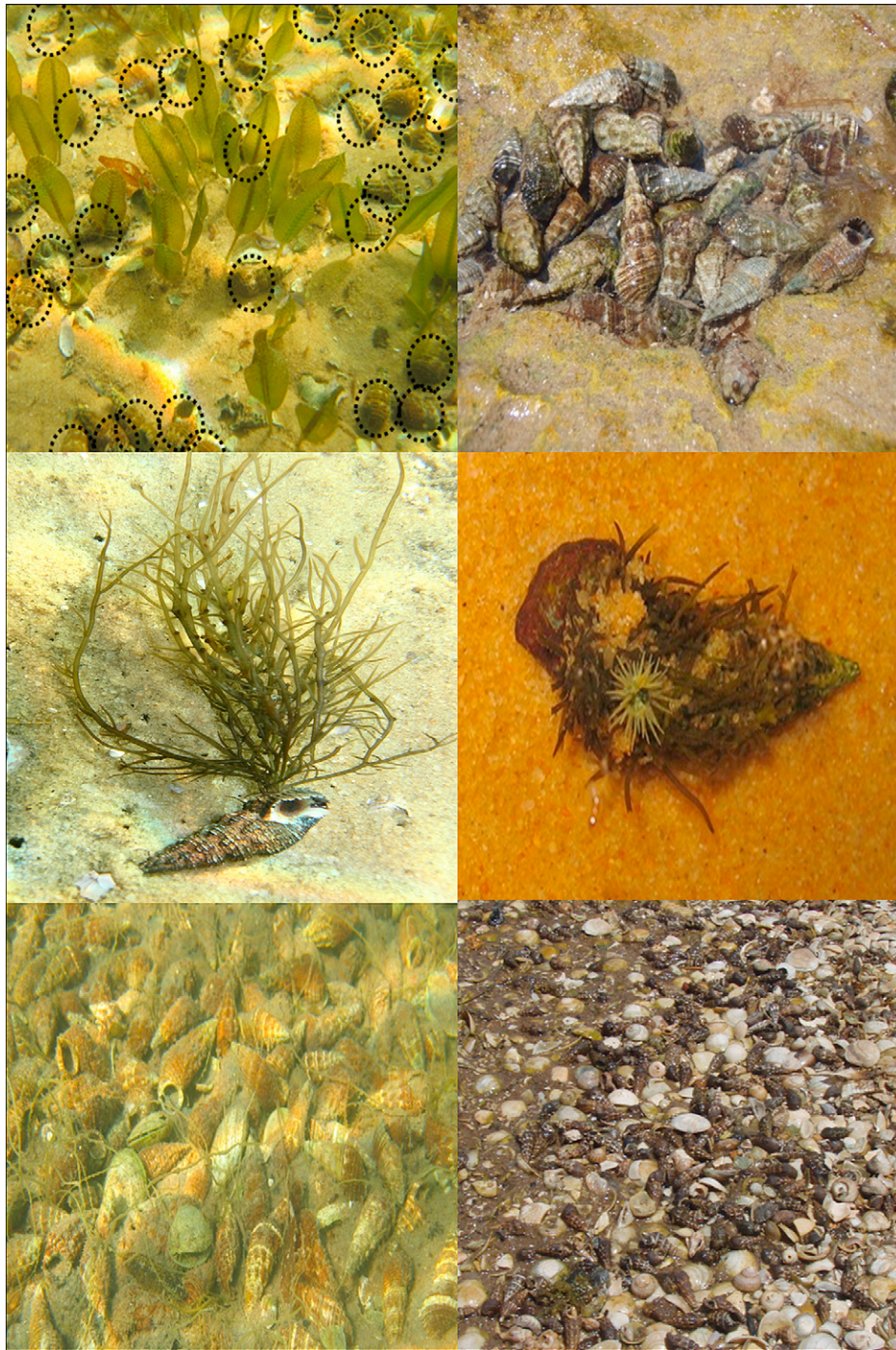


Fig. 3. *Batillaria australis* in the Swan River estuary. Top left: Typical seagrass bed with living *Batillaria* on the surface (highlighted with circles). Top right: Dense aggregation on intertidal rock platform. Middle left: Attached macroalgae (*Gracilaria comosa*) on *Batillaria*. We have also observed seaweed-associated epibiota communities on *Gracilaria*, suggesting the presence of a 'habitat cascade' whereby *Batillaria* create habitat for *Gracilaria* which again create habitat for seaweed-associated polychaetes, crustacean, gastropods and epiphytic sessile organisms. Middle right: Attached sea anemone and *Gracilaria* recruits on *Batillaria*. Bottom left: Recent subtidal accumulation of dead *Batillaria*. Bottom right: Recent beach-cast shell deposits with high proportion of *Batillaria*.

also filtrate the water column for particulate organic matter. Although filter-feeding gastropods are uncommon, the fact that the only two *Batillaria* species tested for this trait so far, both filter feed, suggest that this trait may also exist in the morphologically similar *B. australis*. Assuming that *B. australis* have similar traits, then, theoretically, up to 3 billion liters of Swan River water could be cleared for suspended particles each day. Or, more specifically, *Batillaria* in a seagrass bed at 1 m depth could potentially clear the

entire water column every few hours (Appendix, Table 3, assuming a mixed water column). Similar large-scale ecosystem effects have been suggested for other non-native filtrators, e.g. the sand mussel *M. arenaria* in Ringkøbing Fjord in Denmark (Petersen et al., 2008), the Japanese clam *Potamocorbula amurensis* in San Francisco Bay (Cloern, 1982), and the zebra mussel *Dreissena polymorpha* in the Great Lakes (Strayer et al., 1999). We emphasize that these impact estimates should be interpreted as hypothesis-generating, to be

challenged and tested using experiments from the Swan River and compared to similar ecosystem processes from non-invaded neighboring estuaries.

5. Conclusions and implications

We conclude that *Batillaria* in the Swan River represents a rare example of a poorly studied, but abundant, species of uncertain origin. We provided ball-park estimates of possible system wide impacts of this species, but explicitly designed research projects needs to be initiated to actually test how *Batillaria* affects the functioning of the Swan River. A fruitful approach would include manipulative experiments in the estuary and comparative studies to the adjacent estuaries that lack this species. Indeed, ecological comparisons of seagrass beds and sand flats between the Swan River and nearby non-invaded estuaries may provide much needed theoretical insights into how a single invader may affect large-scale ecosystem attributes (Cloern, 1982; Strayer et al., 1999; Petersen et al., 2008). Based on our literature review, we conclude that all evidence points strongly to a recent human-mediated introduction, and we therefore suggest a “guilty-till-proven-innocent” approach, with immediate implications for management procedures to avoid spread to other estuaries. For example, regulations should be implemented to prohibit direct transport of *Batillaria* but also to minimize indirect transfer via associated species (e.g. shellfish) or trailed boat traffic. If *Batillaria* is verified to be a NIS based on modern molecular analysis of the snail and its parasites (Blakeslee et al., 2008), active population control or even eradication of the smaller Woodman point populations just south of the Swan River could be a method to hinder secondary dispersal to the adjacent estuaries. Finally, we add *Batillaria* to a growing list of ecologically important species (e.g. *L. littorea*, *G. vermiculophylla*, *M. arenaria*, *P. australis*, *Carcinus maenas*), often believed to be native in many places, but today generally recognized as NIS. Targeted searches on more cryptogenic species will likely continue to increase our perception about how human-mediated transport of organisms has transformed the world’s biogeographical regions.

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Appendix. Supplementary material

Supplementary material associated with this article can be found in the online version, at [doi:10.1016/j.ecss.2010.02.014](https://doi.org/10.1016/j.ecss.2010.02.014).

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