

## Gravitational Sensing and Control of Aquatic Flight in *Clione limacina*

Kevin Flick, Department of Zoology (UW)

**Introduction:** Directional control of flight in all animals involves complex relationships between elements in and outside the animal. Externally, there is mechanical and chemical information imbedded in a dynamic fluid characterized by spatial and temporal gradients in viscosity, density, and velocity. Internally, the sensorimotor neural circuitry, the size and orientation of the flight muscles, and the passive mechanical characteristics of the wing and body are integrated to modulate flight performance. In the current study, I examine the relationships between gravitational sensory input and flight steering behavior for an aquatic “flier,” *Clione limacina*.

**Background:** *Clione limacina* (below left) is an opisthobranch gastropod, related to sea slugs and nudibranchs. Thinning and extension the ancestral gastropod foot into wing-like parapodia allowed them to adopt a pelagic



lifestyle, flying in the aquatic sense by generating lift by flapping the parapodia. Sexually mature *Clione* range in size from 5mm to 85mm and continuously hover or swim in the posture shown here, presumably with aid from known statocysts which sense body orientation with respect to gravity. Directed locomotion is of particular interest in *Clione* since it is a specialist predator on another opisthobranch, *Limacina helicina* (above right) and the mechanism by which *Clione* finds its prey is unknown. These studies are aimed to dispel a long-standing anecdotal belief that *Clione* casts randomly to find prey, and cannot change the kinematics of its wings for steering. To that end, I present data from three experiments: (1), a computer simulation of predator-prey dynamics, (2), correlations between body angle and heading for free flying animals, and (3), modulation of wingtip kinematics in response to changes in body orientation with respect to gravity.



**Methodology:** I ran the predator-prey simulations in Matlab on a Macintosh G3 computer. I performed the live animal experiments with animals collected off the breakwater at the Friday Harbor Marine Labs in the spring and early summer of 2000. I stored these animals in filtered seawater (changed at least once daily) at 7-10°C. For the tethered animal preps, I glued an adult *Clione* on its dorsal side to a bent needle and held it at 0°, 45° and 90° (between horizontal and the animal's anterior-posterior axis) while filming its body and wing motions. For the free flying body kinematics, I filmed *Clione* flying in a 10-gallon tank. For all flight experiments, I cooled the animal's tank to 10°C and allowed the animal to acclimate for 30 minutes before filming each trial. For all filming, I used 2 Sony black and white analog video cameras at right angles to each other, both fed to the same tape via a screen splitter, and analyzed the video data in Matlab on a Macintosh G3 or G4 computer.

### RESULTS:

**Predator-Prey Model:** I developed computational model that compared the prey encounter likelihood between a randomly moving virtual *Clione*, and a second virtual *Clione* with a chemosensory based behavior very similar to the bacterial run-and-tumble model. The chemosensing *Clione* found prey 2 times as often as the randomly moving *Clione* with no information on the direction to prey. These data are difficult to interpret for the lack of experimentally derived parameters, but they do serve to cast doubt on the ability to casually observe and detect a bias in the laboratory or field behavior of *Clione*.

**Free Flying body kinematics:** To assess the relative roles of wingbeat steering versus trunk ruddering, I also tracked 3D coordinates of the head, mid-body, and trunk tip in free flying animals. These data show that the motion of the head and mid-section precedes motion of the trunk during turns. This suggests that the trunk does not initiate turns. Further analysis shows no consistent correlation between the angle of the tail with respect to the body and the animal's heading. This suggests that the tail is not used as a rudder and focuses further attention on the wings as the source of directional control.

**Tethered wingtip kinematics:** Analysis of the wingtip kinematics in tethered animals shows that when the animal is tilted towards its ventral side, the wingstroke shifts ventrally as if to restore the animal to an upright position (see figure 1). Variation in the wingstroke kinematics is stronger in the same animal between angles, than between animals at the same angle.

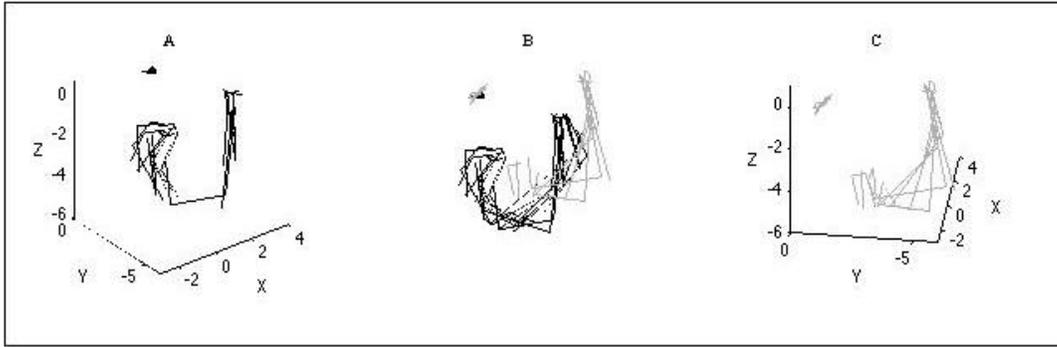


Figure 1: (A) head position and wingtip trajectory of animal at 90°, (B) plots A & C combined, (C) head position and wingtip trajectory of animal at 45° (perspective shifted with animal's anterior-posterior axis).

**Discussion:** What little is known about the spatial ecology of both *Clione* and its food, *Limacina* suggests that both are aggregated and patchy (4). Given the potentially large distances that could arise between clusters of *Clione* and its food, it seems unlikely that random motion is sufficient to bring *Clione* in contact with its prey. My computer simulations demonstrate that a simple chemosensory behavioral switch between casting randomly and moving more concertedly when near prey increases the likelihood of prey encounter two-fold.

The CNS of *Clione* is similar to the CNS in *Aplysia* (5). There are two Central Pattern Generators (CPGs) for swimming (one for each wing the in ipsilateral pedal ganglion) which are coupled *via* interneurons that coordinate the timing of the two wingstrokes (7). A rapid transition to maximum velocity as well as smooth transitions between flying speeds are accomplished by an increased frequency of motor neuron firing (1,2) and recruitment of slow or fast twitch muscle fibers (8). These data and the correlation between gravity sensory input and wingstroke kinematic variation from my experiments demonstrate a coupling between sensory neurons and the wing motor centers. . Since distance chemoreception is well documented for other phylogenetically basal gastropods (6), this suggests the possibility of analogous coupling between putative "*Limacina* tuned" mechano- or chemoreceptors and the wing motor centers.

In flying insects, the wing kinematic arises from the interaction of two sets of muscles. There are power muscles that are responsible for the gross up and down movement of the wing, and steering muscles that are responsible for the control of the wing (3). It is possible that the flight muscles in *Clione* are similarly divided. The role of the CPG and interneurons in stimulating two of the seven muscle groups in the wing has been described (7), yet the function of the remaining five is unknown. One hypothesis is that these five muscles play a role in temporary variations in kinematics and behavior -- turning on and off as necessary. Another hypothesis is that *Clione* changes the pressure of the hemocoel in the wing as a way to change kinematics. In fact, the neural control of pressure regulation in the hemocoel is totally unknown. Any of these pathways might provide sufficient behavioral modulation to increase the probability of prey encounter.

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