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The Western Australian soldier crab, *Mictyris occidentalis* Unno 2008 (Brachyura: Decapoda: Mictyridae): the importance of behaviour in design of sampling methods

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Abstract

Soldier crabs are challenging marine organisms to sample as they do not fit neatly into established faunal behavioural categories. Information on the soldier crab life cycle, ichnological products, and behaviour is a prerequisite to designing appropriate sampling, involving the consideration of the study objective (what to sample), temporal factors (when to sample), spatial factors (where to sample) and sampling method (how to sample). Largely infaunal for most of their life cycle, soldier crabs may be relatively sessile or quite vagile within the substrate, and epifaunal (emergent) for late stages of their life cycle. They also exhibit population partitioning, based on sex and size classes (when there are mixed cohorts); for example, it is mostly adult males that emerge in swarms, and mainly females and juveniles that remain in the subsurface. This behaviour has implications for studies of population dynamics that involve abundance, population structure, and sex ratios. To date, there has been emphasis on sampling while the crabs are emergent (forming so called "armies", or surface swarms), with the assumption that the whole population emerges. When infaunal and mobile, soldier crabs also present challenges to sampling in that they can vary in abundance laterally and vertically in a short time, and they can respond to prolonged sampling, or to researcher-induced perturbations during sampling, by burrowing downwards to avoid being collected (resulting in potentially spurious data with respect to their depth of occurrence and abundance). The complexity in behaviour of soldier crabs, the partitioning of populations, and the response to sampling have not been addressed to date by researchers elsewhere whereas it is an important component in the design of sampling methods.

Keywords: soldier crab, *Mictyris occidentalis* Unno 2008, sampling, crab behaviour, north-western Australia

Introduction

Sampling strategies and methods for marine benthic macroinvertebrates depend on the specific objectives of the study which may range from collections for taxonomic, biogeographical, and physiological studies, to quantitative ecological studies describing population dynamics including abundance, size, and distribution, as well as aspects of life history such as reproduction, recruitment, and mortality. For quantitative studies, accuracy and robustness of results and hence the correctness of conclusions derived from interpreting these data depend on the use of sampling strategies and methods appropriate for the type of organism being sampled, the nature of the organism's habitat and the sampling effort (number of replicates). For a given species, sampling strategies or protocols involve the design of a sampling program, *i.e.*, when, where and how to sample, and use of methods involving particular equipment and techniques appropriate to the objectives of a study. Traditional sampling strategies may include use of random quadrats, or sampling at regular intervals along transects, *etc*. Traditional sampling methods include the use of equipment such as sweep nets, suction devices, grab samplers, dredges and cores. While there have been several examples of generalised sample design (Green 1979; McIntyre *et al.* 1984; Clark & Green 1988; Riddle 1989; Underwood 1997; Underwood & Chapman 2001), and studies of methods for collecting benthic organisms (Holme 1964; Boudouresque 1971; Parker 1975; Ankar *et al.* 1979; Warwick & Clarke 1991; Eleftheriou & McIntyre 2005) in the literature, this paper is the first to describe a sampling strategy and methods specifically for the Western Australian soldier crab *M. occidentalis* Unno 2008, designed in response to information on its life stages and its behaviour. These methods, in fact, are applicable to some degree to other species of *Mictyris*.

Speciation within a genus can result in behavioural differences between the taxa. The species of fiddler crab, *Uca*, exemplify this: with over 50 species of *Uca* worldwide, each species exhibits differences in habitat preferences, depth of burrowing, shape of burrows, and other behavioural characteristics (Crane 1975). At present, there are five species of *Mictyris* described in the Indo-Pacific region (Davie 2002; Unno 2008), and while there are similarities in behaviour between them, it is not to be unexpected that speciation could result in differences in behaviour and habitat preferences of the various taxa within this genus. Thus, while the results of this paper are specifically directed to the sampling of *M. occidentalis*, the principles of adjusting methods to be appropriate to the behaviour of the Western Australian soldier crab, described herein, at the least, can be applied to other species of *Mictyris* in the Indo-Pacific region in that generally there is enough overlap and similarity in the behaviour of the various species, though not necessarily in detail.

The Western Australian soldier crab, *M. occidentalis*, is infaunal to epifaunal and is behaviourally a complex organism (Unno & Semeniuk 2008), and this can result in difficulty in its sampling and ambiguity in a given set of results deriving from sampling. If the complex crab behaviour is not addressed, sampling is likely to result in data that are incomplete, or that are artifacts, spurious, biased, or ambiguous.

In general, for any macroinvertebrate on tidal flats, where studies of abundance, population dynamics, and population structure are undertaken, information on the whole subpopulation, under or on the area of tidal flat being sampled, is required, *i.e.*, for a given area of sampling, all crabs need to retrieved. Further, if a portion of a population becomes emerged (epifaunal), for valid intra-population comparisons of abundance, size classes, and sex ratios, the emergent and infaunal components of the subpopulation need to be sampled concurrently.

Specifically for *M. occidentalis*, since this species spends most of its life cycle as infauna, and emerges generally during the late stage of its life, there can be problems in sampling the populations. Further, its behaviour, whether infaunal or emergent, is variable, and spatially and temporally patchy. For instance, if any adult crabs emerge, there is a proportion of the crabs that may remain in the subsurface. This is particularly so if the population is composed of mixed stages of cohorts, but also is the case even if the population is composed of a single adult-sized cohort. Additionally, even if remaining wholly in the subsurface, the population also may behave variably, with patches working the sediment as near-surface infauna, and other parts of the population remaining inactive (Unno & Semeniuk 2008).

This paper reports on the variety of behaviour of the Western Australian soldier crab *Mictyris occidentalis* Unno 2008 with regard to the way it has responded to various sampling techniques, and in relation to the problems that may arise if researchers do not address soldier crab behavioural variability, with a view to describing the best sampling methods for the soldier crab during various stages of its life cycle.

This paper is structured as follows:

- description of the complex and variable behaviour of *M. occidentalis*
- review of soldier crab sampling methods in the literature
- implications of soldier crab behaviour for sampling strategies and methods
- sampling methods investigated in this study
- results of various sampling methods employed in this study
- conclusions and recommended strategies and methods for sampling soldier crabs

This work is based mainly on three study sites along the Western Australian coast: King Bay (Dampier Archipelago), Settlers Beach (near Cossack), and Broome (Fig. 1A), and detailed work in the Dampier Archipelago (Fig. 1B).

In this paper, the term "box core" is used for a metal open-ended box, with square cross-section, used for coring sediment; "cylindrical core" is a term used for circular pipes, usually of polyvinyl chloride (PVC), but also of metal; and "spading" is used describe the excavation of sediment by spade usually from inside a marked quadrat.

Complex and variable behaviour of *M. occidentalis*

Behaviour of the Western Australian soldier crab on the tidal flat, particularly in relation to the various ichnological products generated by the crab, is linked to its life cycle. Excluding its marine larval stage, the soldier crab life cycle can be divided into three stages: the early, post-settlement stage where the crab has a carapace length of 1–3 mm; the middle, juvenile stage with a carapace length between 3–7 mm; and the late, adult stage with a carapace length of 7–17 mm. This post-larval life cycle takes about twelve months from recruitment to an adult size of 12 mm carapace length.

Throughout most of their life stages the crabs are largely infaunal, maintaining a subsurface air bubble, and can migrate horizontally or vertically through the substrate in this cavity (Unno & Semeniuk 2008). The early, post-settlement stage crab generally is entirely infaunal – the only ichnological clue to its presence is a tiny "clot" of sand on the sediment surface, the result of subsurface feeding and burrowing activities. Juvenile and adult females also are largely infaunal, producing a range of ichnological products as a result of their feeding and burrowing activities, including singular pustular structures, tunnel structures and pustular mats as well as subsurface structures such as air-filled elongate to circular cavities 1–2 cm in diameter (Unno & Semeniuk 2008). Crabs producing pustular structures during a low tide, can be daytime or night activity. Based on aquarium studies, supplemented by field observations immediately after a receding tide, Unno & Semeniuk (2008) documented soldier crabs moving their air bubble cavities deeper into the sediment during high tide, to avoid predators, and during low tide, moving close to the surface to commence feeding activities. If the crabs remain infaunal in the near-surface, these feeding activities produce discard pellets which are pushed to the surface, accumulating to form pustular structures and tunnel structures which, over the course of the low tidal period, may form an agglomerated pustular mat structure of sediment workings spread over large areas of the tidal flat. An index, then, of the crab population proximity to the very near-surface is the appearance of a mat of pustular structures (Unno & Semeniuk 2008). In the aquarium, the crabs remained in a zone 10 cm from the sediment surface for simulated low tide and high tide (Fig. 2).

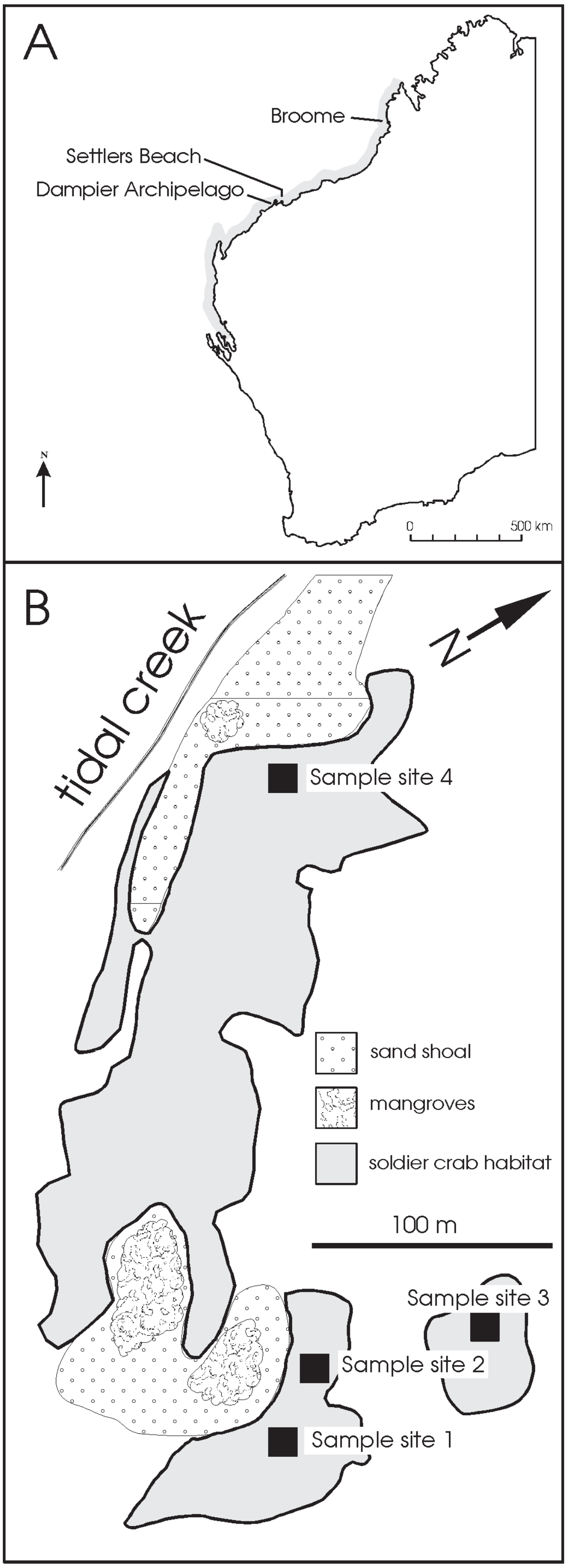

Figure 1. Location map and sampling sites. A. Sampling localities along the coast in Western Australia. Grey border to coast shows the biogeographic extent of *Mictyris occidentalis*. B. Soldier crab habitat (after Unno & Semeniuk 2008) and sampling sites in King Bay, Dampier Archipelago.

When the crabs are in their late adult stage, during some low tidal periods, adults (mostly older blue males) may emerge, forming a swarm, and move about the surface, feeding, and leaving a pelleted surface of discard pellets (Unno & Semeniuk 2008). During this late adult stage, the population may also exhibit a temporary phase of not swarming. When a swarm commences, hundreds of individuals may emerge and feed, but generally do not interact, moving in fact randomly over the tidal flat. However, if a predator (or a human who is perceived as a predator) appears, each individual crab will move in the direction away from the predator, producing an effect that appears to be movement in concert as occurs in an "army". When emergent, adult crabs produce exit holes, craters and rosettes.

The behaviour of *Mictyris occidentalis*, whether infaunal or emergent, is variable, hence activity occurs in a patchy manner. For instance, for every emergence of crabs, there is a proportion of the crabs that may remain in the subsurface. This is particularly the case if the population is composed of mixed stages of cohorts, but also the case even if the population is composed of a single cohort. If remaining wholly infaunal (*i.e.*, remaining in the subsurface), the population also may behave variably, with patches of workings appearing on the sediment indicating near-surface infaunal activity, and other parts of the population remaining lower in the substrate with no surface expression of their activities (*cf*. Figures 8 and 9 of Unno & Semeniuk 2008).

Subsurface activity of infaunal soldier crab populations is variable from day to day with some crabs moving horizontally or vertically through the substrate while others remain relatively inactive. The habitual, undisturbed depth of occurrence in the substrate of the soldier crab is best observed in aquarium studies and is generally between 0 cm and 15 cm (Unno & Semeniuk 2008).

Review of soldier crab sampling methods

A basic prerequisite for present and future comparisons of the various behavioural activities, population dynamics, and partitioning of soldier crab populations in terms of their life stage and sex, is that comparable data are/were collected for the various species of *Mictyris*. To this objective, the various sampling methods for the species of *Mictyris* worldwide were reviewed to provide an assessment of the reliability of the data and information in the literature.

Various aspects of the species *of Mictyris* in the field and in the aquarium have been described in papers from South-east Asia and Australia. Topics for study have included: taxonomy and biogeography (Alcock 1900; McNeill 1926; Takeda 1978; Unno 2008); physiology (Quinn 1980; Sleinis & Silvey 1980; Kraus & Tautz 1981; Maitland & Maitland 1992); ontogeny (Cameron 1965; Fielder *et al.* 1984; Fukuda 1990); ichnology (Unno & Semeniuk 2008); feeding (Quinn 1983); reproduction (Nakasone & Akamine 1981; Takeda 2005); population dynamics (Shih 1995; Dittmann 1998); behaviour (Cameron 1966), and ecology (Cowles 1915; Rossi & Chapman 2003; Webb & Eyre 2004). Most of these

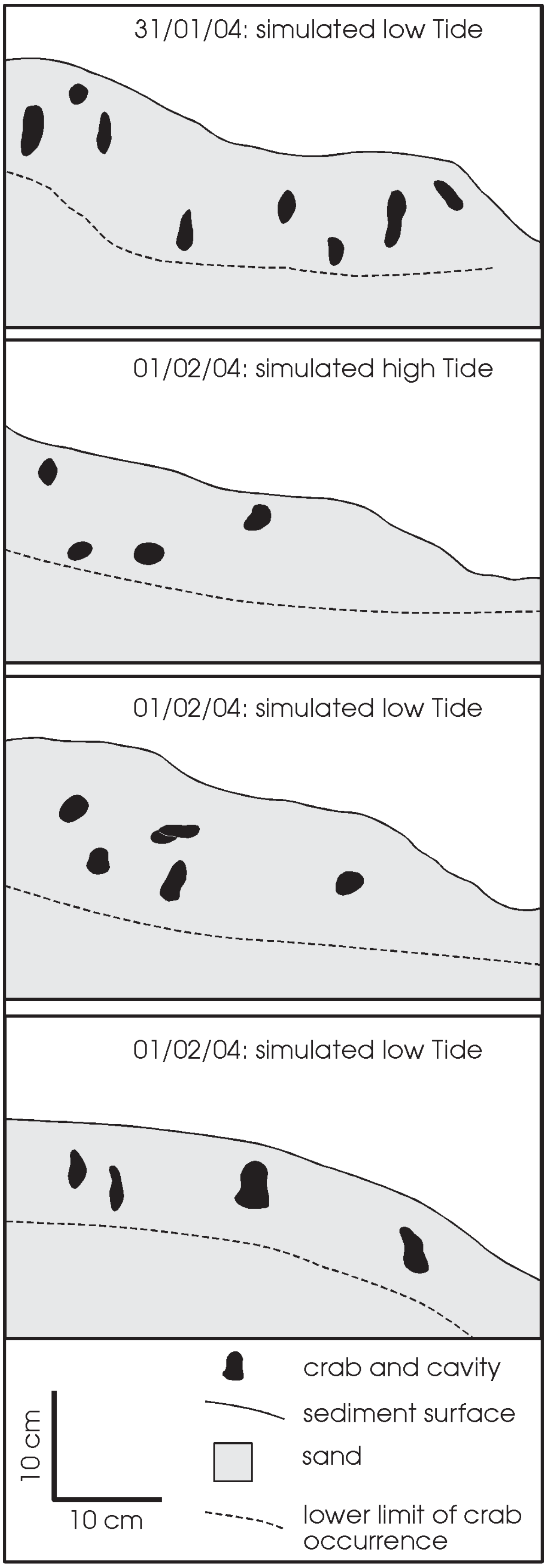

Figure 2. Occurrence of crabs and their subsurface cavity under simulated high tide and simulated low tide conditions in the aquarium. The crabs occur within a topography-conforming zone within 10 cm of the surface.

papers, however, do not describe in detail the sampling methods employed to collect crabs.

A selection of key research papers on soldier crabs that do describe, imply or allude to sampling methods for collection of crabs are reviewed below, with a focus on sampling methods for crabs in their natural tidal flat environment, and the sampling methods therein assessed using criteria, when appropriate, as to whether the sampling appeared to achieve the objective of the paper, whether the whole population or partial population actually was collected, and whether disturbance during sampling possibly triggered a reaction in the crab to "escape from a predator" such that the results were inadvertently biased.

The early work on soldier crabs was taxonomic and involved qualitative observations of burrowing style and burrowing depth. Cowels (1915) focused on the habits, feeding and burrowing behaviour and the ichnological products of *M. longicarpus* Latreille, 1806 in the Philippine Islands (a taxon now assigned in that region to *M. brevidactylus* Stimpson, 1858), including the production of subsurface cavities. Cowles (1915) excavated to at least ~ 10 cm to study the crab (actual depth was not reported but can be estimated from Figure 3 Plate II of Cowles 1915). Information of direct relevance to this paper is that the soldier crab *M. brevidactylus* burrows to a depth of at least 10 cm, and that it undertakes what I term "predator avoidance" by rapidly burrowing.

In a largely taxonomic paper, McNeill (1926) anecdotally described the occurrence and habits of various species of *Mictyris*, drawing on notes and comments of collectors for *M. livingstonei* McNeill, 1926 and *M. platycheles* H Milne Edwards, 1852, but provided direct information/descriptions of the behaviour of *M. longicarpus*. From opportunistic collection in the Botany Bay region from swarms, and supplementary sampling by excavations by spade, McNeill (1926) describes *M. longicarpus* as occurring in the subsurface to depths of 5–9 inches (~ 15–22 cm).

Cameron (1966) reported on visual and filmed observations of swarms of *M. longicarpus* carried out from a hide on the tidal flat. Although primarily a study of swarming behaviour, excavations by spade also were carried out for qualitative determination that there were soldier crabs in the subsurface at the same time that the crabs were swarming. Cameron (1966) confirmed McNeill's (1926) observations that predominately male soldier crabs comprise the swarm but does not describe the method used for this observation/conclusion.

Nakasone & Akamine (1981) described the reproductive cycle of the soldier crab and the growth of juveniles over a year for *M. brevidactylus*, collecting crabs by excavating 50 cm x 50 cm quadrats (reducing the quadrat size to 25 cm x 25 cm if large numbers of juveniles were present) and sieving the sediment through two mesh sizes (a 2 mm mesh, and later, a 10 mm mesh). Depth of sampling was not recorded in the description of the methods. Also, the actual method of excavation was not described in detail, although it is unlikely that a box core with such large 50 cm sides would have been used, and it would seem probable that the quadrat size was a marked area on the tidal flat to delineate the area of excavation. The reported population structure may have been inaccurate due to incomplete collection of crabs. Juvenile recruits < 2 mm would not have been collected in this study. Large adults may also have been under-represented in the reported population structure for subsurface crabs due to the sideways or downward escape movements (see later). No sampling of the subsurface population occurred at the same time as the collection of swarming crabs.

In collecting crabs for physiological studies in the laboratory of the functioning of the lungs of soldier crabs, Maitland & Maitland (1992) reported on the behaviour and burrowing activities of *M. longicarpus* in Botany Bay, and noted that they accorded with the observations of earlier authors. In their own collecting methods, Maitland & Maitland (1992) excavated soldier crabs with a spade to 30 cm, and observed that the crabs occur between 10–30 cm below the sand surface. The disturbance of the sediment due to excavation by spade may have driven the crabs to deeper levels, therefore the maximum depth of 30 cm may not represent the normal habitation level of the soldier crabs.

Shih (1995) undertook a study of the population densities and annual activities of *M. brevidactylus* in Taiwan, providing data on abundance, growth rates, egg-carrying period of the female, and sex ratios. The paper is confusing in the description of methods because while a quadrat 1 m x 1 m x 0.2 m was excavated to retrieve the crabs, the author describes (manually) collecting only obviously visible crabs > 4 mm in size, yet population structures presented in Figures 3 and 4 of Shih (1995) show that animals from 1 mm to 15 mm were apparently collected. The methods make no mention of sieves or sieve sizes involved in the study, though it would be difficult to manually collect crabs in the 1–4 mm size range, and so it must be concluded that a sieve probably was used. Sediment disturbance was not accounted for. The quadrats to sample the subsurface population were relatively large (1 m x 1 m) and would have taken some time to excavate, thereby increasing the chance that the crabs might have escaped by burrowing out, or burrowing deeper to avoid collection by the "predator" researcher. Whether the species naturally occurred at depths > 20 cm, or whether the animal burrowed to depths > 20 cm to avoid collection, is not known, and hence the data on population structure and sex ratios may be biased or incomplete, and as such, the results of Shih (1995), at this stage, should be viewed as potentially spurious or ambiguous.

Dittmann (1998) undertook studies on the behaviour and population structure of *M. longicarpus* in Queensland, collecting crabs from swarms for sex ratios and size class measurements. Sex ratios and size classes were estimated for emergent crabs only, and the structure of the subsurface population under the swarm was not addressed, and hence the true whole-of-population structure had not been documented, and the sex ratio of the whole-of-population also had not been documented. This is an example of the focus on the very obvious swarms on the tidal flat surface with the assumption that the whole population swarms at the same time.

Rossi & Chapman (2003) studied the influence of sediment on burrowing by the soldier crab *M. longicarpus* in Port Jackson and Botany Bay in New South Wales. Abundances were determined by counting crabs collected from sediment excavated from plots 30 cm x 30 cm x 20 cm deep (presumably by spade or similar tool), and sieved through a 2 mm mesh. The authors observed from preliminary diggings that soldier crabs generally excavate the sediment to a depth of 15 cm and selected the plot size for ease of removal with minimum disturbance. Results for abundance and size classes for this study would be accurate for the > 2 mm sized crab population, due to the smaller quadrat size.

In a study of *M. brevidactylus* in Japan, Takeda & Murai (2004) undertook observations on soldier crab feeding behaviour in relation to water levels, and determined abundance and size class measurements as well as sex ratios. They primarily focussed on collecting crabs from swarms and only once concomitantly from the subsurface by excavating 5 blocks of sediment 50 cm x 50 cm x 30 cm deep (presumably by spade – the exact method is not mentioned, but sampling a quadrat 50 cm x 50 cm in size would suggest a quadrat marked on the tidal flat surface and excavated, rather than a large metallic box core to core the sediment). Sediment disturbance is not accounted for since the subsurface population sampling quadrats were relatively large, and would take some time to excavate, thereby increasing the chance of crabs escaping by their sideways or downward mobility. As with Shih (1995), excavating soldier crabs in such large quadrats to a depth of 30 cm similarly would have run the risk that the animals may have burrowed deeper and sideways to avoid collection by the "predatory" researcher. As such, the results of Takeda & Murai (2004) at this stage, similar to the results of Shih (1995), also should be viewed as potentially spurious or ambiguous as the data on population structure and sex ratios may be biased or incomplete.

Takeda (2005) sampled soldier crabs in a study of sexual differences in behaviour during the breeding season of *M. brevidactylus* in Japan. This was not a study of population structure, and as such Takeda (2005) retrieved animals, after they had ceased their surface activities (emergences), only from a quadrat 50 cm x 50 cm to 20 cm depth, over an area where there were soldier crab surface workings (term from Unno & Semeniuk 2008). The description of the methods employed by Takeda (2005) suggests that the 50 cm x 50 cm quadrat was placed (or marked) on the surface to mark the area for excavation only and was not an open-ended metal box (a box core). The sand excavated was washed though a 2.5 mm sieve to collect the animals.

Interestingly, with the same species, *M. brevidactylus*, Shih (1995) and Takeda (2005) both excavated sediment to depths of 20 cm, while Takeda & Murai (2004) excavated to depths of 30 cm. If the crab occurs to depths of 30 cm, Shih (1995) and Takeda (2005), in fact, did not fully retrieve all animals in a given quadrat, and if the animal burrowed to depths > 30 cm, the three studies did not fully retrieve all animals in the study quadrats. If during sampling, the animals were undertaking "predator avoidance" behaviour, and burrowed even more deeply, then Shih (1995), Takeda & Murai (2004) and Takeda (2005) have under-sampled the soldier crab populations.

All methods of sampling described above did not seem to make allowance for crabs burrowing deeper to avoid "researcher predation" and so the maximum depths recorded for observed occurrence of soldier crabs may be an artifact of sampling procedure. In the study by Takeda & Murai (2004), the population numbers may be also be artifacts if the authors did not account for possibility of rapid lateral migration by the crabs to avoid predation. In the studies by Dittmann (1998), only surface swarms were collected, and as will be described later, these may provide a biased sample of the total population size classes and sex ratios if the subsurface crabs were not sampled. Only Rossi & Chapman (2003) appear to have addressed the importance of not disturbing the sediment during excavation of quadrats.

A problem with all the sampling that involved excavation of a quadrat, particularly where the water table is near the surface, is that the sides of a 20 cm or 30 cm wall of sand will collapse, and crabs residing in the sand adjoining the quadrat will slump into the excavation, or migrate in the subsurface into the excavation (see later). In this context, it is important to have a wall that supports the sides of the excavation, *i.e.*, the side of a metal box (a box core), or the side of a large diameter pipe (a cylindrical core).

Implications of soldier crab behaviour for sampling strategies and methods

From the literature, and from field work in northwestern Australian, it is evident that to obtain robust data on population dynamics and sex ratios, sampling of *Mictyris* must involve infauna populations as well as swarms, and must address a number of issues.

The first is 'where to sample'. As vagile organisms, patches of soldiers crabs do not always occur in the same area within the habitat. Sampling within a fixed area within the habitat of size, say, 5 m x 5 m, marked by posts, may result in variable numbers from week to week, or month to month, not reflecting changes in abundance, but the variation in density due to internal adjustment of the density of the population. These types of results, of varying abundance in time reflecting an internally temporally changing density, contrast with organisms such as infaunal bivalves, that may remain resident within a patch of habitat for months, or fiddler crabs, that remain in relatively fixed burrows for weeks and months. Thus, sampling in the same fixed location may provide results showing variation in population density, but this may only be reflecting the very localised immigration and emigration of individuals into and out of the fixed sampling site.

The use of pustular structures as evidence of the crabs in the near-surface is an indicator of the occurrence of crabs in the subsurface within the habitat, or within a fixed sampling site. However, pustular structures are variable in occurrence and density on a tide by tide basis (Figure 9 of Unno & Semeniuk 2008).

The second is 'how deep does the crab burrow. When it is necessary to obtain samples of populations to determine density, density variations, size classes, and sex ratios, it is important to know that the entire subpopulation has been retrieved. Sampling to 10 cm depth by coring, if the crab is burrowing from near-surface to depths of 40–50 cm depths, clearly will produce a biased and inaccurate estimate of abundance, size classes, and sex ratios.

There have been conflicting results about the depth of occurrence of soldier crabs within the substrate and hence how deep to sample to retrieve a representative sample of the population. Sampling of the Western Australian soldier crab shows that the species responds to the sampling regime as though the researcher were a predator, *i.e.* the crab digs deeper into the sediment in an escape response (see later). The depth of occurrence of the crab during sampling often is a function of (or a bias reflecting) sampling style, *e.g.*, slow incremental sampling may drive the crab to deeper depths to avoid what it may perceive as proximity of a predator. Hence, while Maitland & Maitland (1992) reported that the soldier crab was found at a depth of 30 cm, in this instance it appeared that the crab may have been retreating from anthropogenic excavating activity. Ascertaining the normal habitation range of the soldier crab within the substrate and therefore the required length for sample cores should be an important objective of any ecological study.

Thirdly, given that the adults are the main size class that swarms, and that mid-aged individuals, juveniles, and settlement phase individuals largely remain in-faunal, the next group of issues are: 'what proportion of the population swarms', and 'what size class swarm'. Here, it is necessary to obtain information on the swarm as well as on those crabs remaining as infaunal. Simply collecting animals that are swarming will not provide accurate information on the density and size classes within the population.

The fourth issue is 'what proportion of males *versus* females occurs in the population' and 'what proportion of males *versus* females emerges as a swarm'. This requires information on the swarm, the remaining infaunal subpopulation, and the subpopulation prior to swarming. Here again, simply collecting animals that are swarming will provide information on the sex ratio of the swarm, but not accurate information on the sex ratio of the population.

The fifth issue is behavioural variability. This matter is not concerned with static spatial variability in density, which would be addressed through random replicate sampling, but rather the matter of variability in crab behaviour which may result in variation in density of crabs spatially (vertically and laterally) in time, and variability in expression of their ichnological products on the tidal flat surface. This is reflected in behaviour of the crabs where, within the length and breadth of the soldier crab habitat, some crabs may emerge in patches while others create surface workings in patches, and yet others remain inactive.

The sixth issue is 'does the crab population partition with depth with respect to their size classes and to sex ratios'. This issue is not explored in this paper.

The seventh issue is that, at least for *M. occidentalis*, sampling can initiate a "predator avoidance" effect in the species – that is, during sampling, the crab may burrow deeper, and that during low tide while in general it may reside and be active at depths of 1 cm to 20 cm, it may burrow to depths of 40–50 cm to avoid perceived possible predation. There are indications from descriptions in the literature that other species of *Mictyris* generally behave in a similar manner. As a result, if sampling is too prolonged, coring the upper 20 cm may not retrieve all the animals that were residing under the selected sampling quadrat or core site, and excavating the animals from a quadrat by spade may also induce a "predator avoidance" effect, and cause the animals to burrow deeper than 20 cm, often to depths of 50 cm to avoid collection.

As mentioned earlier, the literature shows that there has been an emphasis in sampling swarming soldier crabs, and a number of studies have not recognised that a proportion of the population, in fact, had remained subsurface, that the sex ratio of the emergent crabs were different to the ratios of those that remained infaunal, and that the size classes also differed between emerged crabs and infaunal crabs. A contrast is the work of Takeda & Murai (2004) who sampled emergent and infaunal crabs, and Rossi & Chapman (2003), who sampled the crabs as infaunal animals.

Sampling methods investigated in this study

Various methods of sampling for soldier crabs are described below according to particular objectives including monitoring of fixed sites, monitoring of areas with pustular structures, depth of occurrence of soldier crabs, and the components of populations dynamics consisting of abundance (subsurface population, and swarms), size classes, and how many replicate samples are required. Most of the work was carried out at King Bay, Dampier Archipelago, however, data from Settlers Beach, near Cossack, and Broome are also included.

Sampling was carried out during a low tide period. It would be possible to sample at high tide using a boat equipped with a Van Veen grab or similar such devices, or using divers and hand corers. However, these latter methods would be logistically difficult and potentially statistically inaccurate with crab numbers likely to be under-represented due to crabs potentially being lower in the substrate to avoid predators during high tide, and more liable to escape collection attempts. Hence sampling during low tides is preferred.

A major problem with sampling on tidal flats, however, is that any excavations by spade, and/or enlargement of excavations around box cores to deepen the sampling, involves interacting with the water table. The water table under tidal flats generally is 10 (-20) cm below the surface during low tide (depending on time of sampling after the tide had receded). As a result, if the walls of the excavation were unsupported, sediment can slump into the excavation and, at all times at depth below 10–20 cm, the material being sampled was a sand/water slurry of varying thixotropy. Crabs normally are relatively mobile in the sand, but this mobility is accelerated when the matrix within which they reside has become a slurry. Also, the slurry itself is dynamic, flowing into excavations and wherever there is a positive hydraulic head, carrying with it crabs entrained in the hydraulic flow (this is particularly the case for juvenile crabs). This is a problem that results in artificial numbers of crabs and artificial occurrence of crabs at depth, as will be described later.

To determine the minimum number of replicate samples required to characterise the density of crab populations by coring, 15 box cores were sampled on 4 sites and the cumulative mean and standard deviation were graphed against cumulative number of cores. These results showed that a minimum of five box cores were required to characterise the density of the population (Fig. 3). From time to time, however, when crab densities were low, 10 or 15 box cores were used. Generally, for cylindrical cores, 15 replicates were used.

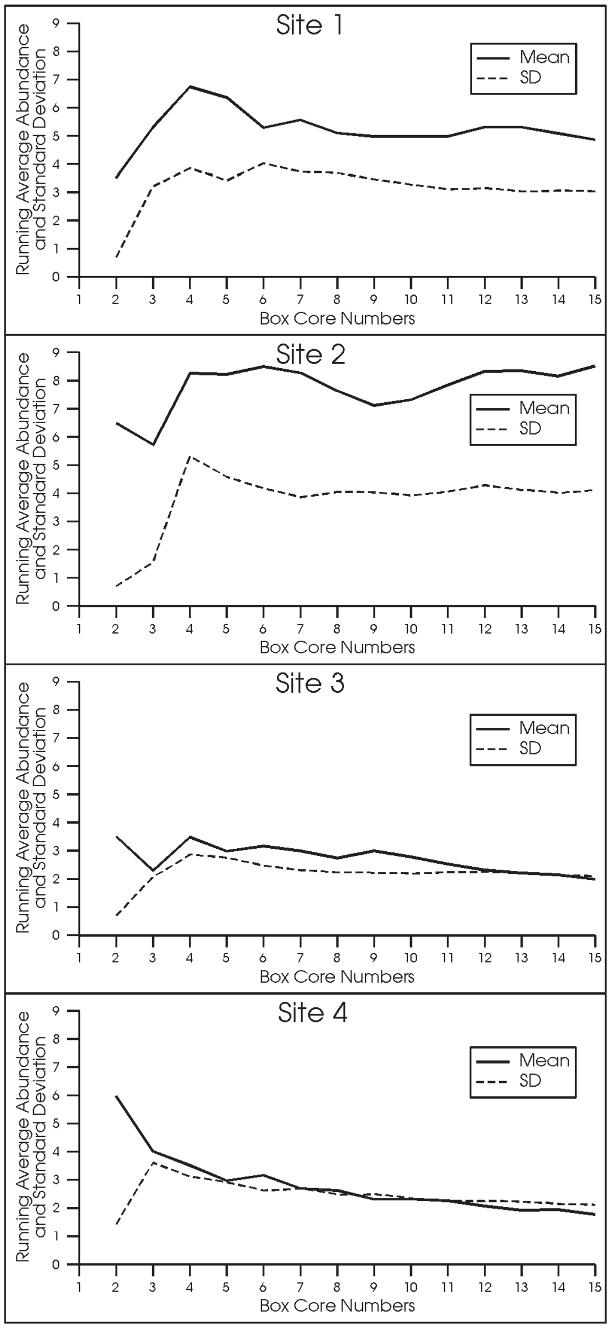

Figure 3. Results of cumulative box core (625 cm^2) sampling showing relationship of mean abundance and the standard deviation to sampling effort.

In all sampling procedures, the sediment retrieved was washed through a 1 mm sieve to retrieve the crabs for counting, measurement, and sex determination. In the earlier part of this study, crabs were returned to the laboratory for measurement. In the middle to latter part of this study crabs were immediately measured in the field and released, or kept and measured over the high tidal period, then released on the next low tide. For crab size, the crab carapace length (Unno 2008) was measured with vernier calipers. Adult soldier crabs exhibit sexual dimorphism and their sex was determined as follows (Unno 2008): male chelipeds are robust and have a large domed tooth on the inner surface of the moveable finger; female chelipeds are more slender and *sans* tooth on the moveable finger; sex can also be quickly determined by gently lifting the abdominal flap to expose either the presence or absence of the male twin peni.

Sampling of fixed sites

Sampling over time within the soldier crab habitat in King Bay, Dampier Archipelago and at Settlers Beach, Cossack (Fig. 1) was generally within a fixed area, marked by posts or position fixing.

The soldier crab habitat in King Bay is reasonably well defined (Unno & Semeniuk 2008). It is a sandy, mid-tidal to high-tidal flat, specifically a sandy ebb-tidal delta located at the mouth of a tidal creek (Semeniuk *et al.* 1982; Semeniuk & Wurm 1987; and Fig. 1 of Unno & Semeniuk 2008). The surface of the habitat is pocked with feeding excavations of stingrays, hence in detail the habitat is undulating, composed of a series of pools and low sand mounds. The sampling sites in King Bay are notated as sites 1, 2, 3 and 4 (Fig. 1B). Within these fixed sites, sampling by 5–15 randomly-located replicate box cores was carried out on consecutive tides, or consecutive days, or separated by two or three days for sites 1, 2, 3 and 4 (Fig. 1B). A two-tailed, unequal variance t-test was carried out to assess the significance of the difference of the means of densities of populations determined during different sampling times (with $p > 0.05$).

For some sampling periods at site 4, subsets of this fixed area were sampled, and these were notated as 4A and 4B. Sampling by box cores on a monthly and quarterly basis also was carried out at the fixed sites at King Bay, but this is the subject of a later paper.

The soldier crab habitat at Settlers Beach is the low-gradient mid-tidal to low-tidal sand flat, with sand mounds and shoals and ripples, at the toe of a moderately sloping sandy beach. Within the fixed sites at Settlers Beach, sampling by 10–15 randomly-located replicate box cores or cylindrical cores was carried out.

Sampling of areas with pustular structures

Given that the crab population appeared to be internally mobile, to ensure that crabs were collected within the habitat, in addition to random box cores on tidal flat surfaces (with or without pustular structures), sampling within a fixed area also focused on areas that exhibited pustular structures, *i.e.*, that there was surface evidence of infaunal crabs. Mapping of pustular structures and other crab workings was carried out and this showed that the areas of presence or absence of workings was variable (Figures 8 and 9 of Unno & Semeniuk 2008). The density of crabs under workings also was determined by transect A'-B' (Fig. 4) where five replicate box cores were sampled every two metres from the centre of an area of workings to an area where crabs appeared wholly absent. The transect A'-B' shown in Figure 4 crossed the area of pustular workings evident on the morning of 23rd July into the zone where crabs were in the subsurface (but would be producing pustular structures in the afternoon), and into the zone where crabs were absent. The results of sampling for crabs along the transect in Figure 4 for the morning of the 23rd July shows the extent of the crab population, as well as the relationship of crab abundance to crab surface workings, and the occurrence of crabs in the subsurface (but no pustular workings for the morning).

Depth of occurrence

These investigations attempted to determine the vertical range or depth of occurrence of the soldier crab within the substrate as this information is required to ensure that the depth of sampling was sufficient to capture a representative sample of the population.

Three types of sampling equipment were used to determine the depth of occurrence of soldier crabs within the substrate: 1. spade; 2. box core; and 3. cylindrical core. Four types of procedures were used: 1. large blocks of sediment removed by spade; 2. simple extraction of sediment from within a box core; 3. removal of sediment by combined box coring and spading; and 4. simple extraction of sediment from within a cylindrical core.

However, in detail, there were variations within these procedures because, as the sampling was being carried out, it became evident that the crabs responded to the sediment extraction by burrowing deeper. As a result, several types of sampling were undertaken: 1. with a view to sample slowly (*e.g.*, excavate layers in a box core, or layers in a quadrat by spade over several minutes); 2. with a view to sample rapidly (*e.g.*, excavate layers in a box core, or layers in a quadrat by spade within a half minute); 3. with a view to create a disturbance while sampling (*e.g.*, insert cylindrical cores forcibly by hammering); 4. with a view to create a minimal disturbance while sampling (*e.g.*, insert cylindrical cores by quickly and gently vibrating the core into the sediment).

When rapidly sampling sediment from the box cores or quadrats by spade the rationale was to extract the sediment containing the crabs at their natural normal depths as rapidly as possible in order to avoid distortion of results or loss of individuals due to their rapid burrowing deeper into the sediment, or laterally escaping in the subsurface, both in an escape-from-predator response. In these circumstances, with the box coring, cylindrical coring, and spading, the sediment was removed *rapidly* in horizontally layered blocks of 5 or 10 cm thick.

There also appeared to be a natural depth difference in the occurrence of the crabs in relation to tidal flats covered in pustular structures, or tidal flats not yet covered in pustular structures, and in relation to the time involved after the tide had receded and the tidal flat was exposed. As such, sampling was undertaken on tidal flats covered in pustular structures for comparison with sampling on tidal flats not yet covered in pustular structures, and undertaken on tidal flats as soon as the

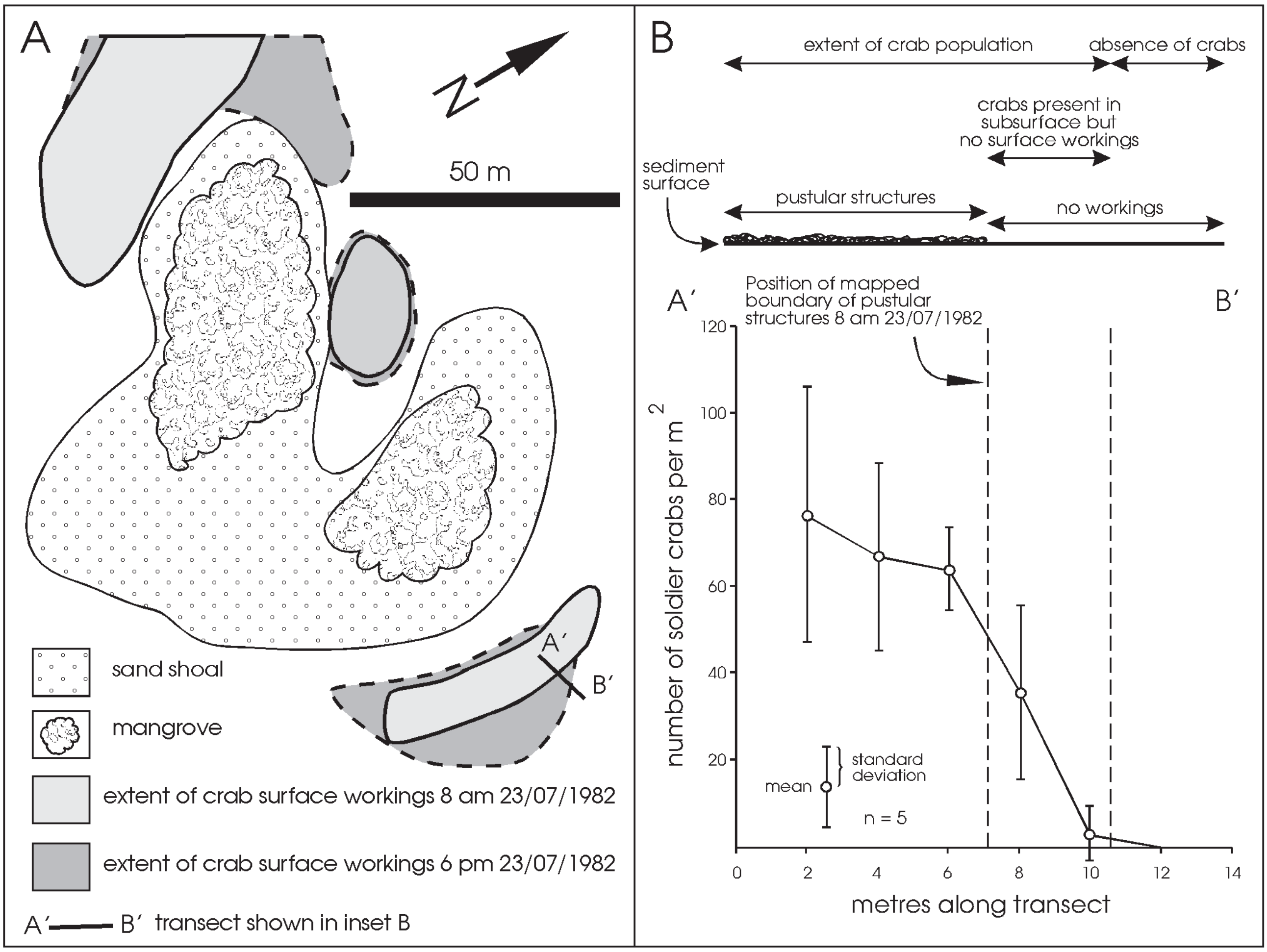

Figure 4. A. Map of the King Bay sampling sites (see Figure 1A this paper; and Figures 1, 8 and 9 in Unno & Semeniuk 2008), and the extent of crab surface workings during the morning and afternoon low tides of 23rd July 1982. B. Results of sampling for crabs along transect for the morning of the 23rd July: extent of the crab population, relationship of crab abundance to crab surface workings, and occurrence of crabs in the subsurface (but no pustular workings for the morning)

receding tide exposed the tidal flats for comparison with sampling on tidal flats hours after the tide had receded.

Since this was not a study of population dynamics and nor a study of the temporal variation in population densities, but of the efficiency of sampling style, box cores, cylindrical cores and spading were not always randomly located on the tidal flat but situated where crab workings were currently or previously evident to ensure that there were crabs in the subsurface. The presence or absence of soldier crab workings were also noted during the investigations. There also was exploration of whether crabs burrowed deeper under areas absent of pustular workings compared to areas with pustular workings.

At one stage, liquid nitrogen also was used to attempt collecting crabs *in situ* within the box core and cylindrical cores (*i.e.*, freeze the crabs *in situ*) to ensure that they did not burrow laterally or vertically, but this procedure was not successful.

Spading: Spading involved the removal of blocks of sediment 20 cm x 20 cm in area by 30 cm deep in two stages – removing a block of sediment 20 cm x 10 cm in area to 30 cm depth, followed by removing the adjoining block 20 cm x 10 cm in area to 30 cm depth. The two blocks of sediment were placed on a table, and squared off to the correct dimensions orthogonally, and then separated into horizontal 10 cm lots which were placed in plastic bags for later sieving. Five replicates using this method were sampled at the one site.

Box coring: Box coring involved use of 25 cm x 25 cm metal box cores, 15 cm, 20 cm, or 45–50 cm deep, inserted fully into the sediment of the habitat. Initially, sediment was rapidly removed with a trowel from the box core in layers of 0–10 cm, 10–20 cm, and for the deeper box cores 0–10 cm, 10–20 cm, 20–30 cm, 30–40 cm, and 40–45 or 50 cm. Later, for more precise determination of soldier crab occurrence in the layers of the vertical profile, the sediment was removed in 5 cm lots for the 15 cm and 20 cm deep box cores, *i.e.*, 0–5 cm, 5–10 cm, 10–15 cm, and 15–20 cm Samples retrieved from a given depth-related 10 cm thick or 5 cm thick layer were placed in a labelled plastic bag for later sieving, so that the subsampling of the box cores could be carried out as quickly as possible. Box coring using the 15 cm and 20 cm deep boxes was undertaken under areas covered in pustular structures, and areas free of pustular structures (just after the tide receded), and under conditions of rapid removal of sediment *vs* slow removal of sediment. Site 4 was sampled in this manner on a number of occasions between 2002 and 2008, with five replicate samples for each sampling time.

Combined box coring and spading: Combined box coring and spading involved inserting a box core into the tidal flat surface, excavating the content, excavating a moat around the box core, and then pressing the box core deeper, until a depth was reached with sampling when no crabs were being retrieved. The sediment was removed from the box cores progressively in 10 cm lots. This procedure was carried out rapidly and, in a second series of investigation, more slowly.

Cylindrical coring: Cylindrical coring involved three different procedures: 1. use of a 50 cm long PVC pipe with a diameter of 90 mm which was manually and gently vibrated rapidly its full length into the sediment; 2. use of a 50 cm long PVC pipe with a diameter of 90 mm which was hammered its full length into the sediment; and 3. use of a 50 cm long PVC pipe with a diameter of 150 mm which was manually and gently vibrated rapidly into the sediment. The sediment was then extruded from the base of the core in 10 cm lots and sieved. Fifteen replicates using this method were obtained. However, using 90 mm diameter cores involved too many replicates to achieve a sampling area comparable to five replicates of a 625 cm^2 per box core, and later in the sampling programme, the core diameter was changed to 150 mm diameter. This produced unexpected results in that the diameter of the core appeared to have an influence on the depth to which crabs were retrieved (see later).

Sampling populations while crabs were in juvenile stages

When the crabs are in their juvenile stage and wholly infaunal, sampling simply involved box coring or cylindrical coring, using five replicates for box cores and 15 replicates for cylindrical cores. The evidence that there have been no emergent crabs is the pustular surface of the tidal flat with no exit holes evident. Ichnological evidence that adults have emerged, and that some crabs are in the adult phase, includes exit holes, abundant discard pellets, and re-entry rosettes (Unno & Semeniuk 2008).

Sampling populations that were infaunal prior to swarming

When the crabs are at a stage when swarming may occur, estimates of population density cannot be accurately obtained when swarms are active on the surface (because a proportion of the population is still infaunal and a proportion of the population has emerged). In this context, it is important to sample prior to a swarm or after a swarm has fully re-entered the sediment. Soldier crabs tend to form swarms 30–60 minutes after exposure of the tidal flat surface. Sampling for population density, and capturing juvenile crabs, and male and female adults, therefore is best carried out after workings appear on the tidal flat surface, but before the swarming, using five replicates of randomly placed 25 cm x 25 cm box cores with sediment rapidly excavated.

In a given fixed area, the density of a pre-swarm infaunal population may be different to that after crabs have swarmed and reburied, as the adult crabs may have moved on from their site of emergence, but this is the natural temporal variation in density of population to be expected for a vagile infaunal and partly epifaunal, rapidly-moving species.

Sampling swarms concurrently with the subsurface population

Sampling of swarms was carried out by manual collection, harvesting up to ten at a time by scooping up the crabs from the surface, *preferably simultaneously by several collectors to ensure a rapid collection of large numbers of crabs before they re-enter the sediment*. Enough crabs were collected suitable for statistical testing (100 at minimum, and usually several hundred). Efforts were made by collectors to take random samples within their collection area and not bias the sample by collecting only the largest specimens. The use of several collectors is advisable as the crabs, after initially fleeing the collectors, will rapidly burrow into the sediment once a swarm is disturbed. Care was taken not to stampede the swarm over the area of workings which would be the site of the subsurface collection under the swarm. Concurrently with collecting specimens from a swarm, the part of the population which had remained resident under the sediment surface was collected by five replicate box cores.

Once the swarm was collected and individuals measured in the field, the swarm was returned to the site of collection so as not to deplete the population, as sometimes several hundred individuals may be involved.

Results of various sampling methods employed in this study

Monitoring of fixed sites

The sampling within fixed sites of the soldier crab habitat in King Bay on consecutive tides, or consecutive days, or separated by two or three days showed that at times the soldier crab population was relatively consistent in density and sometimes it markedly changed (Fig. 5). The crab population at the fixed sites were relatively consistent in density over the following consecutive days: 23rd and 24th March 1981 for site 1, and 29th and 30th December 2002 for site 3 (df = 24, p = 0.51 and df = 18, p = 0.46, respectively) and over two days for 7th and 9th January 2004 for site 3 (df = 9, p = 0.52). The crab population markedly changed in density over consecutive tides on 1st January 1984 for site 1 (df = 28, p = 0.0008), or consecutive days on 6th and 7th January 2004 for site 3 (df = 8, p = 0.13), and over two to three days over the period 21st and 23rd July 1982 for site 2 (df = 13, p = 0.0004), and 6th and 9th January 2004 for site 1 (df = 9, p = 0.001). At site 3, between the 6th and 9th January 2004, the crab population density changed from 154 ± 80 /m^2 to 313 ± 183 /m^2 to 256 ±34 /m^2, showing the diurnal and inter-diurnal variation in numbers of crabs and the variable patchiness of populations (manifest as changes in standard deviation around the mean abundance).

At the time of these sampling episodes, the structure of the population in terms of size classes remained the

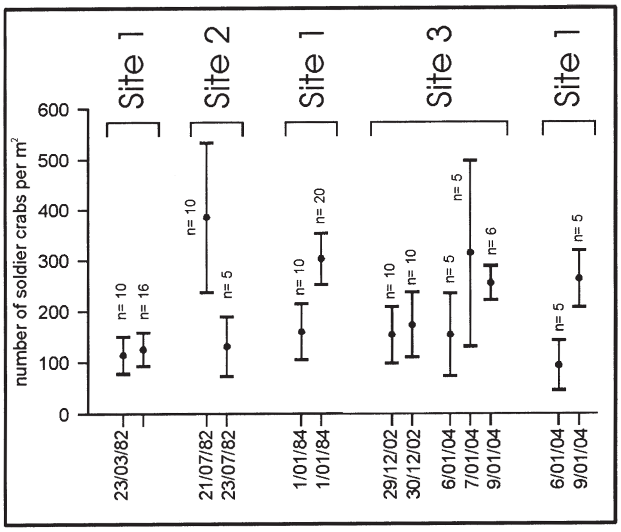

Figure 5. Results of abundance of crabs per m² (mean ± standard deviation) obtained by sampling of sites 1, 2 and 3 (see Figure 1A) over consecutive tides (1st January 1984 for site 1), consecutive days (23rd and 24th March 1982 for site 1, 29th and 30th December 2001 for site 3), or over an interval of two or three days (21st and 23rd July 1982 for site 2; 21st and 23rd July 1982, and 6th to 9th January 2001 for sites 1 and 3).

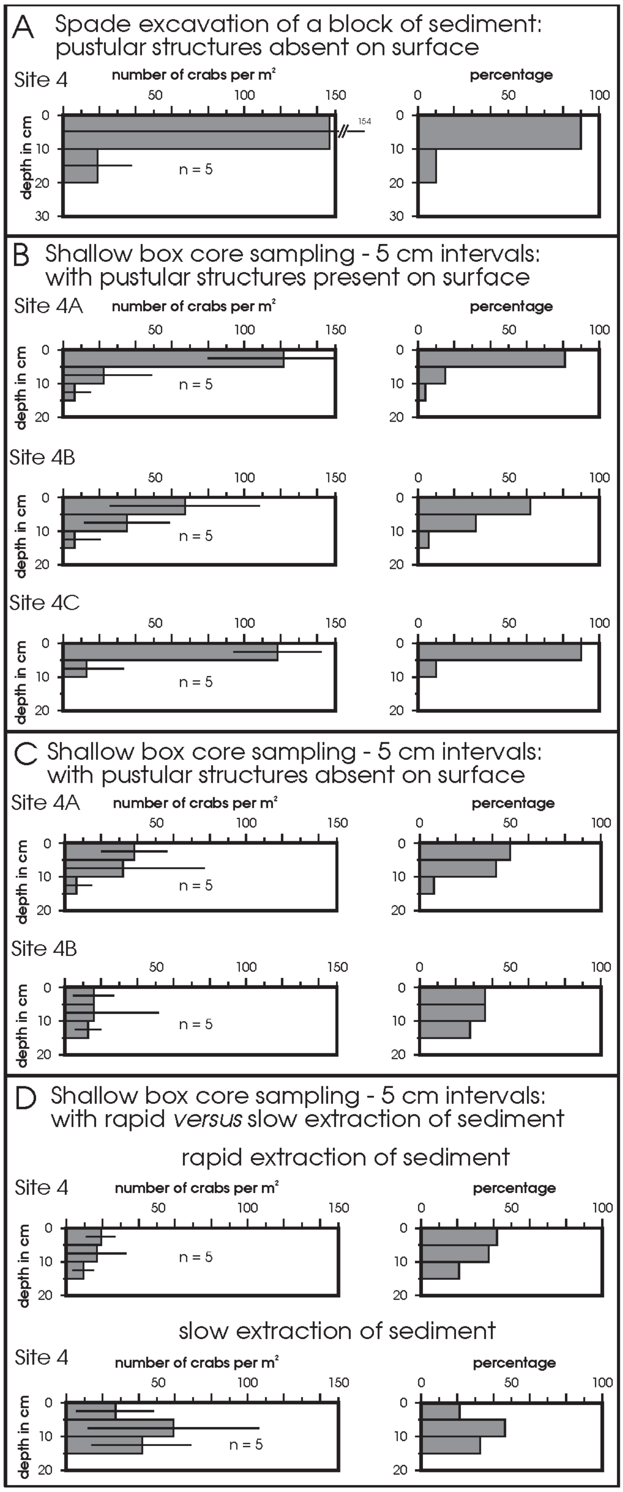

Figure 6. Results of sampling with spading and with shallow box cores to determine depths at which crabs occur under pustular zone and pustule free zones.

same, with no influx of juvenile recruits, and so the results for all sites and all times show the variation in abundance and the patchiness of crabs that occur at a fixed monitoring sites over short time frames.

Sampling of areas with pustular structures

The sampling for crabs along a transect grading from those areas with pustular structures to those without pustular structures showed that there were moderate to high numbers of crabs under the pustular areas during a morning low tide, and moderate to low to zero numbers of crabs in the areas free of pustular structures during that same morning low tide. In the afternoon, the area of pustular workings mapped during the morning extended further east by 4 m (Fig. 4). Crabs that occurred in moderate numbers in the subsurface in the morning, but did not produce workings at that time, were to become active in producing pustular structures in the afternoon.

The daily variability in the extent of working of the near-surface of the sediment by crabs to produce pustular structures has been described by Unno & Semeniuk (2008).

Depth of occurrence

Investigations of the depth of occurrence of the crabs using various methods resulted in variation of numbers of crabs between the various methods used. The reader should focus on the percentage occurrence of the crabs in the vertical profile for a given sampling method, *i.e.*, the capture of the crabs as presented by percentage occurrence down the sediment profile.

During the excavation of the sediment layers within a box core, it was observed, particularly for the slow excavations, that the crabs would be burrowing deeper when the layer above them was removed, exposing them, or placing them now in the very-near surface.

The results presented below show occurrence of crabs in 10 cm interval lots, and in 5 cm interval lots. When the results are presented in 10 cm lots, there is not an accurate estimate of the lower depth to which they occur. With 10 cm interval subsampling, where crabs are recorded at depths of 10–20 cm, crabs may not be present wholly over the interval of 10–20 cm, but may be present

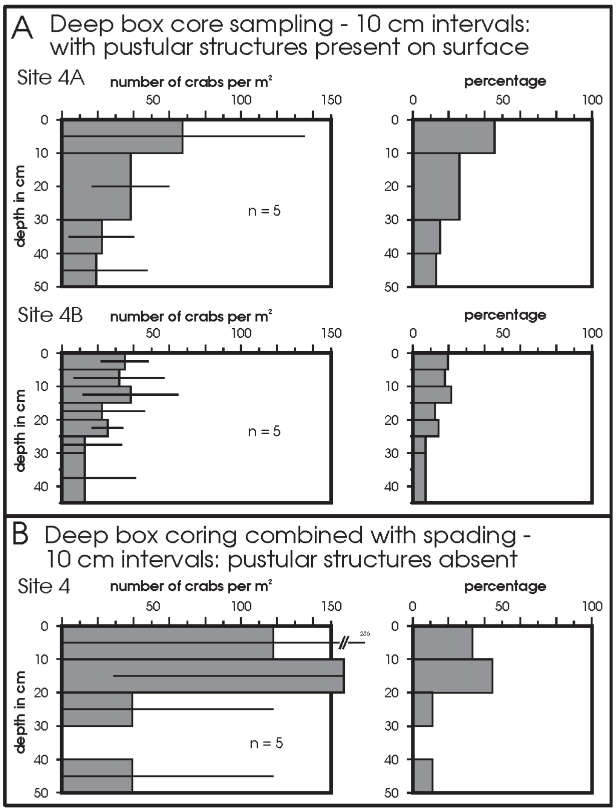

Figure 7. Results of sampling using deep box cores to determine depths at which crabs occur. A. Slow sampling of a deep box core. B. Slow sampling of a deep box core combined with spading.

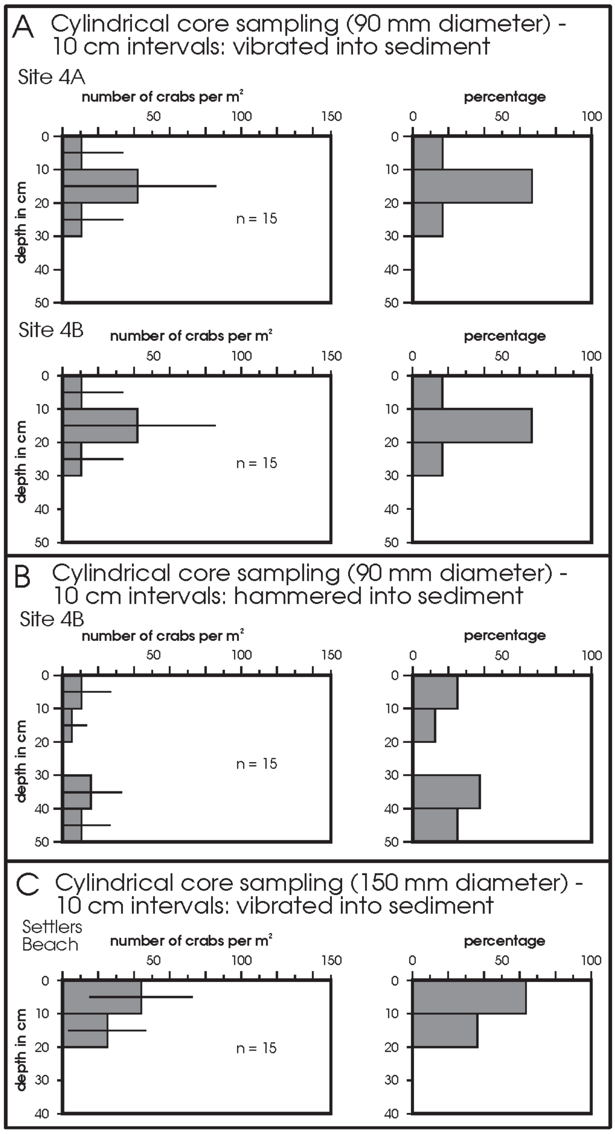

Figure 8. Results of sampling using cylindrical cores to determine depths at which crabs occur . A. 90 mm diameter cylindrical core gently vibrating the core into the sediment. B. 90 mm diameter cylindrical core hammering the core into the sediment. C. 150 mm diameter cylindrical core gently vibrating the core into the sediment.

only to a depth of 0–15 cm – the sampling interval of 10–20 cm may agglomerate the results of *n* crabs between 10–15 cm, and zero crabs between 15–20 cm. The more detailed interval sampling was intended to refine information as to what depth the crabs do occur.

The results of rapid removal of sediment blocks by spading are shown in Figure 6A. The 10 cm intervals of rapid subsampling show the crabs mainly to be confined to the upper 20 cm, and most of these present in the upper 10 cm.

The results from box coring show several patterns. Subsampling of sediment in 10 cm thick layers show that the majority of crabs to reside in the upper 30 cm of sediment, but more refined sampling in 5 cm thick layers showed that the crabs occurred in the upper part of the 20–30 cm level. There is a difference in depth of occurrence of crabs under areas of mats of pustular structures compared to areas where there are no pustular structures (Figs 6B and 6C). The results of sampling site 4B contemporaneously are shown in Figure 6C. Where pustular structures are evident, the crabs are dominantly in the upper 5 cm, and the remainder mostly in the 5–10 cm level. Where no pustular structures are evident, the crabs are still dominantly in the upper 10–15 cm, but more evenly spread in density over the 0–10 cm interval.

There is a difference in abundance and occurrence of crabs with depth with rapid sampling of a box core compared to slow sampling (Fig. 6D). With rapid sampling, denying the crab an opportunity to burrow deeply to escape collection, the crabs are in the upper 15 cm as described above, but more common in the 0–10 cm interval. With prolonged sampling, the crabs were retrieved from the interval 0–15 cm but were more common in the 10–15 cm interval.

The deep box cores penetrating to 50 cm depth showed similar results: the slow excavation of the sediment of a deep box core, with perturbations induced by water table effects and disturbance of the surface sediment, resulted in crabs occurring at deeper layers of the sediment (Fig. 7A).

The combined box coring and spading resulted in two types of results. For rapid sampling, with 10 cm intervals of subsampling, crabs are present in the upper 20 cm. With prolonged sampling, again with 10 cm intervals of subsampling, crabs are present to depths of 50 cm, as a result of their retreating in front of the descending excavation (Fig. 7B).

The results of the cylindrical coring showed interesting results in that the 90 mm diameter cores, if gently but rapidly vibrated in, yielded results that show that the crabs occur within 30 cm of the surface, while hammering in the core, as would be traditional in some sampling protocols to sample infauna, appeared to disturb the crabs and they occurred to depths of 50 cm (Figs 8A and 8B). In addition, the 150 mm diameter core showed crabs occurring in the upper 20 cm of the sediment profile (Fig. 8C), commensurate with the results of rapid box coring. This would indicate that a narrower diameter tube may be disturbing the crabs while it is being inserted and, in response, they burrow deeper.

These results of investigation into depth of occurrence are summarised in Table 1.

During the subsampling in layers it was observed that there is partitioning of size classes vertically. In general, the juvenile crabs tend to be located at shallow depth, and if crabs are located at 20–30 cm, these tend to be mature adults. This aspect of the population behaviour, however, is the subject of a later study.

Sampling populations while crabs were in the infaunal stage

Soldier crabs, when they are in their infaunal stage (juvenile stages), are the easiest to sample and provide the most simple of results. Though infaunally mobile, juvenile crabs largely are confined to the upper layers of sediment, and hence are readily retrieved by cores or spading. The numbers obtained from sampling reflect what crabs are present in the subsurface and these are mostly restricted to the upper 10 cm of the sediment profile. The variation in density temporally reflects their mobility in the subsurface and their removal by predators.

Sampling populations that were infaunal prior to swarming

The results of sampling populations that were infaunal prior to swarming provides estimates of population density in the habitat. Figures 4 and 5 show density of crabs in pre-swarm situations. Figures 9 and

Table 1

A comparison of the results of the various sampling styles.

Sampling style	Summary of results	Comments
rapid spading of sediment blocks, and subsampling in 10 cm layers	90 % of crabs in upper 10 cm; all crabs within upper 20 cm (Fig. 6A)	rapid sampling on a 10 cm sampling interval indicates crabs present within 20 cm of surface
shallow box cores under pustular structures and subsampling in 5 cm layers – rapid sampling	90 % of crabs in upper 5 cm, > 90 % crabs in upper 10 cm; all crabs in upper 15 cm (Fig. 6B))	pustular structures imply crabs are in the near-surface creating surface-parallel tunnels; the sampling confirms this
shallow box cores under tidal flat free of pustular structures and subsampling in 5 cm layers – rapid sampling	90 % of crabs in the upper 15 cm (Fig. 6C)	lack of pustular structures implies crabs are deeper in the subsurface; the sampling confirms this
deep box cores under pustular structures – slow sampling	< 50 % of crabs in upper 10 cm; all crabs decrease in abundance progressively to 45–50 cm (Fig. 7A)	prolonged sampling allows crabs to burrow deeper in front of the descending excavation
combined box coring and spading – rapid removal of sediment	90 % of crabs in upper 10 cm; no crabs present deeper than 20 cm	indicates on a 10 cm sampling interval that crabs present within 20 cm of surface
combined box coring and spading – slow removal of sediment	~ 40 % of crabs in the 10–20 cm depth interval; crabs continue to be present to depths in the interval of 40–50 cm (Fig. 7B)	prolonged sampling allows crabs to burrow deeper in front of the descending excavation and disturbance
cylindrical core 90 mm diameter rapidly but gently vibrated into sediment	~ 80 % of crabs in the upper 20 cm; all crabs within the upper 30 cm (Fig. 8A)	this sampling suggests that crabs occur to depths of 30 cm
cylindrical core 90 mm diameter slowly hammered into sediment	crabs are dispersed along the length of the core, and are most abundant in the interval 30–40 cm (Fig. 8B)	the disturbance of hammering appears to have caused the crabs to burrow deep and their occurrence over 50 cm may be an artifact
cylindrical core 150 mm diameter rapidly but gently vibrated into sediment	~ 65 % of crabs in the upper 10 cm; all crabs within the upper 20 cm (Fig. 8C)	this sampling suggests that larger diameter cores create less disturbance than 90 mm diameter cores, and the results from the 150 mm diameter cores is commensurate with the results of the rapid box core sampling and the rapid spading; with 150 mm diameter cores crabs appear to be restricted to the upper 20 cm

10 show the size structure of populations prior to a swarm. In comparison to size classes that remain in the subsurface when swarming occurs, it is clear that to obtain accurate estimates of density and of whole-of-population size structure, it is important to sample prior to a swarm.

The sampling of the crabs infaunally also shows their dynamic nature in terms of mobility, and density changes and stability on time-frames that are semi-diurnal, daily, across consecutive days, and over several days (Fig. 5). The abundance of crabs within a fixed sampling site of 5 m x 5 m in their habitat can remain relatively consistent over consecutive days, or change markedly between two tides on the same day, or over consecutive days, or over several days.

Sampling the subsurface population concurrently with swarms

Sampling the subsurface population concurrently with swarms showed that the population is partitioned with respect to size and to gender. Only adults swarm, with the juveniles remaining in the subsurface (Figs 9 and 10). Further, it is dominantly the adult males that swarm.

The results from Settlers Beach show the subsurface population is comprised dominantly of juveniles, and some adults. The adults are dominantly female. The emerged crabs are all adults, dominated by males in the size class 9–14 mm, and dominated by females in the size classes 7–9 mm. Pre-swarm sampling shows that the subsurface population is dominated by juveniles, and where sex could be determined, the population was mixed male and female.

The results from Broome show the subsurface population that remained buried during a swarm was dominated by juveniles, with some adults (mainly males). The swarm was dominated by male adults with some female adults in the 9–11 mm size class.

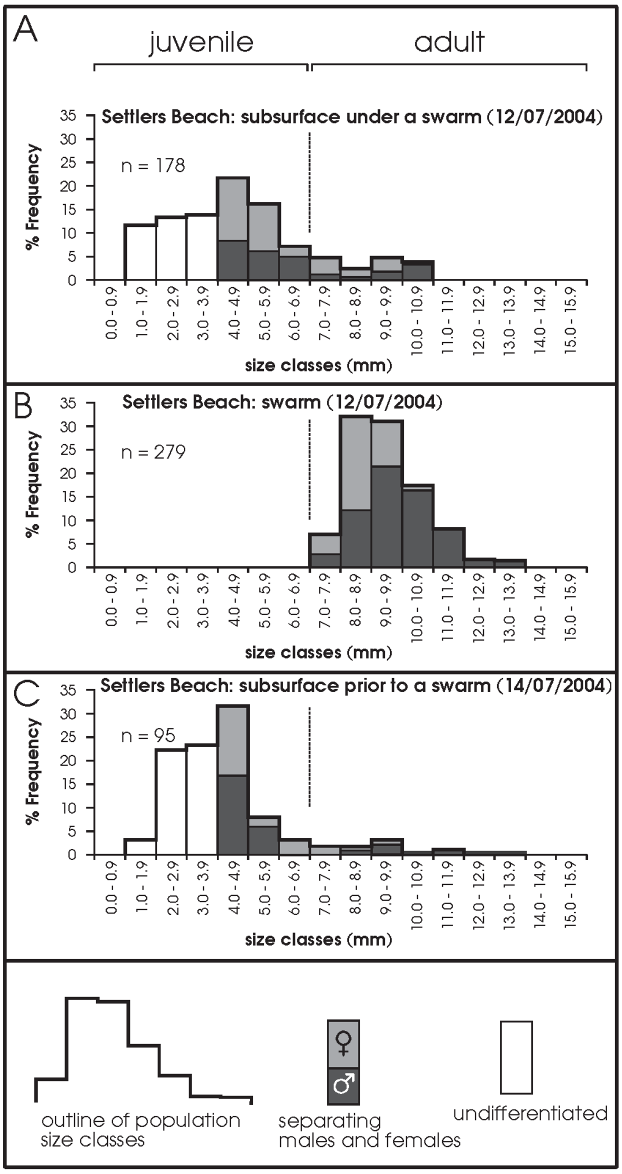

Figure 9. Population structures of soldier crabs at Settlers Beach. The ratio of males to females for a given size class also is shown. A. Population structure of the crabs that remained infaunal during a swarm on July 12th 2004. B. Population structure of crabs that were swarming on July 12th 2004. C. Population structure of crabs as infauna before a swarm emerged on July 14th 2004.

Discussion and Conclusions

The investigation of sampling methods for the Western Australian soldier crab highlighted some difficulties with methods that have been employed elsewhere to date in the general study of the behaviour, population dynamics, population density, and determination of sex ratios of species of *Mictyris*. Notwithstanding that different species of *Mictyris*, when examined in detail, may have varying behaviour and autoecological responses to their environment (as noted in the Introduction), there are many characteristics they share in common (such as swarming, infaunal behaviour, and some aspects of their ichnological products) allowing the principles of this paper to be applicable in a wider generic context. That is, there is enough information in descriptions of the behaviour and population studies of the various species of *Mictyris* and the methods used to study them to indicate that the results of this study have applicability elsewhere, and to compare with the results of this study and to highlight some problems in sampling that have occurred to date.

Generally, soldier crabs have not been perceived to be infaunal, but rather as "crab armies". Many of the studies in terms of population dynamics and determination of sex ratios are carried out only on emergent crabs in swarms, apparently with a perception that the swarms represent the whole of the population (Dittmann 1998, and the initial stages of the work of Takeda & Murai 2004), though there are exceptions to this (*e.g.*, Nakasone & Akamine 1981; Takeda 2005). Consequently, where crabs in a swarm are viewed as representing the whole population, there is no accounting for juveniles and adult females in the subsurface, both of which in fact may numerically comprise the greater proportion of the population. As such, generally, sampling of soldier crabs has not been designed to address the full range of behavioural modes as related to size classes and sex within the population over their life stages.

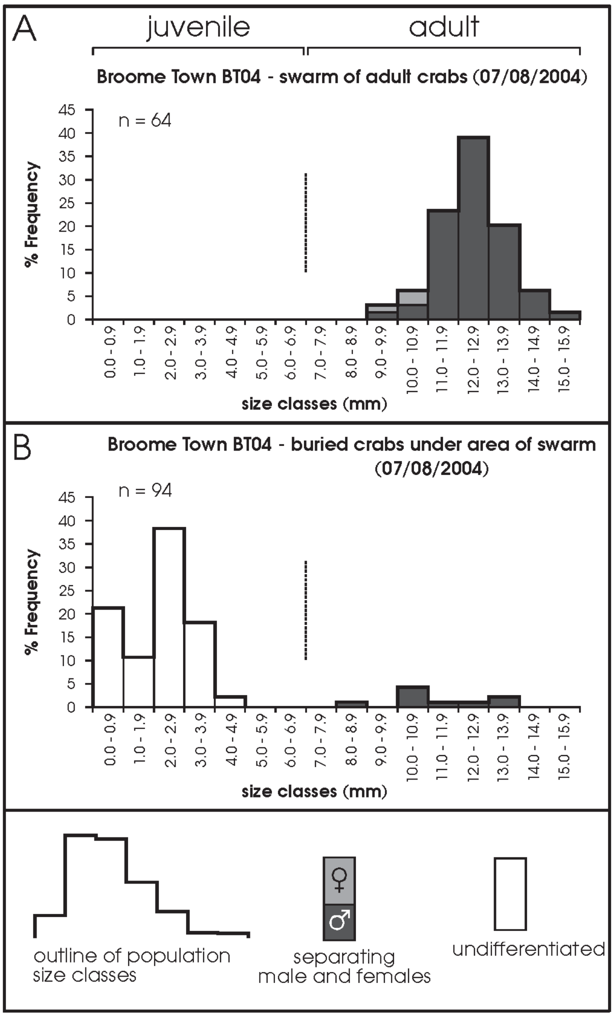

Figure 10. A. Population structures of soldier crabs at Broome. The ratio of males to females for a given size class also is shown. B. Population structure of crabs that were swarming on August 7th 2004. B. Population structure of the crabs that remained infaunal during the swarm on August 7th 2004.

The information deriving from this study and that of Unno & Semeniuk (2008), shows that the Western Australian soldier crab is *largely* infaunal, and emerges only in its late adult stage. Moreover, not all adults emerge for a given swarm. Adult males dominate the swarm with a residual complement of juveniles and female adult crabs remaining in the subsurface. Population studies of soldier crabs need to address the whole-of-population, and thus sampling design has to accommodate the various behaviour of the population as it proceeds through its life stages.

Some of the more specific implications of the sampling results deriving from this study are discussed below.

While many non-sessile organisms on a tidal flat lend themselves to fixed sites for long-term sampling within their habitat because they are not especially mobile or markedly vagile (*e.g.*, species of the crabs *Uca*, *Sesarma*, or *Neosarmatium*, and the thalassinidean shrimp *Upogebia pusilla*, inhabiting relatively fixed or semi-permanent burrows, or worms resident in u-shaped burrows; Lawry 1966, Dworschak 1983, Wolfrath 1992, Emmerson 2001, Layne *et al*. 2003), soldier crabs present themselves as a challenging organism for sampling. While their habitat may be long-term and permanent (for example, the soldier crab habitat in King Bay has been consistently and annually inhabited by these crabs for over 30 years), the soldier crab itself is quite mobile laterally and vertically within this habitat. Sampling for population density will detect fluctuations in abundance that is not necessarily reflecting intra-annual or inter-annual variation in the whole population (resulting, for instance, from local depletion by death or predation, and from regionally-induced recruitment) but rather intra-habitat adjustment and migrations. Thus population density at a fixed site may fluctuate on consecutive tides, or consecutive days, or separated by two or three days (Fig. 11). This factor has to be borne in mind when assessing variation in crab numbers for interpreting population dynamics.

Since the activity of soldier crabs is variable, with workings and/or emergences appearing or not appearing in different locations within the habitat over consecutive low-tidal periods, pustular structures can provide a ready tool for assistance in monitoring a population. The presence of workings is a good indication of the subsurface presence of soldier crabs. However, sampling only where there are pustular structures, and moving away from fixed site areas for monitoring will result in biased sampling. The best approach to obtain a whole-of-population assessment is to map the areas of pustular structures, and then sample in transects across pustular zones to pustule-free zones to obtain an estimate of crab density under the workings *versus* that under pustule-free areas. Estimating density of crab populations needs to involve a process of mapping or delineating the extent that pustular areas are developed and concomitantly collecting crabs by sediment extraction.

Within a fixed site area, the optimum time to sample to estimate population density is after workings have commenced and pustular structures and tunnel structures have appeared on the tidal flat surface. Thus when crabs are nearest to the surface, sampling will ensure that all the crabs under a given sampling quadrat will be retrieved. If exit holes and rosettes are evident, or there are swarms of adult blue crabs, it is too late for sampling the whole population. Approaching a swarm may result in the crabs firstly attempting to run from the perceived predator, and then secondly, rapidly reburying themselves to avoid the researcher and, consequently, the site of coring may have been compromised in terms of natural density of crabs and distribution of size classes. In this context, sampling to estimate the density of the whole-of-population at a fixed site requires pre-swarm sampling.

In the previous studies, it appears that the complex behaviour of the soldier crab in response to sampling procedures also has not been addressed. In this study, different sampling styles resulted in different numbers of crabs being retrieved or different depths that the crab occurred, due to disturbances propagated by the sampling equipment, or the length of time taken to sample, as well as effects due to substrate perturbations during sampling, the effects of a shallow tidal flat water table (on sediment, crabs and sampling), and the watersaturated sand responding to the excavations and sampling, (*e.g.*, the effects of small-scale hydraulic heads developed during sampling, which can entrain small crabs). The greatest effects or perturbations occur where adults rapidly burrow deeper to avoid the "predator" researcher, or where small juveniles (of lesser specific gravity than, but of the same size as coarse and very coarse sand, *i.e.*, ~ 1–2 mm) are entrained in a slurry. The results are that crabs appear to occur deeper than they would occur naturally; not all crabs may be retrieved, and spurious numbers of juveniles may be incorporated into the sample. To circumvent these problems where there are only abundance estimates, size classes, and sex ratios under a given area required in population studies, the sediment containing soldier crabs should be sampled when pustular structures have appeared (in sufficient density to form a mat) by box cores, or with a = 150 mm diameter cylindrical core (both of which ensure that crabs remain confined inside the walls of the core), or rapidly excavated by spade in a large block (*i.e.*, as a large sediment block removed within 10–30 seconds).

Due to the infaunal and vagile nature of soldier crabs sediment, coring with rapid removal of sediment to address the escape response is suggested as the most appropriate sampling method. Square box cores are preferred to cylindrical cores because of ease of sediment removal. The box cores of dimensions 25 cm x 25 cm surface area and 15–20 cm deep ensure a 95 % probability of collecting organisms with living densities > 0.06 specimens per 1000 cm^3 (Dennison & Hay 1967). Preliminary coring carried out in this study to determine the depth of occurrence of soldier crabs during the low tide period, combined with previous field and aquarium observations (Unno & Semeniuk 2008), suggest that soldier crabs are resident within the upper 10 cm of the sediment. A sampling effort of five spatial replicates will result in a total sample volume of = 46, 875 cm^3. Sediment from cores is removed with hand trowels to be washed through a 1 mm mesh sieve to collect the crabs. While spading produced reasonable results when carried out rapidly as shown in Figure. 6A, in practice, it is the least reliable of the three methods because, if carried out in

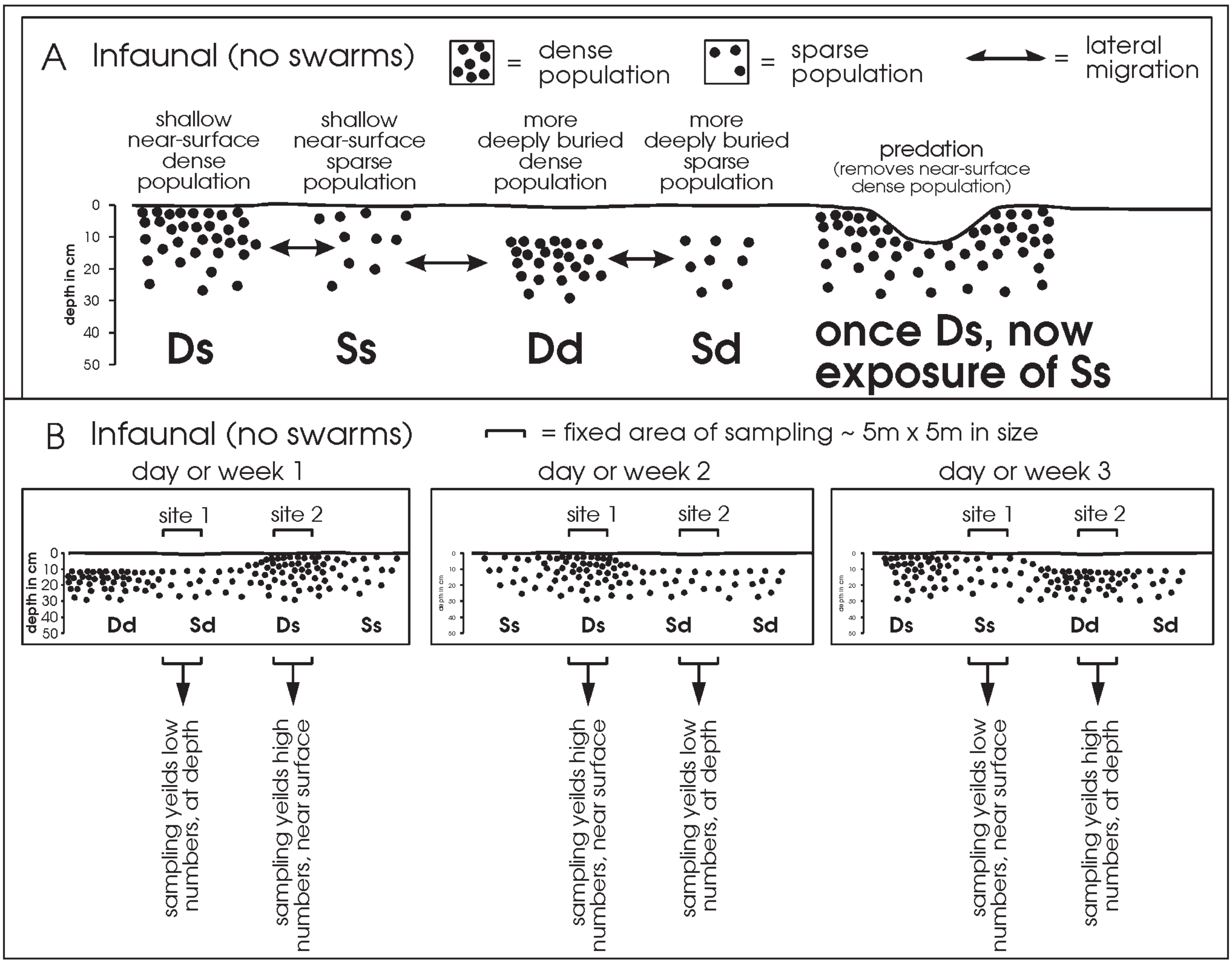

Figure 11. A. Idealised diagram showing the occurrence of dense and sparse infaunal populations of crabs that migrate laterally and vertically, and the effect of predators (that by excavations, expose the deeper occurrences of crabs). B. The varying results of low and high numbers of crabs located at depth or in the near-surface deriving from fixed study sites that intersect the spatially internally dynamic crab population.

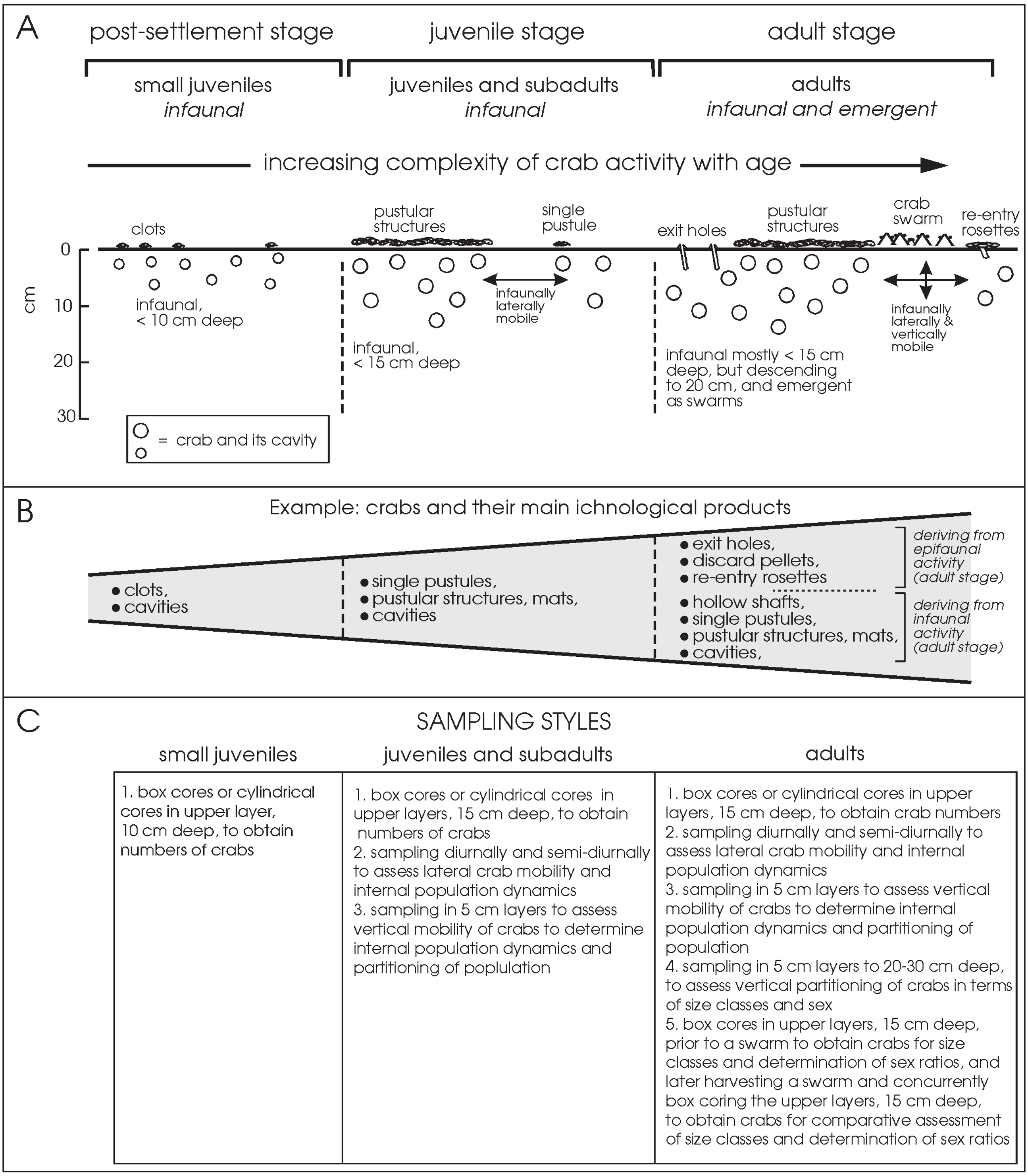

Figure 12. Idealised diagram show increasing complexity of crab behaviour as *M. occidentalis* passes through its life stages, the increasing complexity of information that can be derived and style of sampling required. A. Diagrammatic representation of activities of the soldier crab with respect to its three life stages. B. Example of the increasing complexity of crab behaviour reflected in its ichnological products. C. Suggested sampling that could be undertaken for each of the three life stages.

two stages, there is exposure of a 20–30 cm high wall of sand that is partly submerged by the tidal flat groundwater table, and that has a potential to slump.

The answer to the question of 'how deep does the crab burrow in natural situations?' may be different for the various species of *Mictyris*, and perhaps different for the same taxon in different environments. For the populations in King Bay, it appears to be < 20 cm, and mostly < 15 cm. However, even here, the depth of burrowing changes, depending on whether the crabs are relatively inactive and producing no pustular structures (then they are in the lower part of the interval 0–20 cm), or relatively active and producing pustular structures (then they are in the upper part of the interval 0–20 cm).

Table 2

Suggested investigations and sampling style for the different life stages of the soldier crab.

Infaunal post-settlement juvenile stage

Objective	Suggested methods
depth of burial	determine depth of burial of crabs for a given habitat in a region using box core or cylindrical core, subsampling in 5 cm layers
population density	carry out replicate box coring or cylindrical coring in a fixed site to a depth determined by preliminary assessment of the depth to which the crabs are burying themselves

Infaunal juvenile to subadult stage

Objective	Suggested methods
depth of burial	determine depth of burial of crabs for a given habitat in a region using box core or cylindrical core, subsampling in 5 cm or 10 cm intervals
variation of depth of burial over a diurnal or semi-diurnal period, or a longer period (intra-population vertical migration)	sampling diurnally or semi-diurnally, or over 2–3 days, to determine depth of burial of crabs for a given habitat in a region using box core or cylindrical core, subsampling in 5 cm or 10 cm intervals
population density	mapping pustular structures in a fixed site to assess extent of soldier crab occurrence, replicate coring using box coring or cylindrical coring along transects across the pustular zones into the pustule-free zones (that were determined earlier), to a depth determined by preliminary assessment of the levels to which the crabs are burying themselves
assess intra-population lateral mobility	sampling in a fixed site by box cores or cylindrical cores semi-diurnally or diurnally (*i.e.*, on consecutive tides, or consecutive days), or separated by two or three days
determine partitioning of population in vertical profile in terms of size classes over time of a low-tidal cycle	sampling using box core or cylindrical core, subsampling in 5 cm or 10 cm intervals, from time of first exposure of tidal flat to later high tide inundation
determine partitioning of population in vertical profile in terms of sex over time of a low-tidal cycle	sampling using box core or cylindrical subsampling in 5 cm or 10 cm intervals from time of first exposure of tidal flat to later high tide inundation

Infaunal to emergent adult stage

Objective	Suggested methods
depth of burial	determine depth of burial of crabs for a given habitat in a region using box core or cylindrical core, subsampling in 5 cm or 10 cm intervals
variation of depth of burial over a diurnal or semi-diurnal period, or a longer period (intra-population vertical migration)	sampling diurnally or semi-diurnally, or over 2–3 days, to determine depth of burial of crabs for a given habitat in a region using box core or cylindrical core, subsampling in 5 cm or 10 cm intervals
assessing infaunal intra-population lateral mobility	mapping pustular structures to assess extent of soldier crab occurrence sampling in a fixed site by box cores or cylindrical cores, semi-diurnally or diurnally (*i.e.*, on consecutive tides, or consecutive days), or separated by two or three days
population density in a pre-swarm situation, or population density when the crabs are in a phase of not swarming	mapping pustular structures and ichnological products deriving from emergence to assess extent of soldier crab occurrence replicate coring using box coring or cylindrical coring along transects across the pustular zones to the pustule-free zones, that were determined earlier, to a depth determined by preliminary assessment of the levels to which the crabs are burying themselves repeat sampling semi-diurnally or diurnally (*i.e.*, on consecutive tides, or consecutive days), or separated by two or three days
partitioning of population in vertical profile in terms of size classes, over time of a low-tidal cycle, in pre-swarm situations, or when the crabs are in a phase of not swarming	sampling using box core or cylindrical core, subsampling in 5 cm or 10 cm intervals, from time of first exposure of tidal flat to later high tide inundation
partitioning of population in vertical profile in terms of sex, over time of a low-tidal cycle, in pre-swarm situations, or when the crabs are in a phase of not swarming	sampling using box core or cylindrical subsampling in 5 cm or 10 cm intervals from time of first exposure of tidal flat to later high tide inundation

Table 2 (cont.)

structure of population, in terms of size classes and sex ratios, of the crabs that remained infaunal during a swarm for description and for comparison with the swarm	replicate coring in the area under the swarm, or from where the swarm emerged using box cores or cylindrical cores to determine numbers, size classes, and sex ratios repeat sampling semi-diurnally or diurnally (*i.e.*, on consecutive tides, or consecutive days), or separated by two or three days
epifaunal population characteristics during a swarm for description and for comparision with the crabs that remained infaunal during the swarm	harvesting the individuals during a swarm for determination of size classes and sex ratios

Soldier crabs inhabiting moderately steep sandy beaches, freely and rapidly draining the tidal groundwaters, may burrow deeper than those in King Bay. The imperative before commencing a sampling programme, therefore, is to determine to what depth a given species will burrow in a given habitat for a given region. Effectively, this would be a pilot study of sampling procedures before proper sampling is designed (Principle 5 of Green 1979).

Investigations to determine depth of burial of crabs, and the changes in abundance, or size classes, or sex ratios, vertically (as related to time after low tide, or fall of water table, or day-time *versus* night-time) requires subsampling in layers. This study shows that this can be effectively achieved by rapidly subsampling layers downwards in box cores, subsampling layers from whole blocks of sediment removed rapidly by spade as a single unit, or inserting a cylindrical core extracting it and extruding the sediment from its lower end in 5 cm or 10 cm lots. Where there is investigation of the potential of partitioning of crab size classes and/or sex with depth in the sediment profile, semi-diurnally related to the tides, diurnally, or over seasons, then fine scaled subsampling of sediment layers needs to take place. In all procedures, the sampling and subsampling should be carried out as rapidly as possible. Excavations of large quadrats (*e.g.*, 50 cm x 50 cm or 100 cm x 100 cm), where the sediment is planed off in 5 cm or 10 cm layers runs a risk firstly that where the planed layer is excavated to below the water table the sediment will slurry and be locally mobilised into the quadrat from the wall, or mobilised within the quadrat, thus mixing layers adjacently or vertically by water table effects, and secondly that the crabs will burrow deeper to avoid the researcher " predator", all of which can compromise the results.

Determining depth of burial and that all crabs have, in fact, been fully collected from under a quadrat, or box core or cylindrical core, and that the sample retrieved truly represents a subsample of the population for a given area satisfies Principle 6 of Green (1979).

Given the information above, and the increasing complexity of *M. occidentalis* as it passes through its life stages, a suggested protocol for sampling is shown in Figure 12 and Table 2. The information provided in Table 2 accounts for a range of objectives of any study, and the methods suggested to be employed to document the population features and the population dynamics of the crabs in the various stages of their life cycle. When there are mixed cohorts of the species, the patterns shown in Figure 12 will become more complicated.

Figure 12 suggests that changes in sampling style must follow changes in behaviour effected during the life stages of the crabs, and as the complexity of behaviour and ichnological products of the soldier crab changes, so too the sampling style must adapt, and become more versatile. For instance, soldier crabs in their infaunal juvenile stages are the easiest to sample and provide the most simple of results. These juvenile crabs, though mobile, largely are confined to the upper 10 cm layer of sediment, and hence are readily retrieved by cores or spading. The variation in density temporally reflects their mobility in the subsurface and their removal by predators. Sampling infaunal adult populations prior to swarming, or during the late adult stage when the crabs are in a temporary phase of not swarming, also provides estimates of population density. Such data obtained on population density, whether obtained from juvenile or adult stage crabs will show the dynamic nature of the population in terms of mobility, and density changes and stability on a semi-diurnal, daily, across consecutive days, and over several days. However, when the crabs have matured to the extent that they will swarm, there may be partitioning of the population in terms of size classes and sex both for the complement that emerges and for the complement that remains infaunal. When swarms occur, they are dominated by adult males, with a proportion of adult females and some adult males, and nearly all juveniles remaining in the subsurface, but at this life stage, there also may be some degree of partitioning of size classes and sex in a vertical profile for crabs that remained infaunal during the swarm. Thus, with adult populations with the propensity to swarm, sampling should no longer involve simple coring to collect crabs as it did with juvenile populations, but may have to address a range of complicated patterns to be able to characterise the population in terms of density, size classes, sex ratios, and behaviour.

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