Influence of proximal stimuli on swimming in the sea hare *Aplysia brasiliana*

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Received 22 August 2002; received in revised form 20 November 2002; accepted 30 December 2002

**Abstract**

Although the neurobiology and physiology of sea hares are extensively studied, comparatively little is known about their behaviour or ecology. Several species of sea hares swim, but the function of swimming is unclear. In this paper, we tested the hypotheses that swimming in *Aplysia brasiliana* serves to find food and mates, and to escape predators. Our data strongly support the hypothesis that swimming in *A. brasiliana* is related to feeding. Sea hares deprived of food overnight swam 12 times longer than ones that had been fed. When sea hares contacted food while swimming they invariably stopped, while those contacting a plastic algal mimic mostly continued to swim. Our experiments provided no evidence to support the hypothesis that swimming in sea hares is related to social behaviour. Sea hares deprived of copulatory mates for 3 days did not swim longer than ones held in copulating groups. Moreover, swimming sea hares never stopped swimming upon encountering a conspecific. Our experiments also supported the hypothesis that swimming in sea hares is related to predation. Sea hares stimulated with a standardised tail pinch and exposed to ink of conspecifics swam four times longer than control individuals, and tail-pinched sea hares that released ink swam five times longer than ones that did not release ink. However, because predators of adult sea hares are mostly lacking and because sea hares often swim spontaneously without predators being present, we conclude that swimming behaviour in *A. brasiliana* is primarily related to food-finding.

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**Keywords**: Sea hare; *Aplysia brasiliana*; Swimming
1. Introduction

Marine gastropods of the genus *Aplysia* are among the best studied of all marine invertebrates. They serve as a model system for neurological studies (Kandel, 1979), and have provided natural-products chemists with a rich source of new compounds (Faulkner, 1992). Yet, in comparison with the extensive neurobiological and physiological literature on *Aplysia*, relatively little is known about their behavior and ecology (Carefoot, 1987). Here we focus on one notable aspect of behaviour, swimming.

Of over 30 species of *Aplysia*, less than six are known to swim. Only two have been investigated in any detail, primarily from the standpoints of mechanism of propulsion, and duration, distance, and orientation during swimming. Neither the function of swimming nor the proximal cues to initiate swimming are well understood.

Most of our knowledge of swimming in sea hares comes from the work of Hamilton and colleagues on *Aplysia brasiliana* in the northeastern Gulf of Mexico (Hamilton and Russell, 1982; Hamilton, 1986), and of Susswein and colleagues on *Aplysia fasciata* in the eastern Mediterranean Sea (Susswein et al., 1983, 1984; Ziv et al., 1991a,b, 1994). The two species appear to be closely related (Susswein et al., 1993; Medina et al., 2001). However, while both inhabit subtropical shallow marine waters, they differ in that *A. brasiliana* inhabits seagrass-bed habitats, favours red-algal food, and exhibits crepuscular/nocturnal behaviour, while *A. fasciata* frequents sand and rock areas, eats mainly green-algal food, and shows principally nocturnal behaviour. Swimming bouts in both species are of short duration, averaging about 10 min, although occasional individuals may swim for more than an hour (Hamilton, 1986; Ziv et al., 1994). Swimming is more likely in calm conditions and, in *A. brasiliana* during swims in excess of 4 m distance, is more commonly at the surface and generally in an offshore duration (Hamilton and Ambrose, 1975; Hamilton and Russell, 1982). Theories on the mode of swimming in sea hares include sculling (Farmer, 1970; Bebbington and Hughes, 1973), jetting (Neu, 1932), and hydrodynamic lift (von der Porten et al., 1982).

But where are the sea hares swimming to, and for what reason? Escape from predators, search for mates or food or more suitable habitat, and a mechanism for seasonal migration have all been proposed (Krakauer, 1969; Farmer, 1970; Aspey et al., 1977; Susswein et al., 1984; Hamilton, 1986). Predators are not unknown for *Aplysia* (Pennings, 1990; Rogers et al., 2000) but its repertoire of chemical defenses including purple ink, opaline secretion, and a wide spectrum of secondary metabolites in skin and digestive gland suggests that predation is unlikely to be a major influence on daily behaviour, especially for adults (reviewed in Carefoot, 1987). Likewise, while some laboratory swimming bouts of *A. fasciata* culminate in finding a mate, most do not (Susswein et al., 1984). Swimming in sea hares would most directly enhance reproduction if swimming individuals, on encounter, were to sink together to the bottom and commence copulation, but this has not been reported. *A. fasciata*, however, swims more when isolated than when in groups (Ziv et al., 1991a,b, 1994), and this behaviour could lead to aggregations and increased copulatory activity even if animals were not directly cued to stop swimming by the presence of conspecifics. Migration as part of the life cycle of sea hares has enjoyed past advocacy, but support for this idea has dwindled through lack of evidence (reviewed in Carefoot, 1987).
The most likely hypothesis is that swimming behaviour is related to feeding. In support of this, Aspey et al. (1977) and Susswein et al. (1984) note that laboratory-swimming bouts of *Aplysia* will often terminate on encounter with food. Satiated *A. fasciata* (Susswein et al., 1984) and *Aplysia pulmonica* (Switzer-Dunlap, pers. comm.) also tend not to swim. Inhibition of swimming could be by feedback signals from stretch receptors in the crop, by post-ingestive nutritional cues, or simply by the increased mass of food in the crop.

Here, we investigate the influence of several proximal stimuli on swimming in the sea hare *A. brasiliana*. Because food-finding seemed, a priori, to be the most likely explanation for swimming, and because feeding in sea hares occupies such a large portion of their daily time budgets (Susswein et al., 1983; Susswein, 1984; Carefoot, 1991a,b), we emphasised food-finding in the present study. Also included, however, were tests of mate-locating and predator-escape hypotheses. Questions we addressed included: (1) do fed sea hares swim less readily than food-deprived ones? (2) will swimming sea hares stop when food is encountered? (3) is a sea hare with a full crop-load of food too heavy to swim? (4) do recently mated sea hares swim less readily than ones deprived of mates? (5) will swimming sea hares stop on encounter with a potential mate? and, (6) does tail-pinching to mimic a predator’s attack enhance swimming?

2. Methods

Adult-sized (200–300 g live mass) *A. brasiliana* were collected from harbour and breakwater regions at South Padre Island, Texas in May 2002 and maintained in 60-L plastic tubs at the Marine Science Institute, University of Texas. At this time of the year, the population was dominated by large adult animals, most of which were still vigorous and active. We did observe some senescent animals in the field, but none was collected. Where feeding on intact seaweeds was required, green alga *Ulva fasciata* and red algae, *Hypnea musciformis* and *Gracilaria dibilis* were provided ad libitum. Food-deprived sea hares were kept without food for a 24-h period prior to swimming tests. No individual was used more than once in an experiment.

Some treatments required that the sea hares’ crops be force-filled via intubation (cf. Susswein and Kupfermann, 1975; Pennings and Carefoot, 1995). A short length of plastic tubing (4 mm o.d.) was gently inserted into the crop via the mouth after first touching a small bit of intact seaweed (*Ulva*) to the oral tentacles to initiate reflexive biting by the jaws and to enable passage of the tube past the radula. Once the tube was in place, a process requiring 3–4 min, a 50-ml plastic syringe was attached and a selected volume of test material delivered over a 5-s period. The sea hares were unanaesthetised during force-feeding. Previous work on *Aplysia* spp. using intubation techniques (Susswein and Kupfermann, 1975; Pennings and Carefoot, 1995) showed that a volume equivalent to 10% of an individual’s live mass could be readily accommodated after it was deprived of food for 1 day. Assessment of blood-glucose levels following intubated deliveries of comparable volumes of seawater, agar, or cellulose in past studies of *Aplysia dactylomela* and *Aplysia juliana* indicated no significant stress-effects induced by this treatment or by concomitant handling (Carefoot, 1991a,b).
After an intubated meal, the sea hares were allowed to rest in individual 4-l plastic buckets for 1 h before being used in swimming trials.

Swimming trials were conducted in an indoor circular fibreglass tank (0.5-m depth and 1.5-m diameter) containing non-agitated seawater at 24 °C, with release being just below the surface. After release, we recorded duration of the swim until the sea hare attached, usually to the side of the tank, and ceased beating its parapodia. All experiments used treatment and control individuals matched as closely as possible in live mass, but live mass never explained significant amounts of variation when included as a covariate in our analyses of swimming duration. Swimming trials were conducted at 1600 h, a time when the sea hares were customarily observed to swim in the field and in the laboratory, or at 1000 h, also a time when we observed spontaneous swimming activity in the laboratory. After each swimming trial, the sea hare was blotted dry on a towel and weighed.

2.1. Swimming duration: food-deprived versus fed

We performed two experiments to test the hypothesis that sea hares swim more when hungry than when fed. In the first experiment, nine sea hares were deprived of food overnight while another nine were fed. Both groups were induced to swim the following day at 1000 h. Previous studies have shown that 1 day of food deprivation in Aplysia reduces crop contents to essentially nil (Carefoot, 1991a,b). The sea hares were swum alternately from the two treatment groups. Data on swimming durations were compared with a two-sample \( t \)-test.

To ensure that all fed sea hares had the same relative crop-size of food (i.e., identical stretch on crop proprioceptors), a second group of 30 was intubated, force-fed, then tested. Half were given volumes of seaweed food (Ulva sp. dried at 70 °C overnight, ground to a fine powder in a mortar and pestle, then made up in seawater to a 5% dry mass/volume slurry); the other half, volumes of powdered cellulose in the same dry mass/volume ratio (a cellulase is only weakly present or absent in aplysids: Carefoot, 1987; hence, this control treatment provided identical mass and crop distension to the Ulva meal, but no nutritional signal). Data on swimming durations were compared with a Wilcoxon rank-sum test.

2.2. Effect of meal mass on swimming duration

To test the hypothesis that a fully fed sea hare might be too heavy to swim, we deprived 10 individuals of food for 1 day, then divided them into two groups matched by size. We then fed each group by intubation to 10% crop volume with a mixture of silica and seawater in the following proportions: 0.5 dry g/100 ml seawater (representing a light “meal”) and 50 dry g/100 ml seawater (heavy “meal”). We chose silica because it provides high mass per unit volume, is nutritionally free, and is readily eaten by A. dactylomela, another tropical seagrass-inhabiting species (in which sand may comprise up to 25% of crop volume; Carefoot, 1970). These treatments provided “meals” of 0.1 and 10 times, respectively, the mass of a “normal” intubated meal of Ulva. The heavy meal represented about twice the mass that A. dactylomela would consume in one-night’s feeding (Carefoot, 1970). Data on swimming durations were compared with a Wilcoxon rank-sum test.
2.3. Inhibition of swimming on encounter with food

Fifteen sea hares were deprived of food overnight, then tested the following morning. An individual was induced to swim then, 30 s into the swim, was presented continuously for 120 s with either a 5-g bundle of fresh seaweeds (mixed red and green algae in equal proportions), or with a 5-g bundle of sheet plastic cut into strips to mimic seaweed, held in contact with the oral tentacles. Each sea hare received both stimuli in a paired design, with no rest in between. The stimuli were presented in alternate order for successive sea hares. Data were recorded as time in seconds to attach, or as + 120 s if no attachment. If a sea hare attached to the first stimulus, then we recorded the time, freed it to induce further swimming, waited 30 s, then applied the second stimulus for 2 min. Seaweeds and mimic were replaced throughout the experiment to ensure freshness and neutrality. Data on swimming durations were analysed with a paired \( t \)-test.

2.4. Effect of mate-deprivation on swimming duration

To test whether deprivation from copulatory mates would increase swimming propensity, we held 18 sea hares for 3 days, eight of them in individual containers and 10 in two group-containers (five sea hares in each container). All sea hares were fed ad libitum then swum on the morning of the fourth day. Swimming tests were done at the diel peak of mating behaviour (1600 h) to ensure that the majority of the group-held sea hares had been copulating. Data on swim durations were analysed with a two-sample \( t \)-test. Our expectation was that the group-held sea hares would swim for a shorter time than the solitary ones.

2.5. Inhibition of swimming on encounter with potential mates

To test the hypothesis that sea hares would cease swimming upon contact with mates, we swam 10 sea hares in the manner described for food-encounters. Sea hares were deprived of mates for 2 days before the experiment commenced. The inhibitory stimuli were a hand-held sea hare taken from a copulating pair in one of the group-tanks and a plastic bag that was half-filled with seawater to mimic the physical characteristics of a sea hare. Each test sea hare received both stimuli over successive 2-min periods, with their order of presentation being alternated for successive individuals. A stimulus was held in front of a swimming sea hare so that contact was made almost continuously by the oral tentacles. The stimulus was applied until the sea hare stopped swimming or until 120 s had passed, at which time the test was terminated. The hand-held specimen and plastic bag were replaced from time to time during the trials to minimise stress on the individual being handled and to ensure freshness and neutrality.

2.6. Swimming as escape behaviour

To test the hypothesis that swimming is a means of escape, we compared swimming durations in tail-pinched versus non-tail-pinched sea hares. Thirty sea hares were fed ad libitum overnight, and then paired by size the following morning. One member of each pair was pinched in the tail for 2 s, then passed sequentially through three seawater washes (4-l
plastic buckets) each for 2 s. The seawater washes both cleaned the sea hare of ink released as an alarm response to pinching and exposed following individuals to the same potential “alarm” signal. For this reason, we changed only the second and third wash-waters during the course of the experiment, allowing the first wash bucket to accumulate ink and any chemicals that might serve as alarm signals. Pinching was done using a spring-loaded hose clamp that provided a standardised pinch. Control specimens were passed through a separate set of three 2-s washes in fresh seawater without the pinching. No control specimen inked during this procedure. Sea hares were swum immediately after the third wash and the duration of swimming bouts recorded. Data on swimming duration did not meet the assumptions of parametric statistics and were analyzed with a Wilcoxon rank-sum test.

3. Results

3.1. General observations on swimming behaviour

Swim durations varied depending upon treatment, from zero time for individuals dropping straight to the bottom of the tank, to a few seconds for ones swimming to the side of the tank and attaching, to several minutes (most typical) and to hours (exceptional). On release, the sea hares would generally swim in a direct line to the opposite side of the tank where they would butt their heads or swerve to one side or other, then continue swimming around the circumference of the tank. Although there was no sure way to predict the duration of a swim at the start of a test, we noted that the adoption of a more streamlined shape (oral tentacles rolled over neatly in front, rhinophores lying back along the head, and the edges of the foot curled inwards) usually presaged a long swim. Head-bobbing, or the rhythmical thrust of the head upwards with each parapodial flap (Hamilton and Russell, 1982; Aspey et al., 1977), was done by all sea hares swimming at the surface, but not by sea hares swimming below the surface. The “bob” occurs as a counter-reaction to the downward thrust of the parapodia combined with simultaneous contraction of head musculature (described in detail by Aspey et al., 1977). Most swimming in the tank was done at the surface, accompanied by head-bobbing.

Parapodial flapping was left over right when unimpeded by the side of the tank, and beat frequency was approximately 1 s\(^{-1}\) regardless of how fast the sea hare was swimming or how long it had been swimming (beat initiation in sea hares is from neuronal oscillators in the pedal ganglia and frequency of beat is temperature-dependent: von der Porten et al., 1980, 1982). In a separate experiment, we monitored beat frequency as a function of live mass and showed (as expected from data for wing-beat frequency in relation to size in insects and birds: McMahon and Bonner, 1983) a significant negative scaling (Fig. 1, \(F = 9.9, p < 0.001\), Regression Analysis; regression statistics: \(\log Y = 1.42 - 0.24 \log X, r^2 = 0.44\)).

3.2. Swimming duration: food-deprived versus fed

Sea hares deprived of food overnight swam over 10 times longer than ones that had been fed (Fig. 2, \(t = 3.6, p = 0.008\)).
We could show no significant difference in swimming durations in sea hares intubated and fed meals of *Ulva* - versus cellulose-slurries (Fig. 3, \( p = 0.13 \), one-tailed Wilcoxon rank-sum test); however, a trend was present in the expected direction of longer swimming bouts in the group fed cellulose (i.e., bulk but no nutritional signal).

Fig. 1. Frequency of parapodial flapping in swimming *A. brasiliana* with change in live body mass, \( N = 28 \). Significance of regression: \( F = 9.9, p < 0.001 \). Regression statistics are \( \log Y = 0.521 - 0.236 \log X, r^2 = 0.44 \).

Fig. 2. Duration of swimming in *A. brasiliana* deprived of food and fed overnight. Data are means ± SE. \( N = 8 \) for each treatment.
3.3. Effect of meal mass on swimming duration

We hypothesized that sea hares eating a silica-rich meal might be too heavy to swim. As predicted, sea hares intubated and fed a relatively light “meal” of silica swam almost four times longer than did ones fed a heavy “meal” of silica (Fig. 4, \( p = 0.025 \), one-tailed Wilcoxon rank-sum test).

![Fig. 3. Duration of swimming in A. brasiliana intubated and fed slurry-“meals” of green alga U. fasciata and powdered cellulose. Data are means ± SE. \( N = 15 \) for both.](image1)

![Fig. 4. Duration of swimming in A. brasiliana intubated and fed silica “meals” of different relative mass. Data are means ± SE. \( N = 4 \) for “heavy” and 6 for “light”.](image2)
3.4. Inhibition of swimming on encounter with food

Swimming sea hares presented with tufts of algae grasped the algal clumps and usually immediately stopped swimming (Fig. 5) with a mean swim duration of $4 \pm 0.3$ s out of a maximum 120-s test period. In contrast, swimming sea hares that encountered tufts of plastic (seaweed mimic) sometimes hesitated momentarily, but never stopped swimming immediately. Three individuals continually presented with the plastic mimic ultimately stopped swimming in under 120 s (25, 28, and 28 s), but the remaining 10 sea hares swam for the maximum duration of 120 s despite continuous presentation of the algal mimic (Fig. 5, overall mean of $98 \pm 11$ SE s).

3.5. Effect of mate-deprivation on swimming duration

The duration of swimming bouts of sea hares held alone and in groups did not differ significantly (mean $\pm$ SE for $N=8$ solitary individuals: $32 \pm 12$ min, and for $N=10$ group individuals: $21 \pm 11$ min; $t=0.63$, $p=0.27$, one-tailed test).

3.6. Inhibition of swimming on encounter with potential mates

Swimming sea hares presented with conspecifics or sea-hare mimics (plastic bags partly filled with seawater) all swam continuously over the 120-s duration of the trials. In all tests with conspecifics the sea hare would swim past, over, under, or even through the open parapodia of the stimulus sea hare placed in front of the swimming specimen without

![Graph showing effect on swimming of A. brasiliana on encounter with tufts of algal foods versus plastic-strip food-mimics. Data are means $\pm$ SE. $N=13$ for each treatment.](image)

$P < 0.001$
stopping, and in all confrontations with a sea-hare mimic the test specimen would simply push past it. In no case was the test stimulus investigated even momentarily.

3.7. Swimming as escape behaviour

Sea hares receiving pinch-plus-ink stimuli swam more than three times longer than control sea hares (Fig. 6, \( p < 0.001 \), Wilcoxon rank-sum test). Eight (including the first to be tested) of the 14 pinched sea hares released ink and these individuals swam five times longer (mean = 17 min) than did the six sea hares that were pinched but did not release ink (mean = 3 min, \( p < 0.001 \), Wilcoxon rank-sum test). The generally shorter swim-duration of these sea hares as compared with those in other tests (e.g., Fig. 2) were likely a result of them being fed overnight rather than being deprived of food.

4. Discussion

Our experiments strongly support the hypothesis that swimming behaviour in A. brasiliana is related to feeding. Sea hares deprived of food overnight swam 12 times longer than ones that had been fed. When sea hares contacted food while swimming they invariably stopped, while those contacting a plastic algal mimic mostly continued to swim despite repeated presentation of the mimic. In support of such a food-finding hypothesis, Susswein (1984) observed that laboratory-held A. fasciata swam three times longer when deprived of food over a 2-day period as compared with ones fed ad libitum, and Aspey et al. (1977) anecdotally observed that swimming A. brasiliana would drop to the bottom or attach to the side of an aquarium tank on contact with an algal stimulant (commercial dried laver: Porphyra sp.).
Our experiments provided no evidence to support the hypothesis that swimming in sea hares is related to mating. Sea hares deprived of copulatory mates for 3 days did not swim longer than ones held in groups, despite the fact that the group-held specimens had been copulating almost continuously during the 3-day treatment period. Moreover, swimming sea hares never stopped swimming or, for that matter, even slowed down upon encountering a conspecific. These results contrast sharply with studies of *A. fasciata* by Ziv et al. (1991a,b, 1994) that report increased swimming in the absence of conspecifics.

Previous reports indicate that most surface-swimming *A. brasiliiana* bob their heads with each parapodial beat (Aspey et al., 1977; Hamilton and Russell, 1982), and this behaviour was similarly exhibited by all surface-swimming field and laboratory specimens in our study. Because both frequency and incidence of bobbing in *A. brasiliiana* increased with food deprivation up to about 20 h, Aspey et al. (1977) surmised head-bobbing to be a food-seeking behaviour, but how bobbing at the surface would increase the chance of encountering floating algal food is unclear. Surface-swimming alone would suffice to bring a sea hare in contact with any floating material. These same authors were of the opinion that contact of the head and oral tentacles of a swimming sea hare with paper toweling would stop a swim, but our tests with a chemically neutral plastic seaweed-mimic produced contrary results (see Fig. 5). Why then would a sea hare swim at the surface? Perhaps it allows access to larger areas without the risk of hitting bottom obstructions (this may be particularly applicable to *A. brasiliiana*, which would have to swim through thick stands of seagrasses if it swam along the bottom).

We noted that *A. brasiliiana* is a poor crawler in comparison with several non-swimming aplysoid species that we have worked with in the past. In fact, only once in several weeks did we see an individual crawl in our tanks (and then only a few centimeters), even amongst those deprived of food overnight, yet at the same time we would see several individuals swimming vigorously. An extension of the food-finding hypothesis to include the idea that crawling would be poorly developed amongst swimming aplysoid species would be reasonable were it not for the fact that the closely related *A. fasciata* spends large amounts of time crawling (Susswein et al., 1983; Ziv et al., 1991a,b, 1994). Pedal locomotion is also described for *A. depilans* (reputed to be a swimming species by Bebbington and Hughes, 1973). In view of these observations and noting that *A. brasiliiana* and *A. fasciata* are closely related (Susswein et al., 1993; Medina et al., 2001), we conclude that crawling is likely a highly labile evolutionary feature in sea hares and perhaps not tightly linked to swimming. It may be that crawling behaviour has been largely lost in *A. brasiliiana* because its sandy habitats are less suited to pedal locomotion than are the rocky habitats favoured by most other species of sea hares. A minor difference related to swimming in the species *fasciata* and *brasiliiana* is that while in the former the parapodial lobes overlap right over left in the parapodial cycle (Bebbington and Hughes, 1973), in the latter they overlap left over right (present study).

We found no difference in duration of swimming bouts in sea hares intubated with algal versus indigestible cellulose slurries. This suggests that inhibition of swimming in fully or partially satiated sea hares may be via feedback signals from mechano-receptors in the gut. Previous studies on *A. fasciata* have indicated that inhibition of feeding is similarly via mechano-receptors (Susswein and Kupfermann, 1975), but that inhibition of mating is via chemo-receptors sensing food in the water (Nedvetzki et al., 1998). Inhibition of
swimming, therefore, may be more similar to inhibition of feeding than to inhibition of mating.

Sea hares intubated and force-fed a heavy silica meal swam significantly less than ones fed a lighter silica meal, but we do not know how this might relate to a normal seaweed meal eaten in the field. *A. dactylomela* (a non-swimmer) routinely takes in sand as it feeds on algal turfs, and sand can comprise up to 25% of the volume of the crop and be a principal component of its faeces (Carefoot, 1970), but we know nothing about the effect of this increased mass on locomotion (in *A. dactylomela*, feeding is generally through the night, then at dawn the sea hares seek out crevices and sites under rocks where they rest all day while digesting their food). In comparative terms, a 100-g (live mass) intubated *A. brasiliana* in our experiments received about 5 g of sand, versus about 2 g eaten by the same-sized *A. dactylomela* feeding overnight on turf algae (Carefoot, 1970). In a comparison of diets in several related anaspid opisthobranchs in Florida, Krakauer (1971) specifically notes the presence of sand in the crops of *Bursatella leachi* but not in *Aplysia willcoxi* (= *A. brasiliana*). Whether *A. brasiliana* or other swimming species eat generally smaller meals, eat selectively less of “heavy” algal foods, or preferentially exclude sands from their diet, might be interesting subjects for further study.

Our experiments support the hypothesis that swimming in sea hares is stimulated by aversive stimuli, but we question whether it is linked with predation-events in the field. Individuals stimulated with a standardised tail pinch and exposed to ink of conspecifics swim four times longer than did control specimens, and tail-pinched sea hares that released ink swim five times longer than ones that did not release ink. Similarly, Levy and Susswein (1999) found that swimming in *A. fasciata* increased following application of electrical shocks or exposure to unusually high- or low-salinity seawater. Despite these observations, we doubt that escape behaviour accounts for most field occurrences of swimming in sea hares for several reasons. First, sea hares commonly swim spontaneously in the field and laboratory in the absence of any apparent disturbance (Susswein et al., 1983; our own observations). Second, the types of stimuli observed to induce swimming in *Aplysia* in the laboratory are mostly absent in the field. Even radical changes in salinity would be unlikely in subtidal habitats where most *Aplysia* live. Finally, although a number of predators may eat juvenile sea hares (Pennings, 1990; Rogers et al., 2000), predators of large individuals such as those studied here are virtually unknown (reviewed in Carefoot, 1987). *Aplysia* sequesters large numbers and amounts of secondary metabolites derived from red-algal foods in both skin and digestive gland, and most species additionally possess either, or both, opaline-gland and purple-ink secretions. All are thought to be defensive in function. *Aplysia* species that eat only green or brown algae neither have ink nor the repertoire of potentially defensive, algal-derived secondary metabolites available to red-algal eaters; however, they may produce their own defenses de novo (Pennings, 1994). What this suggests is that if swimming evolved primarily for defensive escape, it might be more common in aplysiids that eat green or brown algae than in species that eat red algae, but there is no convincing evidence for this. Of the four best-known species of swimming *Aplysia*, namely, *brasiliana*, *fasciata*, *gigantea*, and *depilans*, all eat at least some component of red algae except for the last (for this reason *depilans* does not release purple ink). Furthermore, of the other aplysiid species whose diet is restricted to green or brown algae (and, hence, lack purple ink), for example, *juliana* and *vaccaria*, none swims.
Is swimming involved in seasonal migration? The notion of migration in sea hares has invoked much speculation (Eales, 1921; Hamilton, 1986), but there is little or no evidence to support it, and much to argue against it. Firstly, there is no evidence based on population studies that any species of sea hare migrates. Speculation about migration mostly originated as an explanation for casual observations of the sudden appearance of large numbers of adults in shallow waters (Eales, 1921) or stranded on the beach (Hamilton et al., 1982). These sudden appearances are more convincingly explained by changes in sea-hare behaviour associated with reproduction (in which large, persistent, and highly visible breeding aggregations are formed seasonally, followed by the likelihood of post-reproductive and senescent individuals being washed ashore) or by circumstances of weather and sea conditions (in which large numbers of sea hares may be carried inshore by currents and tides: Krakauer, 1969). Secondly, although swimming may be locally directed, as in sea hares orienting into waves in an offshore direction (Hamilton and Russell, 1982), there is no evidence that groups of sea hares consistently swim in the same direction over larger distances; rather, larger-scale swimming orientation appears to be mostly random. Thirdly, observations of swimming bouts in the field indicate that the majority is relatively brief, lasting only a few minutes (Susswein et al., 1984; Hamilton, 1986). These brief swimming bouts would serve well to locate new patches of food within a particular geographic location, but would be poorly suited for long-distance migration. Finally, migration as a means of long-distance movements in adult sea hares, whether by swimming or crawling, seems unnecessary when all species produce a long-lived veliger larva potentially capable of transoceanic dispersal.

The results of this study on A. brasiliana provide an interesting contrast to previous work with A. fasciata by Susswein and colleagues. In both species, swimming increases in the absence of food (Susswein, 1984; Ziv et al., 1991a,b; present paper). Similarly, swimming is stimulated in both species by noxious stimuli, suggesting that swimming could function as a defensive response (Levy and Susswein, 1999; present paper). The effect of conspecifics on swimming, however, seems to differ between the two species. Thus, while swimming in A. fasciata increases in solitary animals versus ones held in groups (Ziv et al., 1991a,b, 1994), we found no effect of conspecifics on swimming in A. brasiliana. It is possible that this reflects a true behavioural difference between the species. Alternatively, differences in methodology may have led to different results. Ziv et al. (1991a,b, 1994) studied spontaneous bouts of swimming at all times of the day, and treated individual behavioral events (>100 events/animal) as statistical replicates, whereas we induced bouts of swimming at specific times, and used individual animals as statistical replicates. Because different behaviours in Aplysia tend to occur at different times of the day (Carefoot, 1987), it is possible that animals might react differently to particular stimuli at different times. Similarly, it is possible that experimental treatments might affect spontaneous and induced swimming behaviour in different ways. Finally, it may be that the effect of conspecifics on swimming is modest, and more readily detected with statistical approaches involving larger replication. Whether this apparent difference in behavior between these two closely related species is real or an artifact is an interesting question, and calls for comparative studies with standardized methodologies.
Acknowledgements

We are grateful to Wayne Gardner, Director of the Marine Science Institute of the University of Texas, and his staff for providing research facilities and accommodations, and for technical assistance. We thank Don Hockaday and the staff at UT Pan American Laboratory on Padre Island for their advice on collecting and transporting sea hares, and for use of holding facilities. We are especially grateful to Ed Buskey for arranging for our visit, and for his generous help and hospitality, and to Rebecca Wagget, Lanny Miller, and Scott Nuñes at the Marine Science Institute for their kind assistance. Comments from an anonymous reviewer greatly improved the manuscript. Research funding for this study was provided through a grant from the Natural Sciences and Engineering Research Council of Canada (NSERC).

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