Radula morphology in veined rapa whelks, *Rapana venosa* (Valenciennes, 1846) (Gastropoda: Muricidae) from Chesapeake Bay, USA

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ABSTRACT

Radula length, width, number of transverse rows of teeth, and rachidian tooth dimensions (central cusp height, central cusp base width, and rachidian tooth base width) were examined in relation to leined rapa whelk shell length. Radula length and width increase linearly with whelk shell length. The number of transverse rows of radular teeth increase with whelk shell length. Within an individual, central cusp height of the rachidian tooth increases with increasing distance from the anterior of the radula. Central cusp height of the rachidian tooth, an indicator of tooth wear or use, was least for teeth in rows 1 and 11. Teeth in radular row 21 appear to be in a transition zone from high to low wear or use. Within a radula and within a size class, the ratio of central cusp base width to rachidian tooth base width does not change. Central cusp base width, central cusp height and rachidian tooth base width were significantly smaller in females than in males indicating sexual dimorphism in rachidian tooth shape for rapa whelks. Patterns of wear as indicated by central cusp base width to central cusp height ratio values were not significantly different between sexes and may serve as an indication that feeding strategies and/or prey may be similar between animals of different sex but similar size.

Additional Keywords: Neogastropoda, rachidian teeth, allometry, ontogeny

INTRODUCTION

The radula is a chitinous ribbon-like series of nearly colorless transverse tooth rows resting atop the radula membrane (Wu, 1965; Radwin and Wells, 1968). Muricid gastropods use the anterior teeth when drilling holes in bivalve prey (Carriker, 1961, 1981; Fujioka, 1985). As anterior teeth are worn down, they are replaced by younger teeth that are formed in the radular sac and gradually moved forward along the radula (Isarankura and Runham, 1968; Carriker, 1981). Muricid radulae have between 100 and 500 transverse rows of teeth (e.g., Carriker, 1961; Radwin and Wells, 1968; Fujioka, 1985). Each transverse row of teeth consists of a central rachidian (R) tooth and two slender marginal teeth (M) in the tooth formation M + R + M (Carriker, 1969). The central rachidian tooth in each transverse row is responsible for most of the rasping and physical shell removal during drilling while the marginal teeth synchronously tear flesh from prey (Carriker, 1969; Carriker et al., 1974; Krutak, 1977). Thus, the rachidian teeth show more wear, or reduction in size with use, than marginal teeth found in the same transverse rows (Carriker et al., 1974). This trend is particularly evident at the anterior end of the radula where the rachidian cusps in the most anterior row(s) may be completely removed by use (Carriker, 1969, 1974; Fujioka, 1985).

Veined rapa whelks (*Rapana venosa*, Valenciennes 1846, Muricidae) are predatory marine gastropods that, while originally native to Japanese and Korean waters (Tsi et al., 1983), have successfully invaded marine and estuarine habitats in the Black, Adriatic, Aegean, Mediterranean (Mann et al., 2004), and North Seas (Vink et al., 2005) as well as the Rio de la Plata (Pastorino et al., 2000) and Chesapeake Bay, USA (Harding and Mann, 1999). At the present time, the Chesapeake Bay rapa whelk population is the only known population of rapa whelks in North America.

Rapa whelks provide an unusual opportunity to investigate allometric changes in radula morphology across a wide size range of individuals because they reach terminal shell lengths in excess of 170 mm (Wu, 1988; Harding and Mann, 2005). Like other muricids (Paine, 1966), rapa whelks experience ontogenetic shifts in diet (Harding and Mann, 2001) as well as predation strategy and resulting predation signatures in prey valves (Harding et al., 2007). Small (<35 mm shell length) rapa whelks drill their prey (Harding and Mann, 2001; Harding et al., 2007) including barnacles

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(*Balanus* sp., *Chthamalus* sp.), mussels (*Mytilus* sp., *Geukensia demissa*), soft shell clams (*Mya arenaria*), and oysters (*Crassostrea virginica*). At shell lengths above 35 mm, rapa whelks eat larger bivalves (Harding and Mann, 2001) including oysters and northern quahogs (*Mercenaria mercenaria*) and typically either edge bore their prey or leave no signatures (Morton, 1994; Harding et al., 2007).

We quantitatively describe radula and rachidian tooth morphology for a size range of rapa whelks from Chesapeake Bay, USA. Rachidian teeth in *Rapana* have a large central cusp flanked by two smaller cusps (Arakawa, 1964; Wu, 1965). Shell length, the maximum dimension from the tip of the spire to the bottom of the siphonal canal, is used as the metric of whelk size. Shell length does not fluctuate with season or other factors. Relationships between shell length and radula dimensions are quantitatively described for male and female rapa whelks. Within each radula, rachidian tooth morphology is described along the length of the radula by measuring ratios of rachidian tooth central cusp base width to central cusp height and central cusp base width to rachidian tooth base width. The resulting ratios are compared between teeth along the length of an individual radula and across radulae from male and female whelks as well as from a size range of Chesapeake Bay rapa whelks.

MATERIALS AND METHODS

Rapa whelks with shell lengths (SL) in excess of 70 mm were obtained from the lower Chesapeake Bay, USA as donations to the Virginia Institute of Marine Science (VIMS) rapa whelk bounty program. Rapa whelks less than 70 mm SL were cultured at VIMS, Gloucester Point, Virginia to supplement the lower SL range of rapa whelks because individuals less than 70 mm SL were not available through the bounty program.

At the time of whelk collection, SL was measured in mm and whelks were assigned to shell length classes that were established to evenly categorize the potential SL range (1–180 mm SL). Petite, small, medium, and large classifications corresponded to whelk SL ranges of less than 45 mm, 45.1–90 mm, 90.1–135 mm, and 135.1–180 mm, respectively.

Whelks were frozen after collection and thawed to facilitate dissection and removal of radulae. Whelks were sexed during dissection and distinguished as male or female on the basis of penis length and gonad color after Mann et al. (2006). For the purposes of discussion herein, true females (penis length = 0 mm, bright yellow gonad) and imposex females (penis length <20 mm, bright yellow gonad) are grouped together per Mann et al. (2006). Typically, radulae were dissected out of the whelk proboscis. However, two control radulae were removed by soaking the proboscis for 24 hours in 10% sodium hydroxide to ensure that dissection removed the entire radula intact. Only intact radulae were used in this study.

After removal from whelks, images of the complete radula were taken using a digital camera mounted on a dissecting microscope for measurement of total radula length, total anterior to posterior distance (mm) and radula width, the maximum lateral distance across the bases of the marginal and rachidian teeth at the first transverse row of teeth (Figure 1). The odontophore was removed and then the rachidian teeth were systematically removed from every 10th transverse tooth row (e.g., Row 1, 11, 21 etc.) along the radulae moving from anterior to posterior (Figures 2 and 3). Tooth rows were removed with a size 10 scalpel blade for larger individuals, and with sharpened needles for cultured individuals less than 66 mm SL.

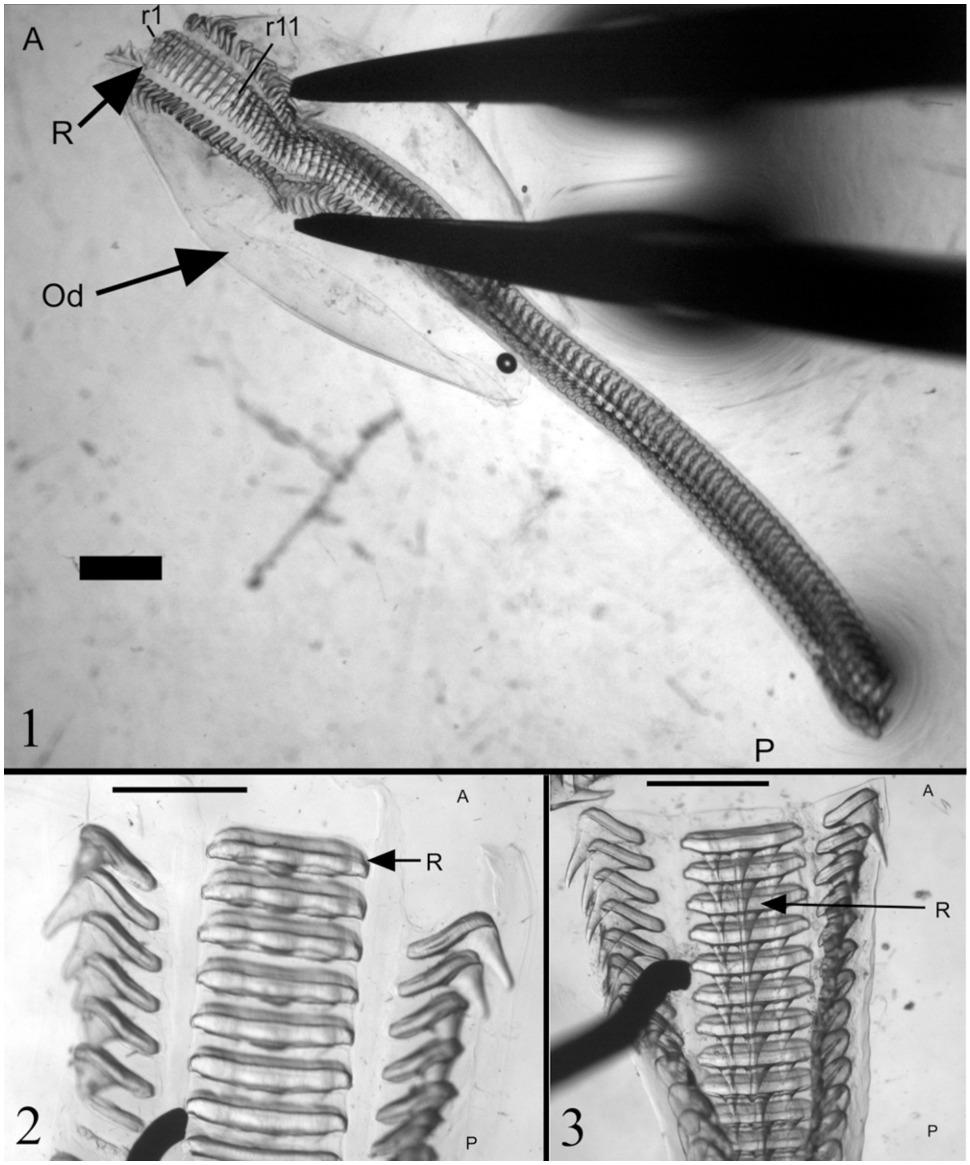
Digital images were taken of each individual rachidian tooth after removal with the tooth positioned convex side down. Typical magnification of individual teeth used for digital images ranged from 50× for whelks with SL greater than 147 mm to 90× for whelks less than 45–50 mm SL. Measurements (mm, Figure 4) of the rachidian tooth central cusp base width (L1), maximum central cusp height (L2) measured from the tip of the central cusp to the midpoint of L1, and the maximum rachidian tooth base width (L3) were made on the resulting images. The terminology used to describe tooth morphology follows that of Kool (1993).

Data Analyses: Significance levels for all statistical tests were set at alpha = 0.05 *a priori*. Fisher's multiple comparison tests were used for *post hoc* comparisons when appropriate.

Radula Allometry and Gross Morphology: Linear and power regression models were used to describe relationships within sexes between rapa whelk shell length and radula length, radula width, and number of rows of transverse teeth per radula. The relationship between radula length and both radula width and the number of transverse rows of teeth within radulae from males and females were also examined with both linear and power regressions. The slopes of all morphological regressions were compared between sexes with t tests (per Zar, 1996) on raw data or on logarithm transformed data if the power model was deemed more appropriate than the linear model.

Rachidian Tooth Dimensions: The relationship between central cusp base width (L1, Figure 4) and size class of the whelk from which it came was evaluated with a three-way ANOVA (whelk size class × tooth row × sex) with the response being the maximum base width of the rachidian tooth. These data satisfied assumptions of homogeneity of variance after the logarithm transformation was applied but not normality.

The relationship between rachidian tooth central cusp height (L2, Figure 4), the size class of the whelk from which it came, and the tooth row was evaluated with a three factor ANOVA (whelk size class × tooth row × sex). These data satisfied neither the assumption of normality nor homogeneity of variance regardless of the



Figures 1–3. Radula of veined rapa whelk. **1.** Radula from an 84.2 mm shell length (SL) whelk showing general morphological features and orientation. **2.** A rachidian tooth from row 1 of the radula from a 134 mm SL whelk showing wear. **3.** An unworn rachidian tooth from row 41 from a 122 mm SL whelk. Scale bar = 1 mm. Abbreviations: **r** = row number; **R** = rachidian; **Od** = odontophore; **A** = anterior; **P** = posterior.

transformation (logarithm, natural logarithm, square root, arcsine).

The relationship between rachidian tooth base width (L3, Figure 4), row number, sex, and size class of the whelk from which it came was evaluated with a three-way ANOVA (whelk size class × tooth row × sex). These data satisfied the assumption of homogeneity of variance without transformation but did not satisfy the assumption of normality regardless of the transformation (logarithm, natural logarithm, square root, arcsine) and were analyzed without transformation.

The ratio of rachidian tooth central cusp base width (L1) to central cusp tooth height (L2) was calculated for each rachidian tooth. Using a ratio that compares base width to tooth height is appropriate in a structure where both the base width and tooth height change along the length of the structure with ontogeny. Not only does the ratio allow for scaling when comparing individual teeth along the radula length, but it can also be used as an index of wear because width does not change with use. In this case a central cusp base width: central cusp tooth height ratio >1 is indicative of wear. The first 81 rows were chosen for analysis because every radula dissected had at least 81 rows. These data satisfied neither the assumption of homogeneity of variance nor normality regardless of the transformation (logarithm, natural

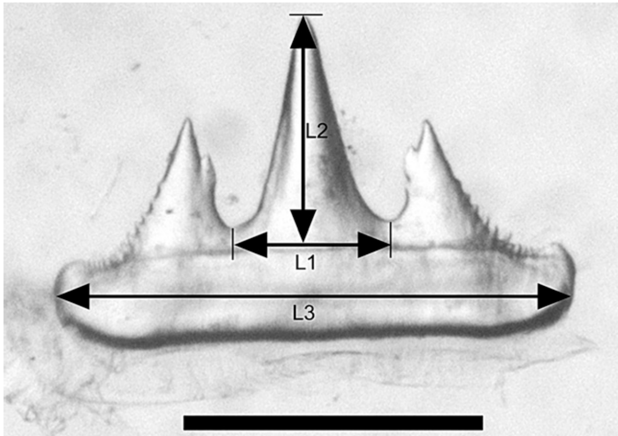


Figure 4. Veined rapa whelk rachidian tooth with the measurements made in this study identified: rachidian tooth central cusp base width (L1), rachidian tooth central cusp height (L2), and rachidian tooth base width (L3). Scale bar = 0.25 mm.

logarithm, square root, arcsine). A three-way ANOVA (whelk size class × tooth row number × sex) was used to evaluate the ratio of central cusp width to central cusp height (L1:L2).

The ratio of central cusp base width (L1) to rachidian tooth base width (L3) for each rachidian tooth was evaluated with a 3 way ANOVA (size class × row × sex) to describe potential changes in tooth shape with ontogeny. Data satisfied assumptions of homogeneity of variance without transformation but not normality (either with or without transformation, e.g., logarithm, natural logarithm, square root, arcsine). Changes in the L1:L3 ratio across whelk size classes reflect ontogenetic changes in tooth morphology that may be related to sexual dimorphism (Fujioka, 1982, 1984) and which may act to disperse relatively greater strike force during feeding in larger whelks.

RESULTS

Only radulae from whelks collected when water temperatures were above 11–12°C and feeding were used (Harding, unpublished data). All radulae examined were intact. Descriptive morphological data were collected from 39 rapa whelk radulae. These radulae were from rapa whelks with shell lengths between 20.2 mm and 174 mm (Table 1, Figure 5). Rapa whelk radula lengths ranged from 4.33 to 51.05 mm with corresponding radula widths of 0.23 to 2.67 mm and total number of transverse rows of teeth of 89 to 210, respectively. Radula length was an average of 21.4% (standard error = 0.61%) of shell length.

Radula Allometry and Gross Morphology: Regression coefficients for the fitted linear and power regression models used to describe relationships between rapa whelk shell length and radula morphology and between rapa whelk radula measurements are given in Table 2A.

The linear model is suggested as a better descriptor of the relationship between rapa whelk shell length (SL) and radula length (RL; Figure 6A) for both sexes since the coefficients of determination from both models are identical (Table 2A) and the linear model provides the simplest description of the data. The slope for the SL–RL relationship in males is significantly higher than that for females (t-test, Table 2B).

The power model more accurately described the relationships between rapa whelk SL and radula width (RW; Figure 6B) by predicting a radula width equal to 0 at a shell length equal to 0. The coefficient of determination for the linear model describing the relationship between shell length and the number of rows of radular teeth was higher (females = 0.63, males = 0.76, Table 2A) than that of the corresponding power model (females = 0.58, males = 0.69, Table 2A) for both sexes and the linear model predicted a positive number of rows of teeth at shell lengths of 0 mm (Figure 6C).

The relationship between radula length (RL) and radula width (RW) was described with a power model for both sexes (Table 2A, Figure 6D) which predicted a radula width of 0 at a radula length of 0 and had a higher coefficient of determination than the corresponding linear model (Table 2A). The linear model describing the relationship between radula length (RL) and number of transverse rows of teeth has a higher coefficient of determination than the corresponding power model

Table 1. Description of rapa whelks used in this study with basic statistics on radulae. Abbreviations used below are as follows: F = female, M = male, Avg = average for female and male whelks combined, SL = shell length, mm, SEM = standard error of the mean in parentheses, RL = radula length, mm, RW = radula width, mm; NRT = number of rows of teeth.

Whelk size class	# of Whelks (F/M)	Avg SL (SEM)	Avg RL (SEM)	Avg RW (SEM)	Avg NRT (SEM)	Avg RL/SL % (SEM)
Petite (<45 mm SL)	F = 5	25.64 (2.64)	5.28 (0.56)	0.48 (0.18)	106 (6.07)	20.59 (0.58)
	M = 5	34.72 (3.07)	7.62 (0.95)	0.71 (0.31)	122.20 (4.78)	21.72 (0.81)
Small (45.1–90 mm SL)	F = 5	70.38 (5.47)	15.93 (2.21)	0.97 (0.15)	133.80 (5.05)	22.38 (1.65)
	M = 6	69.13 (6.21)	17.63 (1.92)	1.22 (0.13)	126.67 (3.86)	25.56 (1.79)
Medium (90.1–135 mm SL)	F = 4	104.75 (5.07)	22.32 (2.52)	1.47 (0.03)	137 (12.71)	21.37 (2.53)
	M = 5	120.2 (5.3)	29.85 (1.58)	2.04 (0.10)	149.2 (7.19)	25 (1.51)
Large (135.1–180 mm SL)	F = 2	153 (10.0)	35.7 (3.2)	1.99 (0.24)	177.5 (16.5)	23.3 (0.57)
	M = 7	153.71 (4.47)	41.12 (2.23)	2.22 (0.10)	182.29 (6.38)	26.76 (1.21)

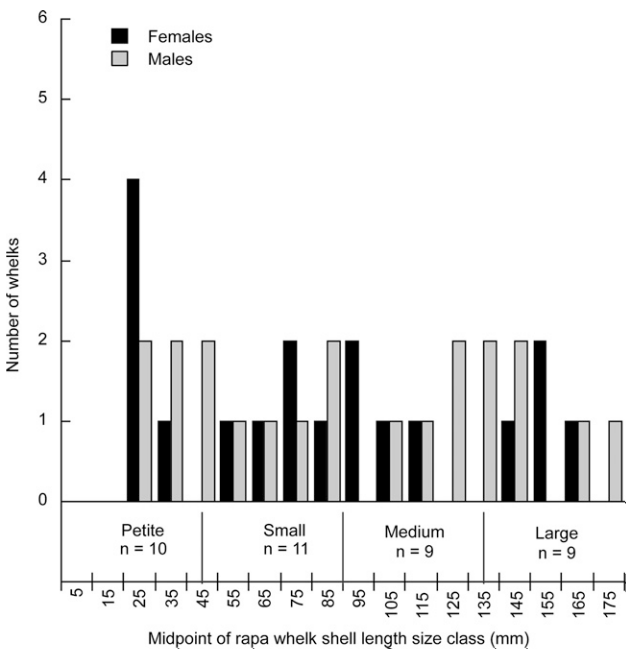


Figure 5. Shell length (mm) frequency distribution for the 39 veined rapa whelks whose radulae were examined in this study.

(females = 0.78 vs. 0.71, males = 0.81 vs. 0.72, Table 2) and predicts a positive number of tooth rows at radula lengths of 0 mm (Figure 6E).

Rachidian Tooth Dimensions: Rachidian tooth central cusp base width (L1, mm; Figure 4) increased significantly with increasing whelk size class (Table 3, Figures 7A and 7D). There were no significant differences in central cusp base width observed between rows within a size class for the 81 rows of teeth that were examined. Central cusp base width was significantly larger in males than in females (Fisher's test, Table 3). Differences between male and female central cusp base width were particularly evident in the medium and large size classes (Figure 7A and 7D).

The height of the rachidian tooth central cusp (L2, mm) varied significantly with size class, row number, and sex (ANOVA, Table 3, Figures 7B and 7E). In general, larger whelks have larger central cusp heights in rows 31 through 81 than whelks of other size classes. Within all size classes and both sexes, central cusp heights from rows 1 and 11 are significantly less than in rows 31 through 81 (ANOVA, Table 3, Figures 7B and 7E). Central cusp heights from rows 1, 11 and 21 in large whelks are significantly different from central cusp heights in petite whelks but similar to cusp heights observed in rows 1 and 21 for medium whelks and row 11 for small whelks (ANOVA, Table 3, Figures 7B and 7E). Female whelks have significantly lower L2 values than male whelks (Fisher's test, Table 3, Figures 7B and 7E).

Rachidian tooth base width (L3, mm) increases significantly with increasing whelk size class (ANOVA,

Table 2A. Summary of regression statistics used to describe rapa whelk radula morphology and wear patterns. The linear model equation was y = (a * x) + b. The equation used for the power model was $y = a X^b$. Abbreviations used below are as follows: coef = coefficient; SE = standard error, vs. = versus; SL = shell length, mm; RL = radula length, mm; RW = radula width, mm; NRT = number of rows of teeth.

		Females					Males				
Relationship	Model	R^2	Coef a (SE)	Coef b (SE)	F Statistic	p Value Regression	R^2	Coef a (SE)	Coef b (SE)	F Statistic	p Value Regression
SL vs. RL	Linear	0.93	0.23 (0.01)	−0.87 (1.47)	186.32	<0.01	0.93	0.27 (0.02)	−1.60 (1.80)	273.30	<0.01
	Power	0.93	0.16 (0.08)	1.07 (0.10)	188.72	<0.01	0.93	0.18 (0.08)	1.08 (0.09)	273.17	<0.01
SL vs. RW	Linear	0.82	0.01 (0.001)	0.16 (0.13)	63.30	<0.01	0.77	0.01 (0.001)	0.31 (0.17)	69.52	<0.01
	Power	0.81	0.03 (0.01)	0.86 (0.13)	61.29	<0.01	0.78	0.05 (0.03)	0.75 (0.11)	73.75	<0.01
SL vs. NRT	Linear	0.63	94.01 (8.73)	0.50 (0.10)	24.20	<0.01	0.76	97.08 (6.87)	0.51 (0.06)	66.41	<0.01
	Power	0.58	47.44 (11.78)	0.24 (0.06)	19.38	<0.01	0.69	40.38 (8.28)	0.29 (0.04)	46.10	<0.01
RL vs. RW	Linear	0.81	0.24 (0.13)	0.05 (0.01)	59.46	<0.01	0.77	0.43 (0.16)	0.05 (0.01)	69.7	<0.01
	Power	0.80	0.13 (0.04)	0.77 (0.12)	57.37	<0.01	0.79	0.19 (0.06)	0.67 (0.10)	78.17	<0.01
RL vs. NRT	Linear	0.78	93.28 (6.29)	2.29 (0.32)	50.66	<0.01	0.81	100.17 (5.58)	1.87 (0.20)	92.44	<0.01
	Power	0.71	67.26 (8.59)	0.25 (0.04)	34.28	<0.01	0.72	65.23 (8.09)	0.26 (0.03)	52.76	<0.01

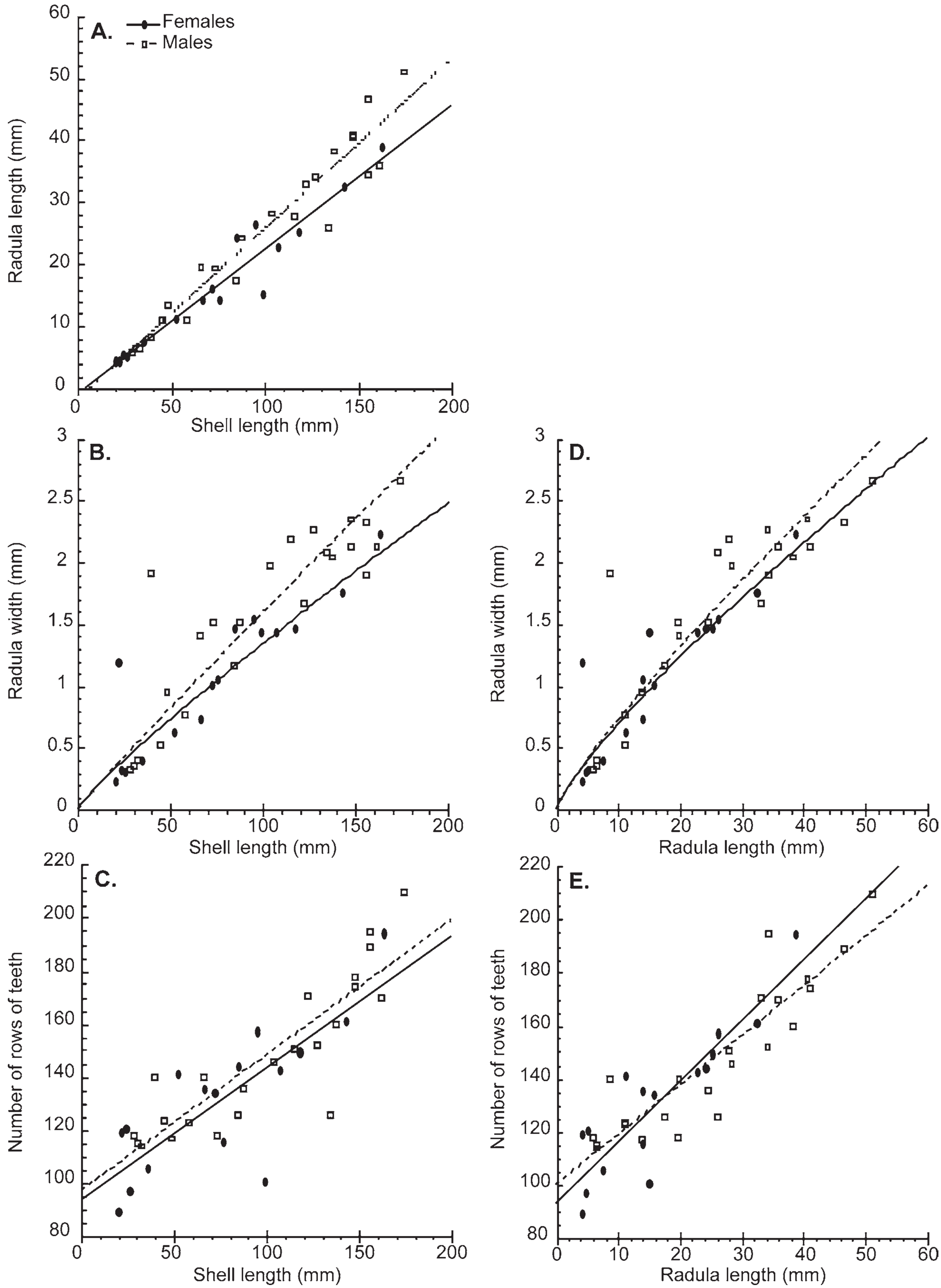

A.
Females
Males
Radula length (mm)
Shell length (mm)
B.
Radula width (mm)
Shell length (mm)
D.
Radula width (mm)
Radula length (mm)
C.
Number of rows of teeth
Shell length (mm)
E.
Number of rows of teeth
Radula length (mm)

Table 2B. Summary of t-tests comparing regression equations for female and male whelks given in Table 2A that are recommended for descriptions of these relationships. T-tests were performed for the power model using logarithm transformed data. Abbreviations are the same as those used in Table 2B above.

Relationship	Comparison	Model	p value
SL vs. RL	Female vs. Male	Linear	$<0.05^*$
SL vs. RW	Female vs. Male	Power	>0.05
SL vs. NRT	Female vs. Male	Linear	>0.05
RL vs. RW	Female vs. Male	Power	>0.05
RL vs. NRT	Female vs. Male	Linear	>0.05

Table 3, Figures 7C and 7F). However, no differences were observed in rachidian tooth base widths between radular tooth rows within a whelk size class and within a sex (ANOVA, Table 3, Figures 7C and 7F). Rachidian tooth base width was significantly larger in male whelks than in female whelks and this trend is particularly evident in the medium and large size classes (Table 3, Figures 7C and 7F).

Large whelks had significantly higher ratios of rachidian central cusp base width (L1) to central cusp height (L2) than all other whelk size classes (ANOVA, Table 3, Figure 8). The first row of teeth in the radulae had significantly higher L1:L2 ratios than all other rows (ANOVA, Table 3, Figure 8). The eleventh row of teeth also had an L1:L2 ratio that was significantly higher than that observed in rows 21–81 (ANOVA, Table 3, Figure 8). Since central cusp base to height (L1:L2) ratios >1 are indicative of tooth wear, the anterior 1–11 rows of teeth are more worn than newer teeth occurring in rows 21 and higher. Within each size class and sex, a wide range of L1:L2 values was observed for row 1 and/or row 11 (Figure 8). This variability was the result of one or two individual whelks per size class having very low central cusp heights (extreme wear) in row 1 or row 11, the rows of teeth that are actively used in feeding. Patterns of wear as indicated by L1:L2 ratio values were not significantly different between sexes (Table 3, Figure 8).

The ratio of central cusp base width to rachidian base width (L1:L3) was significantly affected by size class and sex (ANOVA, Table 3, Figure 9). Within a size class and within a sex, the ratio of central cusp base width to rachidian tooth width did not change significantly with row number. Male whelks had greater L1:L3 ratios than female whelks (Fisher's test, Table 3, Figure 9).

DISCUSSION

Radula length, radula width, and number of rows of teeth in the radula increase with increasing rapa whelk shell length. Ontogenetic increases in radula length and the number of rows of teeth with shell length have also been documented for other muricid species (e.g., *Stramonita floridana*, Radwin and Wells, 1968 (as *Thais floridana*); *Cronia margariticola* and *Morula musiva*, Fujioka, 1984; *Thais bronni* and *T. clavigera*, Fujioka, 1985; *Nucella lapillus*, Kool, 1993).

The relationship between rachidian tooth base width and central cusp base width also changes with ontogeny but does not change in relation to the anterior-posterior location on the radula. That is, within an individual and within a size class, rachidian teeth examined from rows 1 through 81 display similar scaling of central cusp base width to rachidian tooth base width. Rachidian teeth in female rapa whelks tend to have smaller central cusp base width as well as tooth base widths when compared to male whelks within the same size class. Fujioka (1982, 1984) describes similar ontogenetic changes in rachidian tooth shape including an increase in central cusp base width for *Cronia margariticola*, *Morula musiva*, and *Drupella* sp. in relation to sexual dimorphism. The observed ontogenetic changes in rachidian tooth shape may reflect morphological shifts designed to accommodate greater rachidian tooth strike force resulting from the scaling of the buccal complex at increased whelk sizes. Presumably there is an ontogenetic scaling relationship in effect to optimize the force provided by the buccal mass musculature and minimize the damage to rachidian teeth through use that is reflected in the shape of the tooth.

Rachidian tooth wear, as indicated by the ratio of central cusp width (L1) to central cusp height (L2), decreases with increasing distance from the anterior (oldest) end of the radula. Rachidian teeth in the first 11 rows of the radula have central cusp heights that are less than central cusp heights in rows 21 through 81 in all size classes. Carriker et al. (1974) describe rachidian cusps that have been worn off leaving only the tooth base in the anterior rows of rachidian teeth of *Urosalpinx cinerea folleyensis*. In laboratory studies with *Thais bronni* and *T. clavigera,* Fujioka (1985) observed that rows of teeth worn by feeding occupy 5–15% of the total number of radular rows. The whelk *Acanthina spirata* uses approximately 8 to 20 teeth in each rasping stroke as these whelks feed on mussels (Hemingway, 1975). These data are consistent with our observations for rapa whelks, where at least the 1st and 11th rows of the radula were used, and the 21st row acted as a transition between the part of the radula the whelk was actively using to feed and the more posterior section that was unused.

The observed changes in rachidian tooth wear may reflect ontogenetic changes in predation strategy, diet, or possibly both. Differences in predation strategy are potentially reflected in the observed changes in

Figure 6. Relationships for female (n = 16) and male (n = 23) veined rapa whelks ranging from 20.2 to 174 mm SL between shell length (SL) and radula length (RL, A), SL and radula width (B), SL and the number of rows of teeth (C), RL and radula width (D), and RL and number of rows of teeth (E) with fitted regressions (female = solid, male = dashed) that were used to describe the relationships. Linear regression models are plotted for panels A, C, and E. Power models are presented in panels B and D. Regression equations and descriptive statistics are given in Table 2.

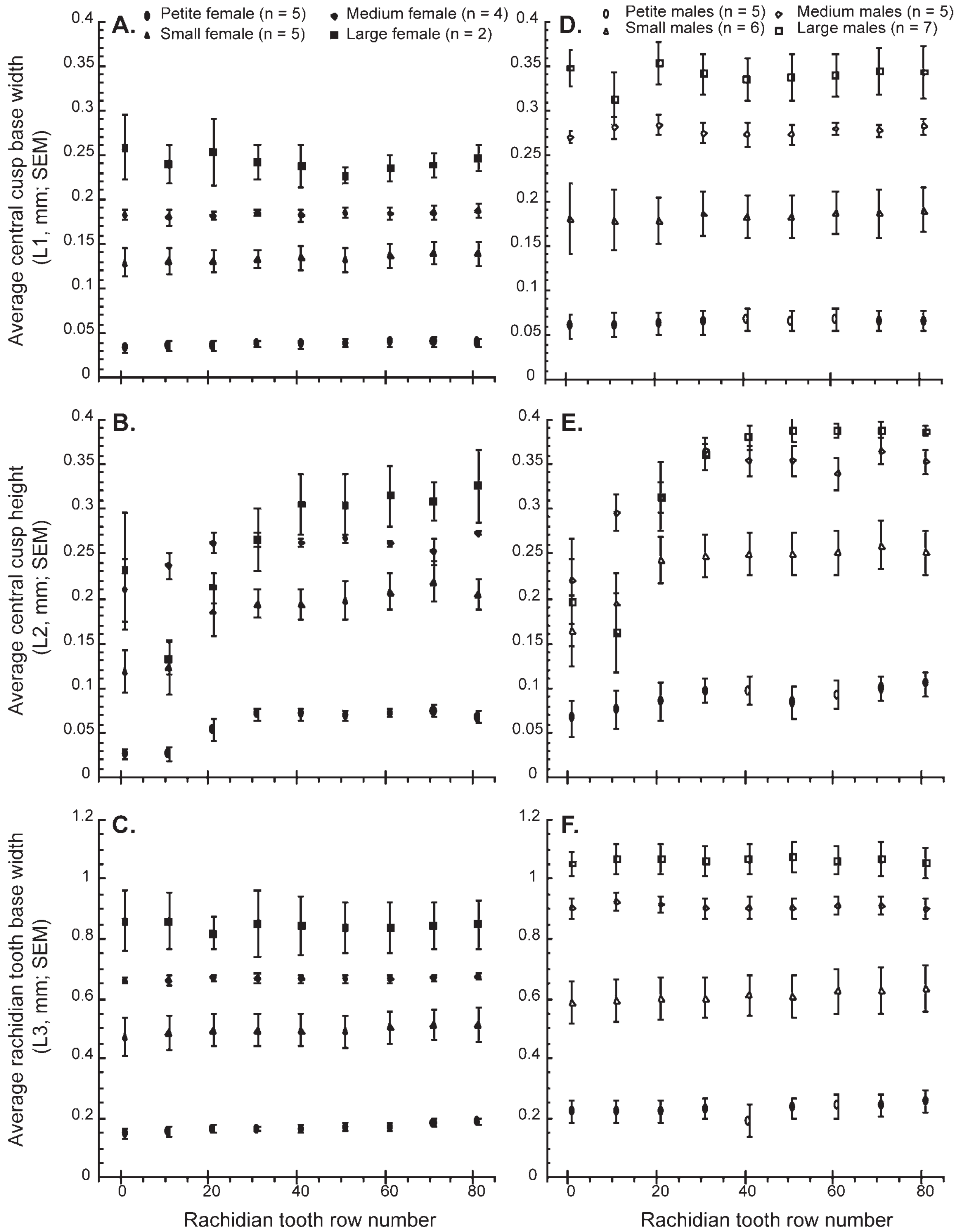


Figure 7. Graphs of rachidian tooth row number in relation to average central cusp width (L1) with error bars (standard error of the mean, SEM) for females (A) and males (D) from all size classes, average central cusp height (L2) with error bars (standard error of the mean, SEM) for females (B) and males (E) from all size classes, and average rachidian tooth base width (L3, SEM) for females (C) and males (F) from all size classes.

Table 3. Summary of ANOVA results comparing tooth morphology across whelk size classes and rows within the radulae. Asterisks indicate statistical significance at an alpha value of 0.05. Abbreviations used below are as follows: 1= petite size class, 2 = small size class, 3 = medium size class, 4 = large size class. NA = Not applicable. Refer to Figure 4 for a description of L1, L2, and L3.

Test	Response	Factors	p value	Fisher's test results
ANOVA	Central cusp base width (L1)	Size class	<0.01*	4 > 3 > 2 >1
		Row	0.80	NA
		Sex	<0.01*	Male > Female
ANOVA	Central cusp height (L2)	Size class	<0.01*	4, 3 > 2 >1
		Row	<0.01*	1, 11 < 31–81
		Sex	<0.01*	Male > Female
ANOVA	Rachidian tooth base width (L3)	Size class	<0.01*	4 > 3 > 2 > 1
		Row	0.99	NA
		Sex	<0.01*	Male > Female
ANOVA	Wear (ratio L1/L2)	Size class	0.02*	4 > 3, 2, 4 = 1
		Row	<0.01*	1 > 21–81; 11> 31–81
		Sex	0.16	NA
ANOVA	Shape (ratio L1/L3)	Size class	<0.01*	4 > 2, 3 > 1
		Row	0.90	NA
		Sex	<0.01*	Male > Female

rachidian tooth wear with ontogeny because the rachidian teeth are actively used during shell drilling. Methods of feeding which require penetration of prey valve shells with the radula (e.g., drilling) will leave more wear on the rachidian teeth than non-drilling methods of attack. Therefore, examination of rachidian tooth wear along the radula and differences in wear depending on size class may give an indication as to transitions in feeding strategies of different size classes of rapa whelks (Figure 8). High levels of rachidian tooth wear (L1:L2 ratio >1) in rows 1 and 11 were associated with the petite and large size classes (Figure 8A). The smallest whelks (<45 mm SL) typically leave drill holes (i.e., wall bores) in the valves of their prey (Harding et al., 2007). Although large (>135 mm SL) rapa whelks do not always leave predation signatures in prey valves, edge bore signatures are left instead of drill holes (Harding, Kingsley-Smith, Mann, unpublished data) when signatures are present. The observed L1:L2 values for rows 1 and 11 in the large size class are driven by one male (Figure 8B). It is possible that this individual had been using its radula to penetrate prey shells and that the other large whelks had not. Since the large whelks used herein were wild caught and had unknown feeding histories, we cannot say this with certainty. Relatively less wear (L1:L2 ratio <1.2) in row 11 was observed in rapa whelks with shell lengths of 45 to 135 mm (small and medium size classes) that do not typically drill their prey (Harding et al., 2007, Figure 8). Similar wear patterns (L1:L2 ratio) were observed for males and females and may serve as an indication that feeding strategies and/or prey may be similar between animals of different sex but similar size.

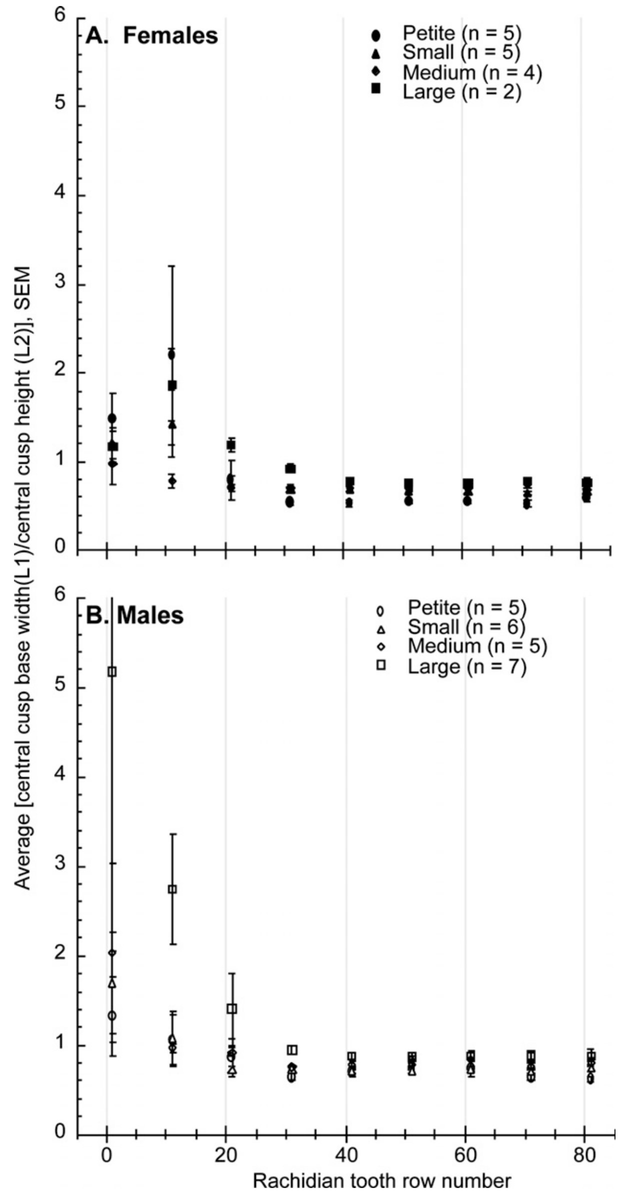


Figure 8. Rachidian tooth wear as indicated by the average ratio of rachidian tooth central cusp base width (L1) to central cusp height (L2) in relation to rachidian tooth row number for females (A) and males (B) from all size classes.

If a whelk is using the radula to penetrate the shell, the chemical composition of the prey shell may affect the level of wear observed on the rachidian teeth. Oyster and mussel shells have more calcite and are relatively softer than other bivalves with predominantly aragonite shells (Carter, 1980). Drilling through aragonite shells has the potential to cause more wear on rachidian teeth than shell penetration of calcite shells. Examination of the radulae from rapa whelks using drilling to consume a species-specific diet is a topic for future research that would provide data to address changes in radula wear with regard to prey shell hardness.

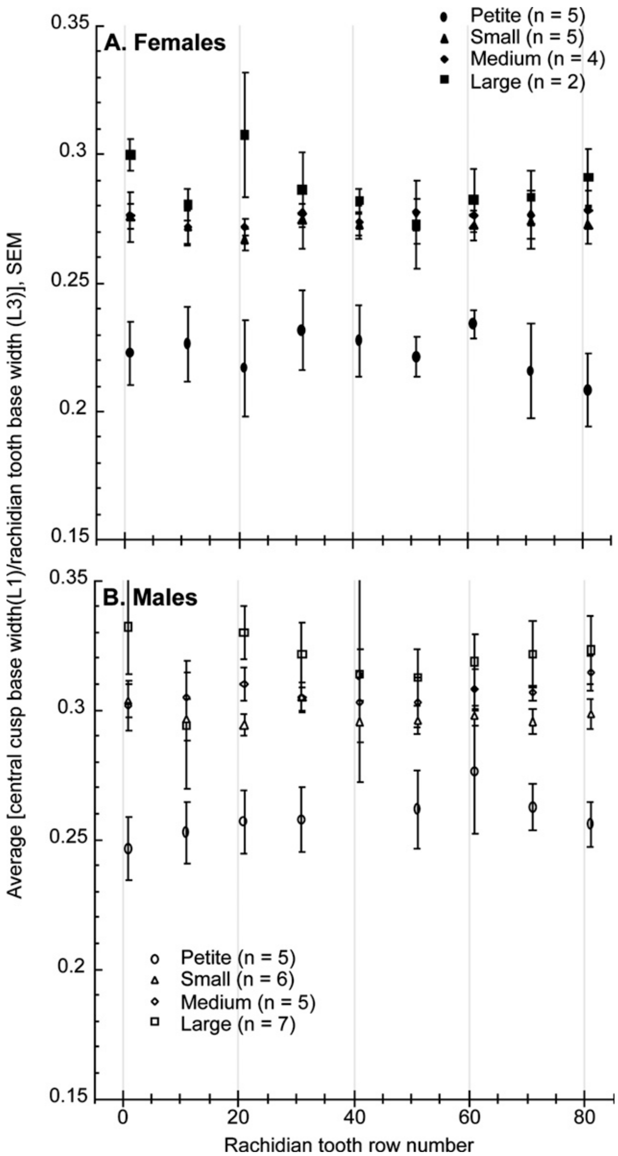


Figure 9. Average ratio of central cusp base width (L1) to rachidian tooth base width (L3, with standard error of the mean, SEM) by rachidian tooth row for females (A) and males (B) from all size classes.

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