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The relative role of intrinsic and extrinsic factors driving alongshore movement of swash-riding smooth plough shells, *Bullia rhodostoma*

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ABSTRACT

Animal movement underpins many ecological processes, and thus plays a key role in maintaining functional ecosystems. Sandy shores are an interesting model system on which to study animal movement because they are physically dominated, and the resident animals are generally very small (<1 mm–5 cm). However, beach macrofauna have a number of key adaptations that may equip them to harness the movement potential presented by the physical environment. Therefore, we aimed to quantify alongshore movement of the smooth plough shell snail, *Bullia rhodostoma*, and identify whether intrinsic (animal size) or extrinsic (beach morphology/swash climate) factors were stronger drivers of this movement. We captured, measured, and marked >2000 snails in each of six occasions (three on neap tides; three on spring tides), released them from a single fixed point, and recaptured them for four consecutive days following release. Each day, a standard suite of physical variables was also measured at low tide. The majority of snails maintained their position along the shore and remained close to the release point, however, some moved up to several hundred meters alongshore per day in both directions away from the release point. Overall, the average maximum daily displacement (daily "step-length") was 100 m; this was independent of animal size and tide state. However, when considering the maximum cumulative distance travelled (furthest distance attained relative to the release point per day), tide state and time were significant drivers of *B. rhodostoma* movement, with animal size playing a secondary role. The latter may be because of differences in animal density and foot size with increasing snail size, translating into differences in tidal migrations and alongshore displacement. Overall *B. rhodostoma*, like other beach macrofauna species, largely maintain their alongshore position at a local scale, but also have the potential to disperse much further even as adults. Of the variables measured, it seems that external forcing (beach morphology and wave/swash climate) is more important for driving *B. rhodostoma* movement than are intrinsic drivers (size). However, there are other intrinsic variables not tested here, e.g., state of hunger, that may be important as well. The limitations of the study notwithstanding, we present a low-cost, low-technology method for estimating beach-animal movement that could be easily applied to test other related questions.

1. Introduction

Animal movement is vital for many individuals to meet their fundamental needs of feeding, escaping predators, and finding mates and shelter, and thus ultimately plays a key role in maintaining functional ecosystems (Nathan et al., 2008). It can facilitate ecological processes, e.g., when animals serve as mobile links, and can shape biodiversity patterns, e.g., by altering intra- and interspecific competition, across a variety of spatial and temporal scales (Jeltsch et al., 2013). Furthermore, the extent to which animals can move has important implications for designing networks of conservation areas because it informs the requirements for reserve size and spacing to provide species with both sufficient protection and metapopulation connectivity (e.g., Green et al., 2015; Pittman et al., 2014). However, animals' observed trajectories are the result of a complex interplay between intrinsic (internal state; movement capabilities; navigational capacity) and extrinsic factors (environmental forcing) driving their movement (Nathan et al., 2008).

Beaches are interesting model systems on which to study animal movement and the relative role of intrinsic and extrinsic factors driving movement. This is because sandy shores are such physically-dominated ecosystems (McLachlan et al., 1993), and the animals inhabiting them tend to be particularly small (mostly <1 mm–5 cm; Harris et al., 2014; Koop and Griffiths, 1982). Consequently, beach fauna need multiple adaptations to survive life at the beach, like: rhythmicity (Jones and Hobbins, 1985; Yannicelli et al., 2001); good capabilities for burrowing, moving and orientating (Brown, 2001; Dugan et al., 2000; Nel et al., 2001; Odendaal et al., 1992; Pardi and Papi, 1952; Yannicelli et al.,

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2002); and excellent olfactory senses (Brown, 1961a; Brown, 1971). These adaptations notwithstanding, it is reasonable to expect extrinsic factors to override any intrinsic forcing of animal movement given the strength of the physical drivers relative to the size of the animals. The alternative, however, is if beach macrofauna can harness the potential for extrinsic-driven movement (e.g., by water movement) through intrinsic factors and their adaptations (e.g., rhythmicity and behavioural responses), as is evident in the across-shore tidal migrations of beach clams (Ellers, 1995) and isopods (Warman et al., 1991).

Most of the existing work on beach-animal movement to date has focused on the across-shore axis (land to sea), i.e., tidal/semilunar migrations and land-sea orientation (e.g., Donn et al., 1986; McLachlan et al., 1979b; Warman et al., 1991), with just a few exceptions (e.g., Dillery and Knapp, 1970; Dugan and McLachlan, 1999). However, alongshore movement (shore parallel), and concomitant spatial distributions, are equally important. It has implications for population connectivity, gene flow, biodiversity dynamics (including the role of patchiness, competition and predation within beaches and among beaches), and consequent ecosystem goods and services provision at local scales. These are all key concepts and effects that we need to start quantifying given the particularly precarious position beach ecosystems are trapped in between burgeoning coastal development (Small and Nicholls, 2003) and rising sea levels (Nicholls et al., 2011). Here, the likelihood of increased habitat fragmentation and degree of separation between functional beaches is an already-observable certainty, additionally resulting in local extirpations (Hubbard et al., 2014).

Beach species without pelagic larvae are of greatest concern because their potential to disperse seems fundamentally less than those with pelagic larvae, and thus are likely to be impacted most by increasing habitat fragmentation (Ketmaier et al., 2003). In this study, therefore, we consider the alongshore movement potential of the Prosobranch plough shell, *Bullia rhodostoma*, a slow-growing, long-lived species. Individuals reach a shell length of 10 mm after one year and 40 mm after 10 years (McLachlan et al., 1979a), with their lifespan estimated at 15–20 years (Brown, 1971; McLachlan et al., 1979a). Although these animals have a larval phase, the larvae are benthic and lecithotrophic. Egg capsules have been observed at 4–12 cm below the sediment surface, with eggs hatching into miniature adults (Brown, 1971). Consequently, *B. rhodostoma* larvae have much less dispersive potential compared to that of free-living planktotrophic larvae, and thus alongshore movement by juveniles and adults may be critical to maintaining population connectivity.

B. rhodostoma snails are key scavengers on wave-swept sandy shores using two modes of movement: surfing and crawling, to reach wave-cast carrion (Brown, 1971; Brown, 2001), e.g., fish, jellyfish, and bluebottles. Because their olfactory senses are so acute, they emerge from the sand almost immediately when carrion strands (Brown, 1961a; Brown, 1971; Brown, 2001). They then catch the up-washing swash with their unusually large extended foot (Brown, 1964), and manipulate their bodies to surf towards the food. *Bullia digitalis*, for example, zig-zags across the triangular plume of scent from the carrion like a tacking boat, until it reaches the prey item (Brown, 2001). Surfing towards carrion often requires riding multiple swashes, and in between swash-riding, *B. rhodostoma* individuals crawl vigorously towards their goal, provided the sand is saturated with water (pers. obs., see also Brown, 1961b; Brown, 2001). Crawling is also observed on spring low tide when the saturation zone is wide, although it is not always clear what the reason is for their movement (pers. obs.). Unlike some other beach species whose movement can be affected by scoto- or phototaxis (e.g., Naylor and Rejeki, 1996; Pardi and Papi, 1952), *Bullia* spp. lack eyes, and a response to light could not be demonstrated in either the laboratory or the field (Brown, 1971). The other time beach-associated *Bullia* spp. move is during their across-shore migrations with semi-diurnal tides (McLachlan et al., 1979b). They do this by surfing with the up-washing and backwashing swashes during both the day and night (McLachlan et al., 1979b). Although the across-shore movement of beach-associated *Bullia* spp. is well documented, the extent of their alongshore movement is unknown.

Therefore, we aim to determine if *B. rhodostoma* snails do move alongshore or if they maintain their position on the beach, and if the extent of their movement (if any) is a function of intrinsic and/or extrinsic factors. Specifically, we: (1) quantify the distance travelled alongshore per day; (2) test whether this movement (if any) is a function of tide (spring/neap), animal size, and/or time; and (3) taking the preceding results into account, and if relevant, attempt to identify a primary driver of the alongshore movement out of a variety of potential environmental variables that may serve as extrinsic drivers, and animal density as a function of size. Although technological advances in biologging make it increasingly possible to track ever smaller animals for longer periods of time (Hussey et al., 2015; Kays et al., 2015), using commercial tracking devices is often prohibitively expensive, requiring researchers to seek more creative solutions to answer fundamental questions. A secondary objective, therefore, was to test the usefulness of a low-technology, low-cost method in addressing these questions. We hypothesize that *B. rhodostoma* can and does move alongshore, and that this is chiefly due to extrinsic forcing, and secondarily due to intrinsic forcing (as a function of body size). Consequently, we predict that alongshore movement will be greatest on spring tides when the tide range and wave height is larger. We also predict that smaller individuals will be carried further alongshore compared to larger individuals because they are smaller and less dense than the adults.

2. Material and methods

2.1. Ethics statement

Ethical clearance was granted by the Nelson Mandela Metropolitan University Animal Ethics Committee: A11-SCI-ZOO-018.

2.2. Study site and data collection

Field work was conducted on Kings Beach, a 1.4-km long dune-backed, microtidal, dissipative-intermediate urban beach in Port Elizabeth, South Africa (Fig. 1). The shoreline is orientated north-south, constrained by a harbour wall in the north, and by the McArthur Baths swimming amenities and a rocky outcrop in the south. At the start of each sampling event, approximately 2000 *B. rhodostoma* were collected by baiting the swash zone with fish (Fig. 1C). We set four size classes for shell length (small: 15–20 mm; medium: 20–25 mm; large: 25–30 mm; very large: >30 mm; animals <15 mm were excluded because they were too difficult to mark and effectively recapture), and tried to collect near-equal quantities of snails in each of these size classes. The length of each snail was measured with Vernier callipers (Fig. 1D), the shell towel dried, and the tip of the shell spray painted with a coloured paint (a different colour for each sampling event; Fig. 1F). Once the paint was dry, all individuals were released simultaneously from a single, fixed release point half way along the shore (−33.970000°; 25.646389°; Fig. 1B, E).

The snails were recaptured at low tide (around 9:00 am on spring-tide days; around 3:00 pm on neap-tide days) on each of four days following marking. The beach was divided into 30-m long sampling units; the first unit (0 m) centred on the release point, and increasing north (+30 m) and south (−30 m) along the shore (see Fig. 2). Snails were recaptured by baiting the saturation zone in each unit and collecting all marked individuals until no more were sighted for 2 min. Because the olfactory senses are so sensitive in *B. rhodostoma*, the response to fish bait is immediate, and 2 min of no recaptures was considered a sufficient cut-off time. Search effort was kept constant by having only two people searching each unit throughout the study period. Searching continued along the shore, north and south of the release point, until no marked individuals were found in three consecutive sampling units in each direction. Once captured, marked individuals were re-measured and released in the centre of the sampling unit from which they were