

SWIMMING BEHAVIOR AND MORPHOMETRY OF THE FILE SHELL *LIMARIA FRAGILIS*

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Swimming has evolved in only a few orders of Bivalves. In this study, the behavior, morphometry, and mechanics of swimming in the file shell *Limaria fragilis* were characterized and compared to the better understood scallops. Absolute swimming speed (cm sec^{-1}) increased with increasing shell height, although relative swimming speed ($\text{body lengths sec}^{-1}$) did not covary with shell height. The increase in absolute swimming speed was due to an increase in the distance covered during each valve clap as clap distance (cm clap^{-1}) also increased with shell height while clapping frequency (claps sec^{-1}) did not covary with animal size. *Limaria fragilis* displayed a variety of morphological changes related to size. Shell length was negatively allometric with shell height indicating the shell became proportionately slimmer in larger animals. Dry shell mass was negatively allometric with shell height, while both dry adductor muscle mass and dry mantle + tentacle mass were positively allometric. Autotomy of mantle tentacles significantly decreased clap distance by 13% without affecting clapping frequency or swimming speed.

Keywords: *Limaria fragilis*; Swimming; Morphometry; Autotomy; Bivalve

INTRODUCTION

Swimming has evolved in only a few orders of Bivalves, including file shells (Family Limidae) and scallops (Pectinidae). The swimming energetics of both file shells and scallops have been well characterized. *Limaria fragilis* (Gmelin) is capable of swimming for extended periods (15 min or more) and swimming is mostly aerobic, but with an anaerobic contribution from arginine phosphate, glycolysis, and ATP stores (Baldwin and Morris, 1983). Their cost of transport is substantially higher than that of other swimming invertebrates, possibly due to the cost of carrying a shell, no matter how light, and to swimming with the extensive mantle tentacles protruding into the water (Donovan and Baldwin, 1999). In contrast, scallop swimming lasts a relatively short time (2–5 min) and is powered, to a larger degree, anaerobically (Gade *et al.*, 1978; Grieshaber, 1978; Livingstone *et al.*, 1981).

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The mechanics and hydrodynamics of scallop swimming have also been well studied. Scallops exhibit a range of swimming abilities, from short-burst, “zig-zag” swimmers such as *Chlamys* (Moore and Trueman, 1971; Donovan *et al.*, 2002) to long-range, gliding swimmers such as *Amusium* (Morton, 1980; Joll, 1989) and *Placopecten* (Caddy, 1968). Swimming ability in scallops is related to shell morphometry, and this varies amongst scallop species (Stanley, 1970). For example, shells of long-range swimming pectinids are thin compared to species that do not swim well and those that do not swim at all (Hayami and Okamoto, 1986). Likewise, long swimming species tend to be upper-convex, in which their upward-facing left valve is more strongly convex than their downward-facing right valve. This allows lift to be generated while swimming through the Bernoulli effect, and is in comparison to poorer swimmers which tend to be equiconvex or lower-convex (Stanley, 1970). Scallop shell morphometry also changes intraspecifically with size, and it is argued that these allometric changes allow larger scallops to produce proportionately more power to compensate for the relative increase in mass that occurs with an increase in height. In this case, relative thinning of the shell occurs as scallops grow, such that relatively less lift must be generated to swim off the substratum (Hayami and Hosada, 1988). As well, shell length is usually positively allometric with shell height in swimming pectinids (that is, shells become relatively broader as scallops grow), which increases the aspect ratio and makes swimming more efficient by decreasing drag (Gould, 1971; Hayami, 1991). Muscle mass is also positively allometric with shell height, increasing the relative power that can be generated by larger scallops (Gould, 1971).

Swimming in Limidae is less well understood. File shells, like scallops, swim by quickly adducting their valves to produce posterior propulsive jets of water. This causes them to swim with their ventral shell margin foremost and dorsal hinge hindmost. File shells typically have long tentacles that extend from the mantle and cannot be withdrawn into the shell. The tentacles are used for defense against predation. When attacked, the file shell is capable of autotomizing its tentacles which are quite sticky due to thick mucus. The mucus is distasteful to predatory fish (Gilmour, 1967). During swimming, these tentacles are also capable of producing thrust by participating in a rowing motion (Gilmour, 1967) and the thin shell is thought to decrease the sinking rate of the animal when it stops valve-clapping (Morton, 1979). However, the behavior and mechanics of swimming in file shells have been described only qualitatively and there has been no description of the effects of animal size or morphometry on swimming ability.

The purpose of this study is to better characterize and to quantify the behavior, morphometry, and mechanics of swimming in *L. fragilis*. We investigated ontogenetic morphometric changes, changes in swimming behavior with file shell size, and the effects of tentacle autotomy on file shell swimming.

MATERIALS AND METHODS

Experimental Animals

Limaria fragilis were collected from under coral boulders on the reef flat at the Heron Island Research Station, Queensland, Australia. They were captured using a plastic tea strainer to prevent loss of mantle tentacles and they were transferred to holding aquaria

(25 cm × 40 cm, 20 cm deep) with a continuous supply of fresh sea water at the research station. Each aquarium had fresh sand and a coral rock on the bottom, and a maximum of two *L. fragilis* were placed in an aquarium. Individual *L. fragilis* were used within one day of collection.

Swimming Behavior

To determine how swimming behavior correlates with file shell size, *L. fragilis* ($N = 14$) were individually placed in a 58 × 10 cm aquarium that was 16 cm deep. A 2 × 2 cm grid was affixed to the long side of the aquarium and each *L. fragilis* was videotaped as it swam the length of the aquarium. To determine number of valve claps, swimming distance and swimming time, the videotapes were reviewed on a large television screen. An individual swimming episode was identified and the number of valve claps was counted. Swimming distance was determined to the nearest 0.1 cm by marking the *L. fragilis*' starting and ending points for the episode on a hand-held 2 × 2 cm grid identical to the one used in the experiment. The distance was then determined with a ruler. Swimming time for the episode was measured by timing with a stopwatch. Three swimming episodes were analyzed for each *L. fragilis*. These three episodes were averaged and mean absolute speed (cm sec^{-1}), mean relative speed ($\text{body lengths sec}^{-1}$), mean valve clapping frequency (claps sec^{-1}), and mean valve clap distance (cm clap^{-1}) were determined for each *L. fragilis*. These were compared to *L. fragilis* height (maximum distance from the dorsal hinge to the ventral margin of the shell; mm) using correlation analysis.

Morphometry

After swimming behavior had been determined as described above, the *L. fragilis* were dissected to measure morphological changes with increasing size. To access soft tissues, the mantle of each *L. fragilis* ($N = 14$) was carefully cut away from the shell with a scalpel then the adductor muscle was cut. The adductor muscle was separated from the rest of the soft tissue and placed on a pre-weighed piece of aluminum foil. The mantle and mantle tentacles were similarly isolated and placed on another weigh boat, as was the shell. The remainder of the soft tissue (gonad and digestive tissues) was discarded. All three components were dried to constant mass in a 60°C oven for 24 h and dry masses were recorded on a Sartorius BP2105 balance with a precision of 0.1 mg.

After drying, a digital picture was taken of each shell. Shell height and shell length (maximum distance from the anterior side to the posterior side of the shell) were measured using image analysis software (NIH Image).

Shell length, dry shell mass, dry adductor muscle mass, and dry mantle + tentacle mass were each log-transformed then regressed against log-shell height. Model I regression was used because there is very little error involved in measuring mollusc shells (Carefoot and Donovan, 1995) and statistical analysis is more convenient with Model I regression. Since the coefficients of determination for Model I regressions were all large (see Results), the difference between Model I and Model II regression is small (Laws and Archie, 1981). When Model I regression equations had been determined, the resulting slopes were compared to the expected slopes for isometry using *t*-tests (Zar, 1996).

Tentacle Autotomy

To determine the contribution of the mantle tentacles to swimming, swimming behavior of *L. fragilis* ($N=9$) was measured before and after tentacle autotomy. File shells were videotaped swimming as described above then, after swimming, each *L. fragilis* was induced to autotomize a majority of its tentacles. The middle fold of the mantle of *L. fragilis* is arranged into rows of tentacles, with the largest tentacles towards the opening between the valves (Morton, 1979). In the present experiment, all of the longest tentacles were autotomized (i.e. the two innermost rows of tentacles) leaving only the short outermost tentacles. Tentacle autotomy was induced by draping them across a finger and gently pulling the finger away from the animal. Some shorter tentacles were removed at the base with fine-tipped tweezers. The *L. fragilis* were then returned to their aquaria and allowed to recover for 24 h. After the recovery period, each *L. fragilis* was again videotaped swimming as described above. Videotapes of a control treatment of different individuals than those used for the experimental treatment ($N=9$) were made of *L. fragilis* swimming on two successive days but without tentacle autotomy.

For the experimental animals, mean absolute swimming speed (cm sec^{-1}), clapping frequency (claps sec^{-1}), and clap distance (cm clap^{-1}) before and after autotomy were compared using paired *t*-tests. For the control animals, means from the first day were compared to means from the second day using paired *t*-tests.

RESULTS

Swimming Behavior

Absolute swimming speed (cm sec^{-1}) increased with increasing shell height in *L. fragilis*, although relative swimming speed ($\text{body lengths sec}^{-1}$) did not covary with shell height (Fig. 1). The increase in absolute swimming speed was due to an increase in the distance covered during each valve clap as clap distance (cm clap^{-1}) also increased with shell height while clapping frequency (claps sec^{-1}) did not covary with animal size (Fig. 2).

Morphometry

Limaria fragilis displayed a variety of morphological changes related to size. Specifically, shell length was negatively allometric with shell height (Table I) indicating the shell became proportionately slimmer as the animal grew. Likewise, dry shell mass was negatively allometric with shell height, with the shell becoming relatively lighter in larger animals. Both dry adductor muscle mass and dry mantle + tentacle mass were positively allometric with shell height. This indicates that both these tissues are proportionately more massive in larger *L. fragilis*.

Tentacle Autotomy

Following tentacle autotomy, clap distance decreased 13%, from 4.70 ± 0.67 to $4.08 \pm 0.52 \text{ cm clap}^{-1}$ (Table II). However, no change in clapping frequency was detected and absolute swimming speed remained unchanged. There were no significant changes in swimming ability in the control treatment (Table II).

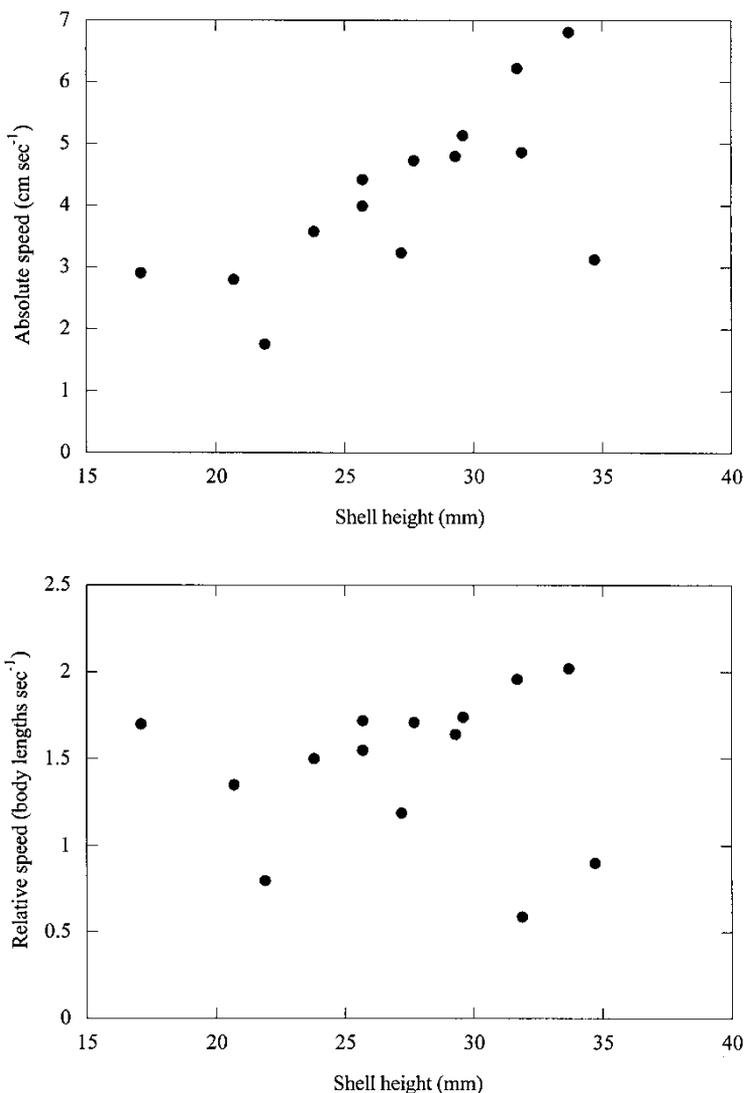


FIGURE 1 Correlation of absolute and relative swimming speed with shell height in *L. fragilis*. Absolute speed showed a positive correlation with shell height ($r = 0.67$, $P = 0.008$), while relative speed did not covary with shell size ($r = -0.003$, $P = 0.99$).

DISCUSSION

File shells are unique amongst swimming bivalves in their ability to produce propulsive thrust with their pallial tentacles to augment jet propulsion produced by valve clapping. In *L. fragilis*, the tentacles account for at least 13% of the distance attained during each valve clap (Table II). In fact, the full contribution of the tentacles is most likely greater since only the longest tentacles were removed in this study. Thus, *L. fragilis* swimming after autotomy still had over half their tentacles with which to row, although the

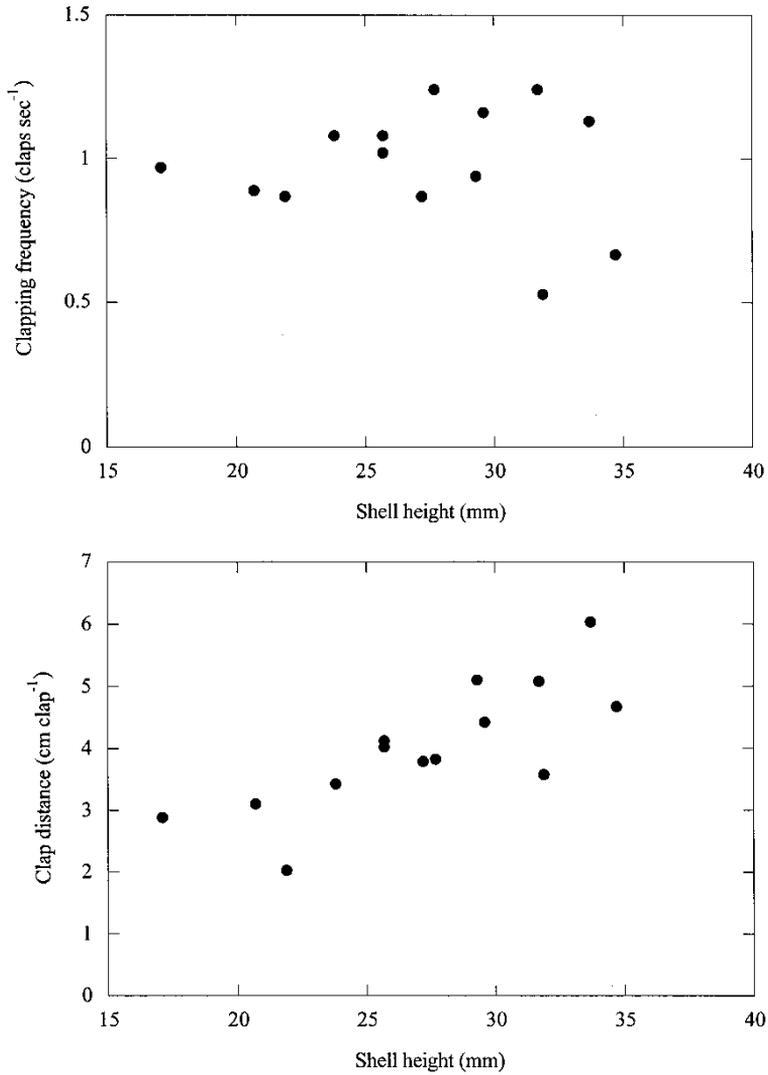


FIGURE 2 Correlation of clapping frequency and clap distance with shell height in *L. fragilis*. Clap distance showed a positive correlation with shell height ($r=0.79$, $P=0.001$), while clapping frequency did not covary with shell size ($r=-0.08$, $P=0.78$).

TABLE I Scaling of swimming-related morphometric relationships in *L. fragilis* ($N=14$). Data were \log_{10} -transformed before a least-squares regression was fit to them. All equations were in the form $\log_{10} Y = \log_{10} a + b \log_{10} X$, where b is the slope of the line and a is the intercept

$\log_{10} Y$ on $\log_{10} X$	$\log a$	b	Expected slope for isometry	r^2	$t_{0.5(2),12}$	P
Shell length on shell height	0.06	0.82	1	0.97	4.38	< 0.001
Shell mass on shell height	-4.14	2.62	3	0.99	5.22	< 0.001
Adductor mass on shell height	-6.61	3.72	3	0.95	2.98	0.01
Tentacle mass on shell height	-5.77	3.56	3	0.98	3.48	0.005

TABLE II Swimming behavior of *L. fragilis* after tentacle autotomy (autotomized group) and after being held in aquaria for 24 h without autotomy (control group). Values are mean \pm sd

<i>Autotomized group</i>	<i>Before autotomy</i>	<i>After autotomy</i>	<i>Paired-$t_{0.05(2),7}$</i>	<i>P</i>	<i>Power</i>
Swimming speed (cm sec ⁻¹)	3.64 \pm 0.91	3.49 \pm 0.72	0.40	0.70	0.06
Clapping frequency (claps sec ⁻¹)	0.77 \pm 0.14	0.85 \pm 0.13	1.09	0.31	0.16
Clap distance (cm clap ⁻¹)	4.70 \pm 0.67	4.08 \pm 0.52	3.51	< 0.01	
<i>Control group</i>	<i>First day</i>	<i>Second day</i>	<i>Paired-$t_{0.05(2),7}$</i>	<i>P</i>	<i>Power</i>
Swimming speed (cm sec ⁻¹)	3.30 \pm 0.74	3.52 \pm 1.20	0.86	0.41	0.03
Clapping frequency (claps sec ⁻¹)	0.74 \pm 0.12	0.84 \pm 0.25	1.72	0.12	0.29
Clap distance (cm clap ⁻¹)	4.44 \pm 0.59	4.21 \pm 0.69	1.60	0.15	0.12

remaining tentacles were less than half as long as the autotomized tentacles. This rowing motion has been described in great detail for *Lima hians* by Gilmour (1967). Briefly, each tentacle is hollow, with extensions of the pallial hemocoel running along its length. Septa, which can be opened and closed via pores, are found at regular intervals. There are also sets of radial and longitudinal muscles along the length of each tentacle. One consequence of this morphometry is tentacles which are capable of complex movements. During swimming, the septa are closed and the hemocoel within becomes a hydrostat so the radial and longitudinal muscles can act as muscular antagonists. Each tentacle is then capable of a rowing motion, similar to that of cilia. In *L. hians*, groups of tentacles participate in specific swimming motions: the ventral tentacles are held stiffly in front of the swimming animal while the anterior and postero-ventral tentacles row (Gilmour, 1967). This behavior is much the same for *L. fragilis* except that a greater number of tentacles participate in rowing (only a few, if any, are held in front of the animal).

The importance of tentacles to swimming is also indicated by their proportional increase in mass as *L. fragilis* increase in size. Mantle + tentacle mass scaled allometrically with shell height (Table I), increasing more than would be expected from a direct linear relationship. In general, as swimming bivalves grow their rapidly increasing mass (dependent on the animal's volume, which scales as the cube of a length) compared to shell size (a length or area) demands that the bivalve generate relatively more lift to leave the substratum and begin swimming. In fact, some scallops lose the ability to swim after reaching a certain size. For example, *Placopecten magellanicus* is highly motile until reaching 100 mm shell height after which swimming is no longer possible (Dadswell and Weihs, 1990). Scallops exhibit a variety of ontogenic morphological changes thought to maximize swimming ability as they get larger. Shell mass becomes relatively lighter compared to shell height, decreasing the amount of lift that would otherwise have to be generated (Hayami and Hosada, 1988). At the same time, adductor muscle mass becomes relatively heavier enabling the scallop to generate more force with each valve clap (Gould, 1971). It is interesting that *L. fragilis* also exhibit both these ontogenic changes (Table I), suggesting that these are common adaptations to enhance swimming ability in bivalves. In this respect, the positively allometric scaling of mantle + tentacle mass would also help larger *L. fragilis* generate proportionately more power than they would otherwise be able to.

One ontogenic change found in scallops that was not found in *L. fragilis* is the relationship of shell length to shell height. In scallops, shell length becomes proportionately greater as the shell increases in height, producing a shell which is relatively more broad (Gould, 1971; Hayami, 1991). Gould (1971) suggests that this

increases the aspect ratio of the swimming scallop, decreasing the amount of drag experienced. The opposite is seen in *L. fragilis*, with shells becoming relatively narrower with age. This difference is expected when we consider the difference in swimming orientation of these two bivalves. Scallops swim with their shell valves horizontal to the substratum while file shells swim with their valves perpendicular to the substratum (anterior margin below the posterior margin) (Fig. 3). Thus, becoming longer and slimmer should benefit file shells by decreasing their profile area in the direction of swimming, while becoming broader would not lead to a decrease in drag because of swimming orientation.

It should be mentioned that the pallial tentacles have other functions beside aiding swimming. In three species of file shells, including *L. fragilis*, Morton (1979) found that the tentacles, especially the postero-dorsal, were typically extended stiffly away from the shell to support the animal at rest. Likewise, file shells are capable of autotomizing their tentacles and Gilmour (1967) reported that the tentacles of *L. hians* are avoided by crab, fish and cnidarian predators probably due to a sticky mucus secreted by epidermal gland cells. The fact that *L. fragilis* cannot completely retract its tentacles into its extremely thin and fragile shell indicates that the shell is not its primary form of defense.

As *L. fragilis* increases in size, absolute swimming speed (cm sec^{-1}) also increases, although relative swimming speed ($\text{body lengths sec}^{-1}$) remains constant (Fig. 1). In scallops, the relationship of swimming speed and size depends on the species. Joll (1989) found that large *Amusium balloti* have faster absolute speeds than small conspecifics. However, absolute swimming speed remains constant over a range of scallop size in *Amusium pleuronectes* (Morton, 1980). Dadswell and Weihs (1990) found that midsized *P. magellanicus* (40–80 mm shell height) were faster than small and large conspecifics due to increasingly unfavorable hydrodynamics of large *P. magellanicus*. Likewise, Cheng and DeMont (1996) found that the minimum absolute swimming speed required to remain in the water column (the balancing swimming speed) of *P. magellanicus* was proportional to scallop height. However, they also found that relative swimming speed remained relatively constant at

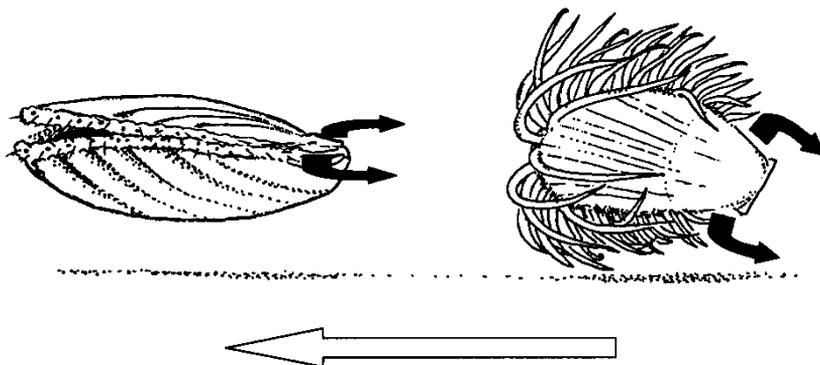


FIGURE 3 Side-view of a swimming scallop and file shell demonstrating the difference in orientation with respect to the substratum. Scallops swim with their valves roughly horizontal to the substratum while file shells swim with their valves roughly perpendicular to the substratum. The black arrows represent water jets being ejected past the hinge and the white arrow indicates the direction of swimming.

5–7 body lengths sec^{-1} throughout *P. magellanicus*'s life in contrast to Dadswell and Weihs (1990) who found that midsized *P. magellanicus* had a faster relative swimming rate (9.0 body lengths sec^{-1}) than smaller or larger conspecifics.

In general, *L. fragilis* displays slower relative swimming rates than do scallops. In this study, relative swimming speed ranged from 0.6–2.0 body lengths sec^{-1} (mean of 1.5 body length sec^{-1}). Scallops vary tremendously in their swimming speed, with long-range, gliding swimmers attaining relative rates of nine or more body lengths sec^{-1} (Joll, 1989; Dadswell and Weihs, 1990). Even the short burst, “zig-zag” swimming scallop *Chlamys hastata* has a faster relative rate (2.0 body lengths sec^{-1} ; Donovan *et al.*, 2002). It is probable that the lower relative swimming rate of *L. fragilis* is a function of the morphometry of the shell and tentacles. Scallops generate hydrodynamic lift (lift due to the convex shape of their shells and due to the angle of attack) while swimming, which augments lift generated by the downward portion of the water jets expelled from their mantle cavities during valve-clapping (Stanley, 1970). In contrast, Morton (1979) suggests that the light shell and the increased volume of extended tentacles reduce the sinking rate of file shells. Thus, the lift that must be generated by the swimming file shell would be reduced. This could be the reason that file shells are able to swim for longer periods of time than scallops, and may also contribute to the aerobic nature of file shell swimming (Baldwin and Morris, 1983) compared to scallop swimming (Gade *et al.*, 1978; Grieshaber, 1978; Livingstone *et al.*, 1981).

Large *L. fragilis* increase absolute swimming speed compared to small *L. fragilis* by increasing the distance covered per valve clap rather than by increasing clapping frequency (Fig. 2). This is similar to the scallop *A. pleuronectes* in which clapping frequency also remains relatively constant with size, although in this case absolute swimming speed does as well (Morton, 1980). *Limaria fragilis* averages 1.0 claps sec^{-1} , which also reflects its lower swimming speed compared to scallops. Scallops in general display a higher clapping frequency, with frequencies between 2 and 3 claps sec^{-1} for both slow-swimming (*C. hastata*, Donovan *et al.*, 2003) and fast-swimming (*A. pleuronectes*, Morton, 1980; *P. magellanicus*, Dadswell and Weihs, 1990) species.

In general, tentacle autotomy probably has minimal effect on the ability of *L. fragilis* to escape predation by swimming. First, autotomy of 100% of the longest tentacles caused a decrease of only 13% of the distance covered per valve clap, with no change in clapping frequency or swimming speed (Table II). This number of tentacles was extreme, and most likely more than would be experienced during a predatory attack. Second, it is unclear to what extent file shells swim to avoid predation. They are rarely seen swimming freely, although many species are capable of swimming when disturbed. File shells burrow into coral crevices or into the sand where they secrete byssus threads to reinforce their burrow. Their preferred method of escaping predation seems to be retreating into their burrows and autotomizing their tentacles (Morton, 1979) rather than swimming.

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