Nudibranch Navigation: The Natural History of *Tritonia diomedea*

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The giant nudibranch crawled slowly forward. Another slug remained stationary on the sea floor some meters away. As the changing tidal flow through the habitat stabilized on a new heading, the second slug was now upstream of the first. The crawling slug turned upstream towards the quiescent animal. Casting left and right with its oral veil, it advanced towards the potential mate. Contact was finally made and both animals began the long process of clockwise circling and mating, before the partners broke apart and crawled off into the distance. For us, the scientists watching these events unfold on a camera system deployed on the ocean floor habitat, two and half hours had passed on board our research vessel. Although slug behavior is slow to the human eye (not to mention tedious if the weather is beautiful above decks), when we reviewed the videos in time-lapse, the slug activities revealed a fascinating complexity. These and other videos recorded in the slug's habitat would advance our understanding of the natural history of nudibranchs and fill an important gap in over 40 years of research on this species.

Over the last four decades the sea slug *Tritonia diomedea* Bergh, 1894 has been a research subject for a small group of neuroethologists, scientists who combine the study of both nervous systems and animal behavior. *Tritonia* and several other species of gastropod mollusks have contributed greatly to understanding neural control behavior (Chase 2002). Why? These slugs and snails have some of the largest neurons on the planet (100 times larger than most mammalian neurons), their nervous system contains "just" tens of thousands of neurons (instead of the billions found in mammals), and their behaviors, although slow, are sufficiently complex to make studying their control interesting. Researchers working with *Tritonia* have been able to explain, at least in part, the nervous control of a variety of behaviors, including crawling, feeding, and most spectacularly, swimming. More recently several researchers have laid the groundwork for studying navigation, working on both the neural control of locomotion (e.g., Redondo and Murray 2005), and the neural pathways involved in sensation (e.g., Cain et al. 2006). They are hoping to gain insight into how

The primary research site was near Vargas Island, in Clayoquot Sound on the west coast of Vancouver Island, British Columbia. Our vessel, the 45-foot ketch *Melibe*, provided the ideal research platform. Ample room above and below decks provided room for SCUBA equipment and the camera system that recorded the slug activities 5m below the surface. She also provided living space and recreational opportunities during the research trips. [photo credit (left): James Murray]

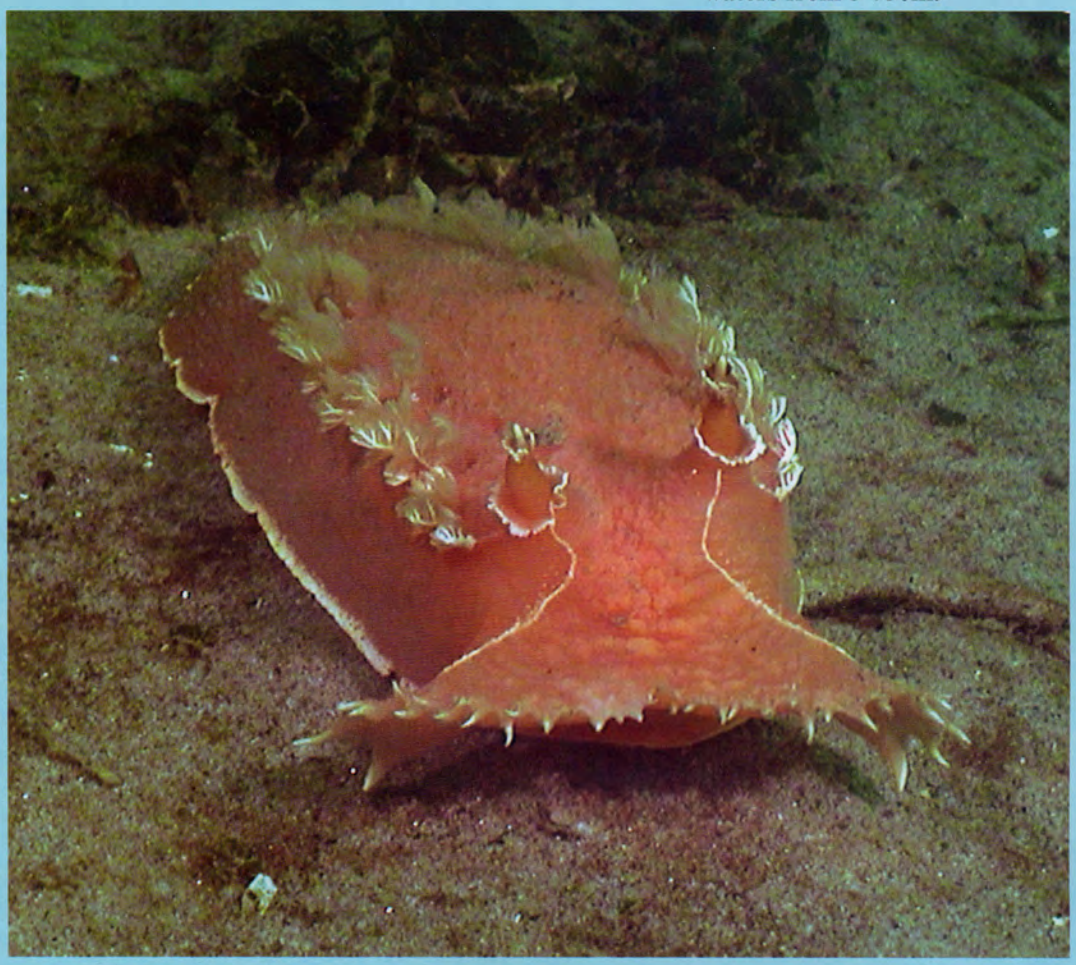
nervous systems are designed to detect an animal's world, process the sensory information, and produce guided locomotion within that world.

This progress, however, emphasized a missing component in our knowledge of *Tritonia*. Despite 40 years of research, no one had made a systematic survey of the slug's natural behaviors. Although it was unlikely the behaviors studied in the laboratory were wholly unnatural, there remained the distinct possibility that either the behaviors were incomplete or that certain behaviors simply had not yet been observed due to some deficit in the sensory environment found in the tanks in the laboratory. Consequently my and my colleague's interest in the slug videos was high.

Our methods were simple in concept. Anchor our boat over a sea pen bed, the natural habitat of *Tritonia*. Deploy waterproof cameras (security cameras used by many convenience stores) on poles thrust into the soft sediment of the sea pen bed. Make sure the video and power cables were all properly connected to a digital video recording system (again, originally designed for use as a security system), press record, and wait for the action to unfold. Of course wind and weather played havoc with our efforts on occasion. Crucially it turned out that we needed three anchors to keep the boat position stable to avoid its 16 tons severing the camera cables, but the system worked remarkably well. In fact, the cameras consistently recorded images slightly *better* than what divers felt

Right: Feeding is a delicate process for *Tritonia*. The slug needs to bite the sea pen before the prey can retract into the sediment. The slug approaches from downstream, with the rhinophores, and presumably the oral veil, used to detect the odor plume spreading downstream from the prey individual. As it nears the sea pen, it raises the oral veil. After the briefest of touches, the slug stops and rears back, readying to strike. The jaws are opened and the flexible radula is thrust out, grasps a leaflet of the sea pen, and then retracts back between the jaws. The jaws are closed, severing the leaflet, and the slug is left with a small meal, while the sea pen continues to contract down into its burrow.

Below: A 20cm *Tritonia diomedea* approaches, looking like a Hollywood creation of an alien for a grade-B movie. This bizarre-looking creature inhabits northern Pacific subtidal waters from 5-750m.



they were able to see underwater and we were able to collect some 510 hours of slug videos. Using a combination of these time-lapse videos and direct observation by divers, we were able to publish a description of many of *Tritonia*'s daytime behaviors in a recent issue of *Biological Bulletin* (Wyeth and Willows 2006a).

We found that *Tritonia* spend much of their time crawling amongst the scattered sea pens of their habitat searching for both food (the sea pens themselves) and mates. They also spend considerable time inactive, remaining stationary on the substratum. They occasionally encounter the predatory sunflower seastar (*Pycnopodia helianthoides*), which they avoid either by crawling away or swimming up into the water column, allowing the currents to sweep them away.

The tidal currents are crucial to their lives in other ways as well. When flow is strong, the slugs will turn to face upstream, reducing drag. They will even bulldoze a berm of sand in front of them, presumably an attempt to further reduce drag and avoid being swept off the bottom. Dislodgement can occur both as a result of oscillating wave motion and strong tidal flows and may have grave consequences since the slugs may not settle back to the sea floor before they are far beyond the bounds of the sea pen bed.

It is when the currents are more moderate, however, that they are most important to *Tritonia*. By careful analysis of our videos (Wyeth et al. 2006), supplemented by some laboratory experiments (Wyeth and Willows 2006b), we were able to determine that the slugs rely on odors carried in the flow in order to navigate. They crawl upstream in the odor plumes generated by both prey and conspecifics, but after feeding or mating with those upstream targets, they crawl randomly with respect to flow. Conversely, they crawl downstream in predator odor plumes. Meanwhile, slugs crawling outside odor plumes are less likely to crawl upstream. They may prefer to crawl cross-stream in search of odor plumes in this situation.

The videos made it clear that in *Tritonia*'s natural habitat, water motion is both continuous and erratic. The regularity of the tides does not translate into predictable flow. Rather the topography of the sea floor disrupts the tidal flow, creating eddies that result in apparently random periods of both consistent and changeable flow from a slug's point of view. Nonetheless, those currents are the most important feature of the natural environment for the slugs, providing the stimuli necessary for navigation as well as carrying the threat of removal far away from both prey and mates.

The major conclusion of our study was that *Tritonia* relies on odors and flow for navigation. This result will help guide further experiments in the laboratories of scientists working to understand neural control of navigation. In addition, the changeable flows encountered by the slugs while navigating towards a potential mate made clear another important point: slow moving animals may need a special strategy for finding the source of an odor plume (e.g., Vickers 2000; Ferner and Weissburg 2005). Most animals trying to find an odor source use a simple strategy, move upstream when the odor is detected. This works because the flow moves the odor from the source to the animal, and therefore to find the source the animal can follow the flow. But what about sluggish animals? The currents are so changeable the animal may lose the scent completely before reaching the odor source. A possibly simple addition to the strategy would be to continue following the upstream heading based on when odor was last detected. A simple strategy, perhaps for a human with excellent vision, but how could a blind slug maintain a constant heading over an uneven sea floor and buffeted by changing flows? The answer may lie in previous research on *Tritonia* that has shown they are able to detect the earth's magnetic field

The giant orange nudibranch *Tritonia diomedea* lives in sea pen beds of the Northeast Pacific. The sea pens, a species of soft coral, form dense aggregations in habitats with both tidal flow and a sandy/muddy sea floor. They alternate between retracting into the sediment and extending their plumes up into the flow to capture planktonic particles carried in currents. *Tritonia*'s only food source is the soft corals, and their adult habitat is therefore limited to the soft coral beds. Despite the restricted diet, adults can reach 30cm or more in length. They crawl using cilia on the ventral surface of their foot. The slugs have two sensory tentacles (the rhinophores) on their head, along with an oral veil (the "moustache") that they use to detect both odors and water flows. The slugs are blind and rely on their senses of smell and flow to find prey and mates and to escape their primary predator, the giant sunflower seastar, *Pycnopodia helianthoides*.

Top two images: Mating for the hermaphroditic *Tritonia* is a long-lasting affair. Almost all mating events are preceded by one slug navigating up an odor plume to find a mate. After contact, the two animals align copulatory organs by clockwise circling. Copulation lasts about an hour, with sperm transferred by both partners. Already-mating pairs are highly attractive to downstream slugs, and occasionally a brief ménage à trois occurs, before the third slug supplants one of the previously mating pair.

Bottom two images: The soft-bodied and almost neutrally buoyant *Tritonia* are particularly susceptible to strong current gusts that can lift them off the sea floor and tumble them away downstream. To prevent this, they bulldoze small berms of sediment in front of them. The berming behavior can sometimes be so pronounced that the animals are almost buried in the sediment.

(Lohmann and Willows 1987). Perhaps the slugs fix a compass bearing on the upstream direction while odor is detected and then continue to follow that bearing even after the scent is lost. At the moment this orienteering behavior is just a hypothesis (Murray et al. 2006). Further experiments both in the natural habitat and in the laboratory will tell whether or not it is a navigation option for *Tritonia*.

Finally, this study has highlighted two broader conclusions. First, it is important to consider the time scale on which an animal lives. At first glance most people have a poor opinion of slug behaviors; they are so slow they must be boring. Yet when seen moving in time-lapse, perhaps 100 times faster than real time, rapt observers frequently compare their activity to mice or rats. The difference lies in that our observation skills are tuned to a certain pace of life, and slugs live at a very different pace from our own. Only by manipulating our observations (speeding up the video) to better suit our own perceptions are we able to properly appreciate the slugs abilities. And this conclusion applies to not just slugs, but to all organisms that live at different time scales. Second, and most importantly, this study reiterates the importance of field biology. The observations made in the natural habitat were able to highlight that odors and flow are the two most important cues for navigating *Tritonia*. Yet *Tritonia*'s sense of smell had been almost entirely neglected in the laboratory. Now further experiments can focus on odor detection and its role in navigation. Natural history, the observation and description of natural behaviors and natural stimuli outside of the laboratory, is critical to guiding further exploration and advancing our understanding of all organisms.

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