

THE BEHAVIOURAL AND SENSORY ECOLOGY OF
AGARONIA PROPATULA (CAENOGASTROPODA: OLIVIDAE),
A SWASH-SURFING PREDATOR ON SANDY BEACHES OF THE
PANAMIC FAUNAL PROVINCE

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ABSTRACT

The genus *Agaronia* includes dominant predators in the eu littoral zone of dissipative sandy beaches of the tropical Eastern Pacific, which show specific adaptations to this environment such as swash-surfing locomotion. We studied *A. propatula* in its natural habitat in El Salvador and Costa Rica, and performed field experiments to obtain insights into its ecology, behaviour and sensory physiology. *Agaronia propatula* is not attracted by carrion and preys mostly on the ubiquitous beach snail *Olivella semistriata*. This, however, reflects community composition rather than prey specialization; *A. propatula* is an investigative hunter and will, quite literally, attack everything that moves (with the notable exception of echinoids). Prey is identified at short range by tactile and, to a lesser degree, by chemosensation located in the propodium. We found no evidence for long-distance sensory capabilities; *A. propatula* rather seems to rely on the regular physical structure of its wave-dominated environment when it moves between its shallow subtidal resting zone and its upper intertidal hunting grounds where potential prey predictably congregates. On the other hand, behavioural patterns such as the rapid yet haphazard cruising of foraging individuals, or the complex prey capture sequence in which the prey is transferred to a metapodial pouch, are similar in *A. propatula* and *Oliva*. Thus, our results lead us to speculate that the development of behavioural features that proved adaptive in the intertidal environment was essential in the evolution of *Agaronia* from *Oliva*-like ancestors.

INTRODUCTION

Sandy beaches are among the most hostile environments for animals and plants (McLachlan & Brown, 2006). They are shaped by physical factors, in particular the rhythm of the waves and tides, and are characterized by the permanent turnover of the sediment on or in which the organisms live (Raffaelli & Hawkins, 1999; Little, 2000). Sandy beach organisms show specific behavioural adaptations to their dynamic environment (Palmer, 1973; Chelazzi & Vanini, 1988; Brown, 1996). Various molluscs, for example, move swiftly by 'surfing' the swash waves, using parts of their bodies as underwater sails. However, the bulk of the available literature focuses on the small number of model species for which quantitative ecological and behavioural results have been produced; in the case of surfing molluscs, these are clams of the genus *Donax*

and *Bullia* whelks (Brown, Stenton-Dozey & Trueman, 1989). Whether these results can be generalized and are applicable to other taxa remains unclear.

The macrofauna of dissipative sandy beaches of the Panamic faunal province (Pacific American coasts from Baja California to northern Peru) is often dominated numerically by one of two swash-surfing suspension feeders, the snails *Olivella semistriata* and *O. columellaris* (Caenogastropoda: Olivellidae) which may reach densities of thousands of individuals per beach metre (Olsson, 1923/1924; Schuster-Dieterichs, 1956; Aerts *et al.*, 2004; own unpublished data). It would appear that the removal of suspended particles from the sea water by these abundant gastropods is a key element of the cycling of organic matter on these beaches, but no quantitative data are available. Similarly, little is known about the most important predators of the *Olivella* species, namely members of the genus

Agaronia (Caenogastropoda: Olividae). Predation by *Agaronia* species on *Olivella* species can be easily observed on Panamic beaches and has been noted by several authors (Olsson, 1956; Seilacher, 1959; López, Montoya & López, 1988; Metz, 1995). However, no detailed information on behavioural and physiological aspects of the predator–prey relationships among the olivid gastropods that occupy key positions in the food webs of Panamic sandy beaches has been published.

Here we report field studies on *Agaronia* undertaken in El Salvador and Costa Rica with two goals in mind. First, we intended to characterize the predator's behaviour and sensory physiology with regard to its prey-capturing capabilities, in order to define this one piece of the food-web puzzle of Panamic sandy beaches. Second, we expected that a better understanding of the sensory ecology of *Agaronia* would contribute to the understanding of the adaptive diversification of olivid gastropods. In many aspects of its morphology and behaviour, *Agaronia* closely resembles *Oliva*, as for example in the peculiar manner in which the foot is used in prey capture and handling (Rupert & Peters, 2011). On the other hand, the genera differ in several important morphological, sensory and behavioural features. For instance, *Agaronia* lacks cephalic tentacles and eyes, whereas *Oliva* possesses both (Gray, 1839; Olsson, 1956). *Agaronia* readily performs 'tail' autotomy in response to attacks, although the 'tail'—the hind part of the foot—plays an essential role in prey capture (Rupert & Peters, 2011); autotomy has not been recorded for *Oliva* so far. *Oliva* species generally are nocturnal, whereas the activities of (at least Panamic) *Agaronia* can be studied during the day. Panamic *Agaronia* species have successfully occupied the eulitoral of dissipative sandy beaches, showing specific behavioural adaptations to this demanding habitat such as circatidal migrations by swash-surfing (unpublished results), a behaviour not observed in *Oliva*.

The taxonomy of *Agaronia* appears plagued by problems similar to those analysed in detail in *Oliva* by Tursch & Greifeneder (2001). The number of Panamic *Agaronia* species and their distinguishing criteria differ from author to author (Keen, 1971; López et al., 1988; Sterba, 2004), making it difficult to establish species identities routinely in the field. At this stage, however, we see no evidence for any ecological or behavioural differentiation among the intertidal, swash-surfing, actively hunting *Agaronia* populations that inhabit dissipative sandy beaches of the Central American west coast. Being unable to resolve the taxonomic issues at this time, we will refer to our study object as *Agaronia propatula* (Conrad, 1849) for pragmatic reasons (compare Rupert & Peters, 2011).

MATERIAL AND METHODS

Study sites and field observations

Observations of the natural behaviour of undisturbed *Agaronia propatula* were made on 29 beaches during seven field trips (four trips to northwest Costa Rica with 12 different locations from the Nicaraguan border to the city of Puntarenas; three trips to El Salvador with 17 locations along the entire coast) from November 2009 to May 2011. Types of behaviour that were observed regularly such as swash-surfing, rhythmic burrowing and the stereotypical prey-capture sequence were photographed and filmed with digital cameras. Videos for publication were prepared with ImageJ v. 1.38x (<http://rsbweb.nih.gov/ij>) and QuickTime 7 Pro (<http://www.apple.com/quicktime/>). Systematic field experiments (described below) were conducted at two dissipative sandy beaches, each of about 5 km length, which had dense *A. propatula* populations as well as suitable infrastructures: Playa Grande in the Marine National Park 'Las Baulas' in northwestern Costa Rica

(10°20'N 85°51'W) and the public beach of El Cuco in eastern El Salvador (13°10'N 88°06'W). At these beaches we obtained prey spectra by recording observed attacks and examining the contents of metapodial pouches.

Field experiments

Field experiments were conducted during the early rainy season in May/June 2010 (Costa Rica) and May 2011 (El Salvador) and focused on the role of mechanic and chemical signals in prey detection by *A. propatula*. For all tests, actively hunting specimens (i.e. animals that crawled over the sediment surface at low or intermediate tide) of intermediate size (shell length 28–40 mm, 2.2–6.9 g) were selected and the responses to stimuli applied at defined directions and distances were recorded. To ensure that each individual was used for one test only, animals that had been subjected to a test were collected and released after our work at a particular beach section had ended for the day. At least two tidal cycles were completed between consecutive working sessions at a given beach section.

To study the response to mechanical stimuli, natural prey and artificial baits that either moved or remained motionless were offered. Actively crawling *Olivella semistriata* of intermediate size (shell length 11–15 mm, 0.16–0.39 g) were picked up carefully and placed in the path of hunting *A. propatula* at 5–6 cm distance from the anterior edge of the hunters' propodium. These *O. semistriata* usually continued to crawl and, if they did, served as moving natural prey. Other *O. semistriata* were 'immobilized' by rolling them between finger tips, which caused them to retract and remain in their shells for up to 3 min. These specimens were also placed in the paths of hunting *A. propatula* and served as motionless natural prey. The responses to moving and motionless natural prey were compared to the responses to a variety of artificial baits (compare Fig. 3A below): plastic sticks (7–8 cm long, 0.70–0.80 g), wooden sticks (7–8 cm, 0.32–0.39 g), plastic-covered paperclips (bent to 7–8 cm length, 1.24 g), cotton swabs (4 cm, 0.16–0.19 g when wetted with sea water) and empty turritelliform shells (3.0–3.5 cm, 1.1–1.4 g) taken from the beach. To serve as a moving artificial bait, an item was held so that one of its tips touched the sediment 3 cm in front of a hunting *A. propatula* and was gently but rapidly vibrated. Motionless baits were items that were simply laid into the path of a hunter at about 6 cm distance. Each cotton swab was used only once to avoid carrying mucus or scent substances in the cotton material. The other items consisted of more inert materials; they were thoroughly washed with sea water after each test and reused. The proportion of tests in which an item evoked an attack response was recorded.

Responses to olfactory stimuli were tested using water that had been loaded with the scent of potential prey species. To obtain scented water, 20 *O. semistriata*, 40 *Echinolittorina conspersa/dubiosa*, 15 *Donax* sp. or 5 *A. propatula* were incubated in 40 ml sea water in a plastic tube (3 cm diameter) for at least 10 min. Similarly, one medium-sized (4–5 cm diameter) sand dollar (*Mellita* sp.) was kept in 10 ml sea water in a plastic Petri dish for the same period. Droplets of the scented fluids were placed either in front of a hunting *A. propatula*, or 5–8 cm above and 3 cm in front of the animal on the beach slope so that the scented water ran into the path of the hunter (compare Fig. 4 below). The number of cases in which this stimulus evoked an attack strike was recorded and compared to the attack rate evoked by the control (plain sea water).

To identify body regions in *A. propatula* that were responsive to mechanic and olfactory stimuli, a moving artificial bait (plastic stick as described above) or droplets of *Olivella*-scented sea water were applied at different positions next to the hunters' bodies as detailed in Figure 6 below.

Statistical analysis

Categorical data that could be represented in 2×2 contingency tables were compared using Fisher's exact probability (FEP) test (two-tailed). A helpful online calculator with explanations can be found on the website maintained by Richard Lowry at <http://faculty.vassar.edu/lowry/fisher.html> (accessed last on 7 January 2012). Mean values of continuous data were compared using Student's *t*-test (two-tailed).

RESULTS

General observations: functional morphology of foot

Agaronia propatula shows the typical features of the genus, lacking a defined head, tentacles, eyes and an operculum (Olsson, 1956). The anterior of the foot is shaped like a double-sided ploughshare. A pronounced groove separates the narrow propodium from the large metapodium (Fig. 1A). The latter has two lateral folds that can cover the anterior portion of the shell and the entrance of the mantle cavity. More posteriorly, the metapodium is flat and visually divided in most specimens by a distinctly pigmented transversal line, which marks an autotomy plane (Rupert & Peters, 2011). Irrespective of these morphological subdivisions, the foot represents two biomechanical elements, as becomes apparent when the snails perform searching movements while being held up in the air. In this situation, the anterior part of the foot, consisting of propodium and the anterior metapodium, forms a pointed 'snout' that probes the surroundings, while the posterior metapodium flattens and becomes concave ventrally (Fig. 1B; Supplementary material 1). The biomechanical antagonism of the two foot components in locomotion becomes apparent when hunting specimens accelerate by switching from the usual smooth gliding mode into a 'galloping' mode in which the posterior and anterior foot portions move forward alternately; we clocked 'galloping' snails such as the one seen in Supplementary material 1 at velocities in excess of 9 mm/s. *Agaronia* burrows by thrusting stepwise into the sediment at a shallow angle, indicating that it employs the common 'penetration anchor' *vs* 'terminal anchor' mechanism analysed by

Trueman & Brown (1992; Supplementary material 1). As in other burrowing marine gastropods, the subdivision of the foot of *Agaronia* provides the antagonistic actuators required (posterior foot: penetration anchor; anterior foot: terminal anchor).

The two elements of the foot are essential for the prey capture mechanism of *A. propatula*, which resembles that described previously for *Oliva* species (Marcus & Marcus, 1959; Olsson & Corvo, 1968; Taylor & Glover, 2000; Kantor & Tursch, 2001; Supplementary material 1). However, in contrast to most *Oliva* species, *A. propatula* hunts on beach sediments that are wet but exposed to air between incoming waves. Prey capture of *Agaronia* is therefore easily observed in the wild. Once a potential prey item is located below the sand surface, the snail extends the anterior foot rapidly to grasp the prey. If the detected prey is located above the surface, the anterior foot is raised during its rapid forward movement so that the prey is grasped from above. Such above-surface strikes make a surprisingly violent impression on the unsuspecting observer; they are particularly fast and powerful if they are carried out in the forward direction, because in this case they are supported by a simultaneous backward movement of the posterior metapodium, which balances the momentum of the striking anterior foot. In contrast, strikes to the left or right are visibly slower. In most cases in which the initial strike is unsuccessful, the snail immediately launches a second and sometimes even a third strike. These, however, usually are directed some 10–30° to the left or right of the direction of the initial attack (Supplementary material 2).

After a successful strike, the anterior foot with the captured prey bends ventrally and backward. At the same time, the posterior foot turns concave ventrally and bends ventrally and forward; like a dredger bucket, it takes up sediment and water but also encloses the oncoming anterior foot, which holds the prey item. This movement of the posterior metapodium is so powerful that it usually causes the animal to 'somersault' forward. The anterior foot is then pulled forward out of the pouch formed by the posterior metapodium, leaving the prey within the pouch. Next, the pouch contracts which, under favourable conditions, becomes visible as a forceful expulsion of water and sediment from the pouch (this can be seen in the

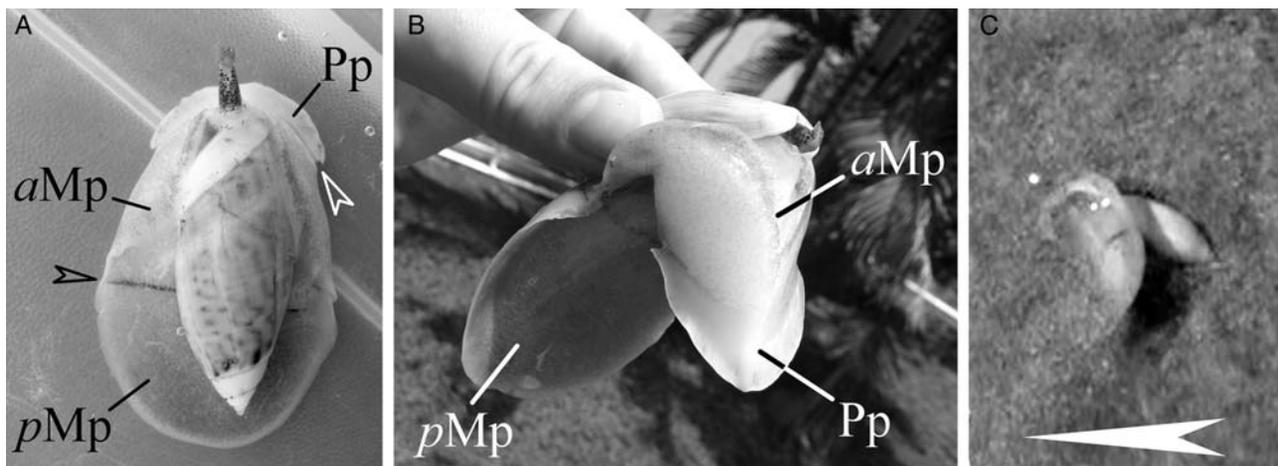


Figure 1. Functional morphology of the foot of *Agaronia propatula*. **A.** Dorsal view of a crawling animal (shell length 34 mm). The small propodium (Pp) is separated by a groove (white arrowhead) from the metapodium (Mp). The metapodium is divided visually into an anterior (aMp) and a posterior (pMp) portion by a distinctly pigmented, transversal hoop (black arrowhead) that marks an autotomy plane. **B.** Large specimen (shell length 46 mm); the anterior half of the foot performs searching movements in the air (compare Supplementary material 1) while the posterior half has assumed a spoon-like shape. This 'spoon' can be closed like a drawstring bag to form the metapodial pouch. **C.** Individual swash-surfing on a beach. Direction of water flow indicated at the bottom. The entire foot is expanded and functions as an underwater sail. The animal is lying on its right side as the shell is dragged along the sediment surface. Photographs taken at Playa Grande, Costa Rica.

movie by [Rupert & Peters, 2011](#): Supplementary material). Finally, the snail burrows rapidly into the sediment, dragging the prey within the metapodial pouch to a depth of several centimetres, where it can be safely consumed. Burrowing always follows a successful attack; we never observed *A. propatula* collecting multiple prey items in the pouch during a continuing raid as reported for several *Oliva* species ([Taylor & Glover, 2000](#); [Kantor & Tursch, 2001](#)). Since burrowing with, as well as without, prey occurs at similar speed in a stepping fashion, the most posterior, pouch-forming portion of the foot does not seem to be an essential functional element of the penetration anchor.

Similarly, the expansion of the posterior foot is not functionally essential for swash-surfing. Normally, surfing animals expand the complete foot and then are dragged along the sand surface by the water flow, lying on their right or left side (Fig. 1C). However, at 2 to 1 h before low tide, large numbers of *A. propatula* utilize the backwash of the last waves that reach across the intertidal plane to surf back to the lower beach zone that will remain submerged. We found that up to one-third of these swash-surfing individuals carry prey in their pouches, even when little or no hunting activity had been observable at the same location since the preceding high tide. This is circumstantial evidence suggesting that burrowed *A. propatula* keep captured prey in their metapodial pouches over prolonged periods rather than swallowing it. Thus it appears that *A. propatula* consumes prey while holding it in the pouch, as *Oliva* species do ([Marcus & Marcus, 1959](#); [Kantor & Tursch, 2001](#)).

Field observations: prey species and their detection

At Playa Grande (Costa Rica), the prey most frequently attacked and subdued by *A. propatula* (88% of all observed attacks and examined pouches) was the ubiquitous *Olivella semistriata* (Table 1). Equal proportions of the remaining attacks were directed at burrowing clams (*Donax* sp.), unidentified small (<1 cm) crustaceans and smaller individuals of its own species. The prey spectrum at El Cuco (El Salvador) was more diverse (Table 1, Fig. 2) which seemed to reflect the composition of the beach community. Common taxa of Panamic beaches such as burrowing clams (*Donax* sp.) and mole crabs (*Emerita* sp.) can be found at Playa Grande, but one has to search for them. In contrast, these animals literally are ‘all over the place’ at El Cuco and are collected effortlessly by the local population for food. *Olivella semistriata* was still the most frequently attacked prey species at El Cuco, but its proportion was reduced to some 60%, with bivalves contributing almost one quarter of all prey items (Table 1). While

Table 1. Prey spectrum of *Agaronia propatula* at Playa Grande (Costa Rica; $n = 89$) and El Cuco (El Salvador; $n = 54$).

| Prey species | Prey taxon frequency | |
|--|----------------------|-------------|
| | Playa Grande (%) | El Cuco (%) |
| <i>Olivella semistriata</i> (Gastropoda) | 88 | 61 |
| <i>Agaronia propatula</i> (Gastropoda) | 3 | 2 |
| <i>Donax</i> sp. (Bivalvia) | 4 | 18 |
| <i>Tivela</i> sp. (Bivalvia) | — | 4 |
| <i>Pitar</i> sp. (Bivalvia) | — | 2 |
| Unidentified small (<1 cm) crustaceans | 4 | 4 |
| <i>Emerita</i> sp. (immature, <2 cm; Crustacea) | — | 2 |
| <i>Emerita</i> sp. (mature, >5 cm, with soft exoskeleton; Crustacea) | — | 7 |

Prey frequencies include directly observed attacks and prey removed from metapodial pouches. Pouches never contained more than one item.

gastropods subdued by an *A. propatula* were always small relative to their predator (Fig. 2C, D), the less mobile bivalve prey items frequently reached the size of the *Agaronia* that had captured them (Fig. 2E, F). Interestingly, all mature *Emerita* sp. that we found under attack by an *A. propatula* were very much larger than their attacker (Fig. 2G, H) and had a soft and elastic carapace, indicating that they just had moulted. In all observed cases, the *Agaronia* were struggling, without immediate success, to burrow into the sand with the oversized prey. Whether such attacks on large mole crabs ultimately lead to the death of the prey remains unclear.

Among the echinoderms on Pacific sandy beaches of Central America, lunulate sand dollars of the genus *Mellita* are common ([Harold & Telford, 1990](#)). We found the animals regularly in the lower eulittoral of Playa Grande and El Cuco. Since we had never observed *Agaronia* attacking *Mellita* sp., we tested their interaction by placing a sand dollar in the path of a crawling snail so that they moved towards each other. Upon contact, the sand dollar continued on its way unimpressed, whereas the snail stopped briefly and then moved to the left or right, apparently to evade the sand dollar (five tests with different animals gave the same results). Thus, *A. propatula* seems to avoid echinoids. Similarly, carrion appears of little interest to *A. propatula*, as we never observed snails approaching, let alone feeding on, the dead jellyfish, crabs, fish, sea turtles, birds or fishery and kitchen wastes that we found washed-up on the beaches. This is an obvious contrast to the scavenging habits of South African *Bullia* whelks, the standard textbook example of swash-surfing snails ([Brown, 1982](#)).

Agaronia propatula preferred wet sand occasionally inundated by incoming waves and numerous animals crawled about the sediment of the lower and mid-eulittoral at low and intermediate tide. Evidently, these crawling specimens were actively hunting, as they almost always attacked moving prey that crossed their paths. In contrast, individuals that were resting motionless on the surface—this was most frequently observed on relatively dry sand when the tide was lowest—or that had started to burrow into the sediment seemed to be in a ‘peaceful’ mode, as we never observed them attacking approaching prey; neither could we provoke these animals to tackle artificial baits or respond to the scent of prey (compare field experiments below).

Interestingly, *A. propatula* typically attempted to burrow into the sand when they had landed at the end of a swash-ride, even if the spot where a surfing snail came to rest was located within a dense accumulation of *O. semistriata*. As we did not observe a single instance of an animal starting to hunt immediately after swash-surfing, it appears that *A. propatula* do not initiate swash rides to pursue specific prey items detected over long distances, as has been reported for *Bullia digitalis* ([Odendaal et al., 1992](#)). This conclusion is supported by the fact that long-shore distributions of hunting *A. propatula* and *O. semistriata* did not correlate. While generally abundant, the local densities of *O. semistriata* varied along the beaches, with high-density spots that moved or dispersed and reassembled elsewhere with each tidal cycle. *Agaronia* often formed similar hotspots but, contrary to our initial expectation, dense accumulations of *O. semistriata* were of no guiding value when we searched for locations with high densities of *A. propatula* to perform the field experiments described below.

Crawling, motivated hunters never probed the sediment surface with their siphon, and generally appeared unaware of prey at distances >3 cm. Potential prey animals were usually attacked when they were moving within about 2 cm in front of the predator. In contrast, motionless *O. semistriata* were frequently ignored, in some cases even if the hunting *Agaronia* literally bumped into them (Supplementary material 3). Crawling *O. semistriata* leave characteristic tracks in the sand.



Figure 2. *Agaronia propatula* and its prey. Prey species often can be identified within the *Agaronia*'s metapodial pouch; the aperture of an *Olivella semistriata* is faintly visible through the wall of the pouch in **A**, while the pouch has assumed the typical triangular shape of the captured burrowing clam (*Donax* sp.) in **B**. As a rule, captured gastropods are significantly smaller than the predator; **C** shows an *O. semistriata* and **D** a small *A. propatula* that we removed from the pouches of the large *A. propatula* seen to the right of their prey items. In contrast, captured bivalves retrieved from pouches often reached the size of the hunter; **E**, *Pitar* sp.; **F**, *Donax* sp. Other relatively immobile prey items such as mature mole crabs (*Emerita* sp.) shortly after moulting are attacked even by significantly smaller *A. propatula*; **G** shows an *Agaronia* together with the mole crab with which it was found struggling. In **H**, an *Agaronia* attempts to burrow into the sand with a mole crab too large to fit into its metapodial pouch. Photographs were taken on the beach at El Cuco, El Salvador.

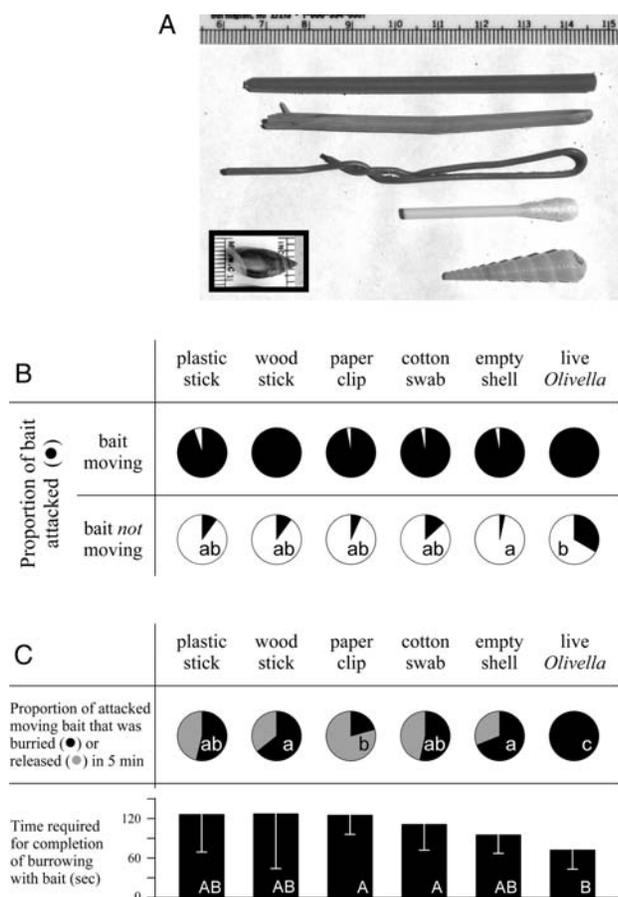


Figure 3. Response of *Agaronia propatula* to mechanic stimuli. **A.** Artificial baits used (from top to bottom: plastic stick, wood stick, paper clip, cotton swab, empty shell); the inset shows the natural prey, *Olivella semistriata*, at the same scale. **B.** Proportion of attacks on the five artificial baits and *O. semistriata* that were moving (upper row) or motionless (lower row); $30 < n < 36$. All differences between the responses to the same bait (moving vs motionless) are significant at $P < 0.0001$ (FEP test). In the lower row, pie charts carrying the same letter are not significantly different at $P < 0.01$ (FEP test). **C.** Upper row, proportions of the baits attacked that, within 5 min of the attack, were either successfully buried or released; $25 < n < 31$. Pie charts carrying the same lower-case letter are not significantly different at $P < 0.01$ (FEP test). Lower row, time taken for completion of burrowing with different ‘prey’ items; bars represent means with SD, $6 < n < 21$. Bars with the same capital letter are not significantly different at $P < 0.01$ (Student’s *t*-test). A movie clip showing an attack on the plastic stick is available as Supplementary material 4. These experiments were conducted at Playa Grande, Costa Rica.

On a few occasions we observed *A. propatula* striking at recently made *Olivella* tracks (Supplementary material 3) or following these tracks over significant distances (up to 40 cm) finally to make a catch. In most cases, however, tracks that an *Olivella* had left—sometimes only seconds before a hunting *Agaronia* crossed them—evoked no response whatsoever from the predator (Supplementary material 3). These observations suggested that prey detection occurred over short distances only and depended mostly on tactile cues, possibly supported by olfactory stimuli under certain conditions. We decided to clarify the situation by controlled field experiments.

Field experiments: tactile stimuli

When active *O. semistriata* were picked up from the sand and placed in front of a hunting *A. propatula* so that their paths

crossed shortly afterwards, the crawling *Olivella* was always attacked when it approached the front of the *Agaronia* to < 2 cm (Fig. 3B). However, when the prey was first ‘deactivated’ by rolling it between finger tips for a few seconds, which caused it to retreat into its shell, and then placed into the path of a hunting *Agaronia*, the attack rate decreased to about 30% (Fig. 3B). We repeated this experiment with five types of non-living bait: sticks of plastic and wood, paper clips, cotton swabs and empty gastropod shells (Fig. 3A). When any of these baits was gently vibrated while it touched the sand roughly 2 cm in front of the anterior edge of the foot of a hunting *A. propatula*, it was almost always attacked (Fig. 3B). Placing the same baits motionless about 6 cm before an *Agaronia* reduced the attack rate to some 10%, although the hunters always made contact with the bait item shortly after we had placed it in their paths (Fig. 3B). Evidently, motion transduced by the water-saturated sediment as a tactile stimulus is an essential signal that hunting *A. propatula* employ to distinguish live potential prey from random dead objects that they encounter in their environment.

Agaronia propatula that had ‘caught’ an artificial bait performed the usual behavioural sequence. The ‘prey’ was transferred to the metapodial pouch and the successful hunter attempted to burrow into the sand (Supplementary material 4). This behaviour did not require further movement of the artificial prey, indicating that while potential prey was identified by its motility before the launch of an attack, the subsequent handling of the captured prey did not depend on additional prey-specific signals. Because the artificial baits were much larger than the standard prey *O. semistriata* (Fig. 3A), they could not be enclosed completely in the metapodial pouches, as similarly observed with mature *Emerita* sp. (Fig. 2G, H). Nevertheless, the hunters kept their catch in close grip and could be lifted from the sediment by the bait (Supplementary material 4). However, while *A. propatula* that had captured *O. semistriata* in their pouches always burrowed into the sediment successfully, hunters that attempted to burrow while clinging to an artificial bait item frequently released the bait before burrowing was complete (Fig. 3C). Those burrowing attempts that were finished (as defined by the complete disappearance of the animal, not the bait) tended to take longer with artificial bait than with *O. semistriata* (Fig. 3C). These results suggested that *A. propatula* released artificial bait items because it had difficulties handling very large prey, rather than because it could distinguish between real prey and artificial objects once an object classified as prey had been captured. We concluded that *A. propatula* identified moving objects as prey even if these objects consisted of materials and had shapes of which the predators had no prior experience.

Field experiments: olfactory stimuli

Motionless *O. semistriata* were attacked more frequently by *A. propatula* than any of the five motionless artificial baits, although the statistical significances of the differences varied ($0.058 > P > 0.005$, FEP test; Fig. 3B). This indicated that *A. propatula* had a limited capability of identifying natural prey and distinguishing it from dead objects in situations in which the primary criterion for prey identification—motion—was absent. To test whether this capability was based on olfactory stimuli, we prepared ‘*Olivella* water’ by incubating *O. semistriata* in a small volume of sea water. When two to five droplets of this water (which we presumed to contain *Olivella*-specific scent substances) were placed carefully about 2 cm before a hunting *A. propatula*, strikes were triggered in some 80% of the trials (Fig. 4A). Control tests with sea water did not usually result in attacks (Fig. 4A; see also Fig. 5). Obviously, hunters performing ‘*Olivella* water’-induced strikes literally clutched at thin air (Supplementary material 5). We concluded that *A.*

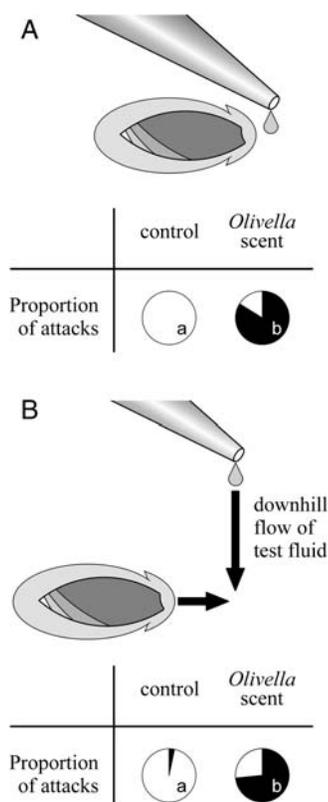


Figure 4. Response of *Agaronia propatula* to olfactory stimuli from *Olivella semistriata*. Test fluids were sea water (control), and sea water in which *O. semistriata* had been incubated ('*Olivella* scent'). **A.** Proportion of attacks (represented by black pie chart sectors) when droplets of the test fluid were placed about 2 cm in front of a hunting *A. propatula*. **B.** Proportion of attacks in experiments in which a hunting *A. propatula* crawled into a stream of test fluid placed uphill of the snail. Pie charts carrying different letters in **A** or **B** are highly significantly different at $P < 0.0001$ (FEP test; $29 < n < 32$); the difference between the results of experimental series **A** and **B** is insignificant ($P > 0.3$; FEP test). A movie clip showing an attack following stimulation as in **A** is available as Supplementary material 5. These two sets of experiments were carried out at Playa Grande, Costa Rica.

propatula can identify its main prey, *O. semistriata*, by a water-soluble substance(s) emitted by the prey.

Although the above results (Fig. 4A) appeared unambiguous, we decided to exclude the slightest possibility that strikes that seemed to be provoked by scent substances in '*Olivella* water' were actually triggered by vibrations that occurred when the droplets were placed on the sediment. To this end,

we selected hunting *A. propatula* that moved more or less perpendicular to the slope on relatively steep parts of the intertidal zone. Series of droplets of '*Olivella* water' were placed 5–8 cm uphill of and about 3 cm in front of the crawling *A. propatula*, so that the flow of the fluid into the path of the hunting snail could be followed as sediment particles were moved downhill. When the hunting *Agaronia* reached the freely flowing '*Olivella* water', strikes were launched in three quarters of all trials (Fig. 4B). In contrast, attacks occurred at a negligible rate in control experiments with sea water (Fig. 4B). Thus, our conclusion that *A. propatula* is capable of sensing *O. semistriata* olfactorily was corroborated.

In the experiment shown in Fig. 4B, strikes always occurred in the forward direction, i.e. in the direction in which the snail moved. After their vain attacks, the hunting snails never turned uphill but continued on their original path. This implied that the direction of flow of the scented water as such was not perceived as meaningful information by *A. propatula*.

Echinolittorina conspersa and *E. dubiosa* are small Panamic periwinkles restricted to the rocky supralittoral fringe (Williams & Reid, 2004), and therefore are unlikely to meet *A. propatula* in its habitat. However, *Echinolittorina*-scented water evoked the same responses as *Olivella*-scented water (Fig. 5; in the field, we did not distinguish between the two similar *Echinolittorina* species which formed mixed populations on the rocks adjacent to our study beaches). Evidently, the capability of *A. propatula* to identify potential prey olfactorily is not restricted to the species it encounters regularly. The predator also responded to the scent of *Donax* sp. as well as to that of its own species (Fig. 5). The lower attack rate in response to these stimuli as compared to the responses to *Olivella* and *Echinolittorina* scents (Fig. 5) cannot be interpreted as evidence for a lower sensitivity, because the actual concentrations of the relevant scent compound(s) were not controlled in our tests. Water carrying the scent of sand dollars (*Mellita* sp.) failed to induce attacks but caused *Agaronia* to turn away from the stimulus in some 20% of the trials (Fig. 5). This reaction, which we never observed following exposure to scents of other potential prey species, resembled the response to live *Mellita* specimens described above. While the reason for this avoidance of echinoids remains unclear, we can conclude that prey identification in *A. propatula* is supported by an olfactory sense which is versatile enough to allow for the exploitation of unusual prey such as an unlucky *Echinolittorina* flushed from its rock onto an adjacent sandy beach.

Field experiments: localization of tactile and olfactory receptors

We had frequently observed that close encounters and even collisions between *A. propatula* and *O. semistriata* provoked no reaction from the predator, especially when the potential prey approached the predator from the side or back

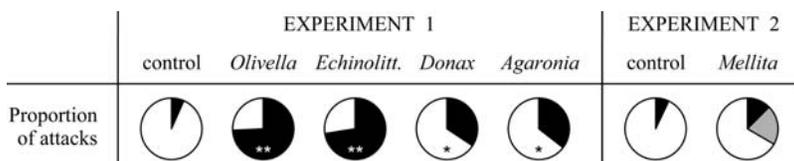


Figure 5. Response of *Agaronia propatula* to olfactory stimuli from five potential prey species, determined in two independent sets of experiments at El Cuco, El Salvador (Experiment 1; *Olivella semistriata*, *Echinolittorina conspersa/dubiosa*, *Donax* sp., *A. propatula*), and at Playa Grande, Costa Rica (Experiment 2; *Mellita* sp.). Test fluids were sea water (control), and sea water in which the prey species had been incubated. Attack rates (represented by black sectors) in pie charts carrying one or two asterisks differ from their corresponding controls at $P < 0.01$ (*) or $P < 0.0001$ (**; FEP test); $30 < n < 41$. Attack rates in response to *Mellita* scent did not differ from the control ($P > 0.3$; FEP test); $19 < n < 24$. The grey sector in the *Mellita* pie chart indicates the proportion of tests in which *Agaronia* turned and moved away in a new direction; this avoidance reaction was never observed in response to other scents. The results shown for *Olivella* and the controls do not differ significantly from the corresponding ones in Figure 4 ($P > 0.3$; FEP test).

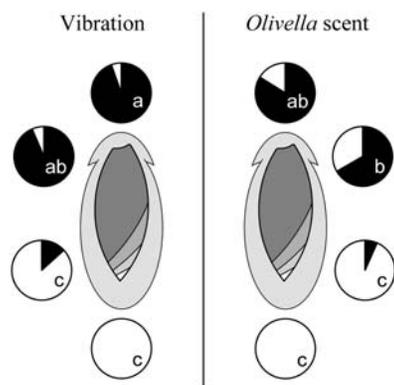


Figure 6. Sensory receptors responsible for prey identification in *Agaronia propatula* monitor a forward-facing sector of the animal's surroundings. Pie charts show proportions of attacks following tactile (left) or olfactory (right) stimulation of hunting *A. propatula*. The location at which the stimulus (either the gently vibrating tip of a plastic stick or droplets of *Olivella*-scented sea water) was applied was (i) 2 cm in front of the snail; (ii) 1 cm from the lateral edge of the foot at the level of the anterior tip of the shell (equal numbers of tests on the left and right sides of the animals); (iii) 1 cm from the lateral edge of the foot at the level of the shell apex (equal numbers of tests on the left and right sides of the animals); and (iv) 1 cm behind the posterior tip of the foot. Since responses to stimulation at positions (ii) and (iii) showed no significant differences between the left and right side of the animals, pooled data are shown for each position. All strikes were directed towards the source of the stimulus; to carry out the few strikes recorded in response to stimulation at the level of the shell apex [position (iii)], the snails turned backwards rapidly. Pie charts carrying the same letter are not significantly different at $P < 0.01$ (FEP test); $29 < n < 38$. Attack rates following stimulation of the front part of the foot (letters a, b) differed highly significantly ($P < 0.0001$; FEP test) from rates following stimulation of the hind part of the foot (letter c). This set of experiments was performed at Playa Grande, Costa Rica.

(Supplementary material 3). Moreover, the leading edge of the propodium of crawling *A. propatula* often performed rapid ruffling movements that are suggestive of a continuous probing of the environment (Supplementary material 5). These observations suggested that *A. propatula* surveys only a limited, forward-facing sector of its immediate surroundings by means of sensory organs in the propodium. To test this hypothesis, we compared the reactions to tactile (vibrating plastic stick) and olfactory ('*Olivella* water') stimuli that were applied at four different positions around the hunting predator. Both types of stimulus provoked attacks at high rates when applied in front of the snail and on its left or right side at the level of the anterior end of the shell (Fig. 6). When applied behind the crawling animal or laterally at the level of the shell apex, attack rates were negligible (Fig. 6). We concluded that the tactile and olfactory receptors that enabled prey identification in *A. propatula* were restricted to the most anterior part of the foot, probably the propodium.

Interestingly, all strikes observed in these experiments (Fig. 6) were directed towards the location at which the stimulus had been applied, implying that *A. propatula* is capable of the exact localization of nearby sources of sediment vibrations as well as attractive smells.

DISCUSSION

The genera *Agaronia* and *Oliva* have always been considered to be closely related (e.g. Gray, 1839; Olsson, 1956; Tursch & Greifeneder, 2001: 67). Therefore it is no surprise that our investigations into the behavioural and sensory ecology of *A. propatula* revealed close similarities to some of the behavioural

patterns found in *Oliva*. For example, the anterior and posterior parts of the foot can act as biomechanically independent units or even antagonists, as becomes evident when prey is seized by the anterior foot and then transferred to the posterior foot for storage in the metapodial pouch. This complex action proceeds in a practically identical manner in both taxa (Marcus & Marcus, 1959; Olsson & Corvo, 1968; Taylor & Glover, 2000; Kantor & Tursch, 2001; Rupert & Peters, 2011; Supplementary material 1). It should be noted that a similar behavioural sequence has evolved in naticids (Gonor, 1965; Edwards, 1969). Similarly, *Oliva* as well as *A. propatula* seem incapable of accurate long-distance localization of their prey, which needs to be in the immediate vicinity of the leading edge of the propodium for proper identification (Marcus & Marcus, 1959; Zeigler & Porreca, 1969: 11; Kantor & Tursch, 2001; Fig. 6). While the habitat of at least three *Oliva* species extends from deeper water into the eulittoral (*O. undulata*, Olsson, 1956: 164; *O. tigriddella*, Taylor & Glover, 2000; *O. oliva*, Tursch & Greifeneder, 2001: 194; Yu.I. Kantor, personal communication), most members of the genus dwell in subtidal sediments (Van Osselaer *et al.*, 1994). On the other hand, *A. propatula* performs swash-surfing, a highly specialized behaviour of intertidal sandy beach molluscs, which has not been reported from *Oliva* so far. Thus, *A. propatula* appears like an *Oliva* that has adapted to the conditions of the sandy beach intertidal more completely than the other *Oliva* species found in this habitat. This idea suggests an evolutionary scenario in which a clade represented by modern *Agaronia* separated from the *Oliva* main line(s) through the development of behavioural features that enabled a more efficient exploitation of the harsh intertidal environment. It will be interesting to determine whether the ecology of *Agaronia* species in other faunal provinces supports this hypothesis. This comparative approach should be expanded further by studies on swash-surfing, South American *Olivancillaria* (Olividae) species, which apparently have also conquered the sandy eulittoral (Caetano, Veloso & Cardoso, 2003).

Comparing food spectra of *A. propatula* and *Oliva* species, one may conclude that the former differs from the latter in its preference for one prey species. On our study beaches, *O. semistriata* was by far the prey most frequently taken by *A. propatula*, in agreement with remarks in the literature (Seilacher, 1959; López *et al.*, 1988; Metz, 1995). However, these observations do not necessarily imply a specialization or preference of the predator for this particular prey. *Olivella semistriata* is the numerically dominant macrofaunal element on many northern Panamic sandy beaches and accumulates in the backwash zone, where it can apply its specialized suspension-feeding mechanism (Seilacher, 1959; this author mistook *O. semistriata* for *O. columellaris*, but his observations, interpretations and excellent drawings are highly instructive nonetheless). Consequently, the dominance of *O. semistriata* in the prey spectrum of *A. propatula* may simply reflect the relative abundance of potential prey species in the community in which *Agaronia* hunts (for general discussion of related problems in ecology, see Underwood, Chapman & Crowe, 2004). Several findings support the idea that *A. propatula* is an opportunistic predator. First, species other than *O. semistriata* contribute significantly to the prey spectrum at Playa de Cuco with its rich species composition (Table 1). Second, the scent of *Echinolittorina conspersa* and *E. dubiosa*, upper rocky-shore species whose habitat does not overlap with that of *A. propatula*, triggers the same attack responses as that of *O. semistriata* (Fig. 5). Third, various artificial objects are attacked if they displayed a key character that distinguishes most living objects from dead ones—autonomous movement (Fig. 3A, B). Since *Agaronia* always attempts to reach a feeding position underneath the sediment surface once it has 'caught' such an artificial object (Fig. 3C), it seems that the familiarity of size, shape, smell or taste is no requirement

for prey identification. This ‘investigative hunting’ style of *A. propatula* provided us with an opportunity to teach a cheeky know-all tourist on Playa Grande some respect for the key predator on the beach, as *Agaronia* can be provoked to strike at human toes set before them. In this context, the avoidance of *Mellita* sp. is intriguing. These echinoids must possess a very powerful deterrent indeed to keep a predator at bay which unhesitatingly pounces on unknown objects and prey specimens several times its size. We may speculate that *Mellita* is toxic for *A. propatula*, but this hypothesis requires experimental corroboration.

The crawling speed of *O. semistriata*, as well as that of *A. propatula*, increases with body size (unpublished observations). This fact, together with the observation that gastropods found in metapodial pouches were always smaller than the predator, whereas subdued bivalves often reached the predator’s size (Fig. 2C–F), suggests that prey mobility, but not prey size, is a limiting factor for hunting success in *A. propatula*. This interpretation is further supported by the low proportion of highly mobile crustaceans in the prey spectrum and the relatively small body sizes of the few crustaceans that actually were found in metapodial pouches (Table 1). Adult mole crabs seemed to be an exception (Fig. 2G, H), but all the individuals attacked had not yet hardened their exoskeleton following moulting. These mole crabs were unable to move and burrow efficiently, due to the transiently nonfunctional state of their exoskeleton. Given their agile nature, it seems inconceivable that a biomechanically fully functional, adult mole crab could fail to escape an approaching *Agaronia*.

On wet sand, *A. propatula* monitors a narrow band of about 2 cm width around the edge of its anterior foot, within which potential prey is detected reliably by tactile and olfactory receptors that appear to be localized in the propodium (Fig. 6). Due to its rich innervation, the leading edge of the propodium has been suggested to be the “most important sense organ” in *Oliva* (Marcus & Marcus, 1959). Chemosensory sensitivity of the propodial edge also has been demonstrated for *Bullia* whelks (Hodgson & Brown, 1985), which resemble *Agaronia* in their swash-surfing habits and the fact that they forage on wet sand. Within the narrow surveillance zone around the propodium, *A. propatula* determine the position of the source of a stimulus quite precisely: in experiments in which the stimulus was applied within 1–2 cm of the edge of the propodium, attacks were generally directed towards the source (Fig. 6). Such precision seems to result from the snail’s ability to interpret the point on its propodium where the stimulus is perceived first as a marker of the direction towards the source of the stimulus. This interpretation is supported by experiments in which snails crawled towards a stream of *Olivella*-scented water that flowed perpendicular to the snail’s path (Fig. 4B). Strikes carried out when the snail moved into the stream of scented water were always directed forward in the direction of the snail’s movement, presumably because it was the most anterior portion of the propodium that came into contact with the stimulus first. The flow of the scented water as such did not provide useful information for hunting *Agaronia*, as the animals never turned towards the source of the stream in these experiments. Evidently, the snail’s ability to integrate spatially the information acquired by the propodial chemoreceptors is limited, despite the precision in localizing stimuli originating from within the surveillance zone of the propodium.

Although hunting *A. propatula* screen only a small forward-facing area of not more than 5–10 cm², they crawl rapidly on more or less random trajectories with speeds approaching 1 cm/s, thus increasing the chance to contact potential prey. Similarly, *Oliva* species “often pass by a morsel two or three times before finding it” even if it is only centimetres away (Zeigler & Porreca, 1969: 11; compare Kantor & Tursch,

2001), probably because food identification requires direct contact with the receptors in the propodium (Marcus & Marcus, 1959: 119). Interestingly, *Oliva* species make up for their lack of efficient long-distance food localization by speed of movement, which often enables them to reach food through haphazard paths before slower competitors with superior navigation capabilities arrive on straight trajectories (Kantor & Tursch, 2001). In contrast to *A. propatula*, most *Oliva* species forage under water and take up water through their siphons, apparently detecting the presence—as opposed to the location—of food using chemoreceptors on the osphradium (Olsson & Corvo, 1968; Zeigler & Porreca, 1969; Kantor & Tursch, 2001). Osphradium-based sensory capabilities play no detectable role in *A. propatula* hunting on tidal planes exposed to air, but this does not necessarily exclude the possibility that the perception of water-borne chemical stimuli is relevant for the approach to potential prey while an *Agaronia* is submerged. Such long-distance perception could be hypothesized to operate when *Agaronia* perform swash-surfing to reach the beach zone where feeding *O. semistriata* concentrate. However, our field observations provided no support for this idea. *Agaronia propatula* showed no tendency to home in on particularly dense accumulations of its prey—as they should if they were attracted chemically to the prey over long distances. In addition, *A. propatula* reliably started to burrow into the sand at the end of each swash ride, which would not be expected if swash rides were undertaken to reach food items precisely located over long distances.

The lack of evidence for long-distance chemoperception of prey in *A. propatula* may be surprising, as it well known that gastropods employ olfactory signals in a multitude of physiological and ecological contexts (Croll, 1983). Various marine gastropods use chemical signals to detect the presence of potential predators (Harvey, Garneau & Himmelman, 1987; Marko & Palmer, 1991; Rochette *et al.*, 1998; Jacobsen & Stabell, 2004; Aschaffenburg, 2008). Marine gastropods may also find their food thanks to their chemoreceptive abilities, a fact that has long been exploited in whelk fisheries (McQuinn, Gendron & Himmelman, 1988). Moreover, *Buccinum undatum* (Rochette, Morissette & Himmelman, 1995; Rochette, Dill, Himmelman, 1997) as well as *Littorina scutulata* (Keppel & Scrosati, 2004) have been shown to perform risk assessment if olfactory cues signal the presence of both food and predators. Nonetheless it is unlikely that *A. propatula* utilizes chemoreception of water-borne substances to detect its prey over significant distances on the beach, not only because we have not found supporting evidence, but also because of the fundamental physical problems involved in long-distance perception in this unique environment. If a foraging gastropod is to detect and approach food over significant distances with the help of its olfactory capacities, water must flow continuously from the food to the gastropod (Weissburg, 2000; Weissburg *et al.*, 2002; Webster & Weissburg, 2009). This ‘informative flow’ may be turbulent (Ferner & Weissburg, 2005) but it must not cease or change direction, or else the forager loses its bearings (Lapointe & Sainte-Marie, 1992). Obviously, this requirement is not met on dissipative sandy beaches where the water is permanently mixed and changes its direction of flow continuously. Consequently, *A. propatula* and other intertidal gastropods may well ‘smell’ that food is present somewhere on the beach, but it is hard to see how they could locate their food over significant distances through the detection of water-borne chemicals. This conclusion seems to disagree with the report that the intertidal scavenger *Bullia digitalis* locates dead mussels by chemoreception followed by directed swash-surfing towards the food (Odendaal *et al.*, 1992). However, Odendaal *et al.* (1992) studied *Bullia* approaching carrion floating in the swash. As these authors explained, a cloud of scent substances may

remain stable relative to the position of its emitter if the emitter moves in unison with the water body in which it floats. This situation is distinct from the case of stationary emitters such as congregations of *O. semistriata* at the water line. It also is worth noting that in the experiments performed by Odendaal *et al.* (1992), *B. digitalis* detected food only when it was closer than 2 m, and that the bait was approached successfully in <30% of the trials even when the initial distance between snail and bait was <0.5 m.

Our interpretation agrees with the conclusion drawn by Kitching & Pearson (1981) from field observations in the naticid *Polinices incei*, a predatory gastropod that hunts bivalves on sandy beaches of eastern Australia. "It is plausible ... that the adoption by some intertidal species of a non-olfactory method of prey detection is likely to be adaptive given the special environmental conditions which obtain on certain shores." At intermediate and low tide, the sandy beach eulittoral "is washed frequently by incoming waves. For a predator and prey operating just below the sand surface, this will have the effect of washing out any chemical emissions, obviating the possibility of prey detection by olfaction, especially for a slow moving predator like the snail. Mechanoreception ... presents an alternative which will be unaffected by wave action" (Kitching & Pearson, 1981: 320). In this context it is of interest that *Navanax inermis*, an efficient opisthobranch predator of the intertidal and shallow subtidal of the North American west coast appears to rely entirely on contact as opposed to distance chemoperception to locate acceptable prey (Paine, 1963).

While wave action certainly does not interfere with mechanical prey detection in those phases in which the sandy intertidal is exposed to air (Kitching & Pearson 1981), intertidal organisms may actually utilize wave action as a beneficial abiotic factor if they exploit the physical regularity that it establishes. This was recognized by Brown (1971) in a review of the lifestyle of swash-surfing *Bullia* species. Upon chemical detection of the presence of carrion, *Bullia* tend to emerge from the sand and surf towards the water line. There, they begin "crawling around almost at random". In doing so, they never venture further up into drier beach zones or move back into the water, thus remaining within "a relatively narrow strip of beach—precisely that area in which washed-up animal remains are most likely to come to rest" (Brown, 1971: 303). It must be stressed that in this interpretation, as in the case of hunting *Oliva* (Kantor & Tursch, 2001), the smell of food betrays its presence, not its exact location. However, *Bullia* whelks can 'predict', as it were, the approximate location of the food item due to the regular physical properties of their habitat. Surfing in *A. propatula* appears to serve a similar purpose through a similar mechanism. Hungry individuals position themselves in the beach zone in which smooth backwash flows regularly occur, which is where the suspension-feeding *O. semistriata* congregates due to its own feeding requirements. Even without long-distance perception, *Agaronia* can 'predict' where prey accumulates at highest densities, and follow the prey during the tidal cycle. This requires migrations over a few hundred metres each day on typical dissipative beaches and swash-surfing is an energy-efficient mode of locomotion that enables *A. propatula* to remain in beach zones of maximum prey density. On the other hand, our finding that numerous specimens surfing downwards at retreating tide had prey in their pouches indicates that nonhunting individuals prefer lower beach zones, possibly to avoid predation by birds, terrestrial animals and larger members of their own species. Swash-surfing locomotion therefore not only facilitates the approach to prey, but enables *A. propatula* to utilize the different parts of dissipative sandy beaches with their dynamic yet predictable zonation.

Evidently, long-distance senses are not required for *A. propatula* to make sense of its environment; these snails can move over long distances between beach zones of high prey density and relatively safer locations, relying on the regular physical structure of their habitat alone. In terms of its sensory ecology, *A. propatula* seems to live in a mostly tactile world. This appears sufficient and appropriate as *A. propatula*'s world is structured by factors that can be sensed and monitored by mechanoreceptors. Temporal structure is provided by fast and slow cycles of fluid-mechanic forces (waves and tides, respectively), while spatial structure is established by the direction of water flow (defining the physical and ecological gradients along the beach slope) and the sediment surface (separating the fluid phase in which to move from the semisolid phase in which to rest). Swash-surfing gastropods generally possess reduced sets of sensory organs, as indicated by the lack of eyes not only in *Agaronia* but also in *Olivella* and *Bullia*. It appears that their adaptation to the life on sandy beaches included the loss of sensory capabilities that became dispensable due to the physical regularity of this habitat.

SUPPLEMENTARY MATERIAL

Supplementary material is available at *Journal of Molluscan Studies* online.

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