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DEPTH AND DEVELOPMENT OF THE SONIC SYSTEM IN DEEP-SEA MACROURID FISHES ON THE CONTINENTAL SLOPE

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**DEPTH AND DEVELOPMENT OF THE SONIC SYSTEM IN DEEP-
SEA MACROURID FISHES ON THE CONTINENTAL SLOPE**

A thesis submitted in partial fulfillment of the requirements for the degree of Master of
Science at Virginia Commonwealth University.

by

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Table of Contents

	Page
Acknowledgements	iv
List of Tables	vii
List of Figures	viii
List of Abbreviations.....	ix
 Chapter	
1 Introduction	5
2 Materials and Methods	8
3 Results	10
Swimbladder	11
Sonic Muscle	11
Analyses of species.....	12
4 Discussion	15
Figures for Results	17
Reference List	38
Vita.....	41

List of Tables

	Page
Table 1: List of head length, fish weight, and sex ratio	17
Table 2: List of location, date of collection, coordinates, and depth	18
Table 3: Regression equations for <i>Nezumia bairdii</i>	19
Table 4: Regression equations for <i>Coryphaenoides rupestris</i>	20
Table 5: Regression equations for <i>Nezumia equalis</i>	21

List of Figures

	Page
Figure 1: Drawing of swimbladder and its structure.....	22
Figure 2: Relationship of fish weight and head length of all species	23
Figure 3: Relationship of fish weight and head length of all species	24
Figure 4: Swimbladder and sonic muscle analyses of <i>Coelorhincus carminatus</i>	25
Figure 5: Swimbladder and sonic muscle analyses of <i>Nezumia bairdii</i>	26
Figure 6: Swimbladder and sonic muscle analyses of <i>Nezumia bairdii</i>	27
Figure 7: Swimbladder and sonic muscle analyses of <i>Coryphaenoides rupestris</i>	28
Figure 8: Swimbladder and sonic muscle analyses of <i>Nezumia equalis</i>	29
Figure 9: Drawing Swimbladder and sonic muscle analyses of <i>Coryphaenoides armatus</i>	30
Figure 10: Swimbladder and sonic muscle analyses of <i>Coryphaenoides carapinus</i>	31
Figure 11: Swimbladder and sonic muscle somatic indices for all species	32
Figure 12: Gonasomatic indices for <i>Coelorhincus carminatus</i> , <i>Nezumia bairdii</i> , and <i>Coryphaenoides rupestris</i>	33
Figure 13: Gonasomatic indices for <i>Nezumia equalis</i> , and <i>Coryphaenoides armatus</i> and <i>Coryphaenoides carapinus</i>	34
Figure 14: ANCOVA of SBSI	35
Figure 15: ANCOVA of SMSI	36
Figure 16: ANCOVA of GSI	37

List of Abbreviations

GSI: Gonasomatic Index

GWt: Gonad Weight

HL: Head Length

Hz: Hertz

SBL: Swimbladder Length

SBSI: Swimbladder Somatic Index

SBW: Swimbladder Width

SBWt: Swimbladder Weight

SML: Sonic Muscle Length

SMSI: Sonic Muscle Somatic Index

SMW: Sonic Muscle Width

SMWt: Sonic Muscle Weight

TL: Total Length

Wt: Total weight

Abstract

DEPTH AND DEVELOPMENT OF THE SONIC SYSTEM IN DEEP-SEA MACROURID FISHES ON THE CONTINENTAL SLOPE

By Jonothan Bennett Wrenn, B.S.

A thesis submitted in partial fulfillment of the requirements for the degree of Master of Science in Biology at Virginia Commonwealth University.

Virginia Commonwealth University, 2016

Major Advisor: Michael L. Fine
Associate Professor and Graduate Director, Department of Biology

Work on sound production of deep-sea fishes has been limited to anatomy, and no sounds from identified species have been recorded on the continental slope. Here I examined the sonic muscles of six species in the family Macrouridae by depth (*Coelorhincus carminatus*, *Nezumia bairdii*, *Coryphaenoides rupestris*, *Nezumia equalis*, *Coryphaenoides armatus*, *Coryphaenoides carapinus*). Due to increasingly limited food with depth, I hypothesized that sonic muscle development would decrease with depth. Sonic muscles were intrinsic and occurred in males and females. Swimbladder and sonic muscle dimensions increased linearly with fish size, but there were no clear differences with depth suggesting sound production remains important in deeper species.

Introduction

Little research has been conducted on fish sound production in the deep sea. Marshall (1967) described sonic anatomy of deep sea fish families Ophidiidae and Macrouridae on the continental slope. He noted the presence of muscles on the swimbladder and suggested they function in sound production, but development of sonic muscles has not been quantified.

Fishes produce sounds through various mechanisms that evolved independently (Ladich & Fine 2006; Fine & Parmentier 2015; Parmentier & Diogo 2006). The most common method of sound production in fishes utilizes superfast sonic muscles that deform the swimbladder (Skoglund 1961; Fine *et al.* 2001; Connaughton, Taylor & Fine 2000; Connaughton 2004; Millot, Vandewalle & Parmentier 2011), which functions as the sound radiator (Fine and Parmentier 2015). Muscles can be either extrinsic, typically coming from the head, or intrinsic and attaching only the bladder. The swimbladder and position and contraction of sonic muscles control sound amplitude, frequency and directionality by its shape and movement (Fine *et al.* 2001). In oyster toadfish, a 200 Hz sonic-muscle contraction is translated to a 200 Hz fundamental frequency from bladder oscillations (Ladich & Fine 2006; Nguyen, Parmentier & Fine 2008).

Sounds produced by slow sonic muscle contraction have been observed in carapid fish (Parmentier *et al.* 2006). In comparison to the 10 ms twitch exhibited by the toadfish (Skoglund 1961; Fine *et al.* 2001), a carapid twitch requires 500 ms, and the muscle tetanizes around 10 Hz. The carapid swimbladder is comprised of three components: an

unattached anterior lip, a posterior part fused to the spinal column, and a flexible fenestra that connects the two. A swimbladder plate, a specialized epineural rib, couples with rapid movement of the anterior lip to excite the posterior region of the bladder (Parmentier et al 2006). The anterior portion of the swimbladder is pulled slowly toward the cranial region by sonic muscle contraction, after which the swimbladder is released and rapidly rebounds setting bladder and plate into vibration (Parmentier et al 2006).

A combination of these two, a fast muscle combined with a slow snap-back mechanism occurs in the genus *Glaucosoma* (Mok et al. 2011). The anterior swimbladder and fenestra are extended by fast muscles placing a tendon under strain. The stretched tendon in turn causes the bladder to snap back rapidly causing an intense sound upon relaxation. Sound is caused by a fast rebound of the tendon, similar to the slow muscle mechanism in carapids (Parmentier et al., 2006; Mok *et al.* 2011).

The family Macrouridae, grenadiers or rattails, is found in the order *Gadiformes*. Ninety percent of macrourid species occur in the subfamily Macrourinae; other subfamilies include Bathygadinae, Macrouroidinae, and Trachyrincinae. The Macrouridae contains around 385 species within thirty-four genera (Iwamoto, 2008). The genera *Coryphaenoides*, *Coelorinchus*, and *Nezumia* contain the greatest number of species. The presence of sonic muscles on the swimbladder suggests the ability for acoustic communication in the vast, barren, and dark environment. Females have heavier and stouter bodies than males (Marshall, 1962). The impacts of evolutionary adaption to heightened hydrostatic pressure and limited food resources are not known.

In this study I will describe and quantify swimbladder and sonic muscle development of six macrourids of varying depths from several hundred to 3,000 m. Due to decreasing food availability with depth (Gartner, 1997), I hypothesized that sonic muscle size will decrease with depth.

Materials and Methods

Six species of macrourids were obtained from the fish museum of the Virginia Institute of Marine Sciences (VIMS, Gloucester point, VA). Specimens were fixed in 10% formalin and maintained in 90% ethanol. Specimens came from depths ranging from 300 to 3000 m and were collected 80 – 350 km off the mid-Atlantic coast (except for one collection of *Nezumia bairdii* from the southern Greenland coast) from the late 1960s to early 1990s (Table 1, 2).

Fish were measured for total length (TL), head length (HL) and weighed. Head length was measured from the most anterior point of the snout to the most posterior opercular point. Swimbladders, sonic muscles and gonads were removed and placed in 0.9% NaCl solution to ensure uniform hydration before weighing in milligrams.

Smaller samples were taken from the sonic muscle and gonad, and cross sections were cut at 10 μ m cryostat. The sex of individuals was determined microscopically or females were sexed externally by the presence of a cloacal opening behind the anus. Gonad and sonic muscle weights were regressed against fish weight and linear dimensions against HL. HL was used in regression analysis because slender tails often break off or are damaged. Gonasomatic index (GSI), swimbladder somatic index (SBSI) and sonic muscle somatic index (SMSI) were calculated using:

$$GSI = \frac{\text{gonad weight}}{\text{fish weight}} \times 100\%$$

$$SBSI = \frac{\text{swimbladder weight}}{\text{fish weight}} \times 100\%$$

$$SMSI = \frac{\textit{sonic muscle weight}}{\textit{fish weight}} \times 100\%$$

In species for which males and females were present, I used analysis of covariance to determine sexual differences.

Results

See Table 1 and 2 for species examined and their collection depths. Species are listed in order of collection depth, and many of our samples were biased toward males. *Coelorhincus carminatus* ranged from 43.1 to 70.6 cm HL and 16.1 to 85.4 g and included 10 males and 2 females. *Nezumia bairdii* ranged from 12.3 to 50.8 cm HL and from 1.2 to 29.5 g and included 55 males and 6 females. *Coryphaenoides rupestris* ranged from 52.3 to 98.1 cm HL and 57.7 to 240.7 g and included 14 males and 4 females. *Nezumia equalis* ranged from 32.2 to 48.5 cm HL and 17.7 to 33.5 g and included 6 males and 5 females. *Coryphaenoides armatus* ranged from 25.8 to 62.0 cm HL and 5.4 to 64.8 g and included 11 males. *Coryphaenoides carapinus* ranged from 40.9 to 56.7 cm HL and from 26.8 to 65.2 g and included 4 males.

All species appeared sexually monomorphic externally, and females were identified by the presence of an external cloacal opening found behind the anus. The relationship of weight to HL increased exponentially in all species (Fig. 2), and regressions formed a cluster with no obvious relationship between depth and relative weight (Fig. 3). For instance *C. carminatus*, the shallowest species, was lightest per unit weight, *C. armatus* one of the deeper species was at the lighter end, and *C. carapinus*, the deepest species, was in the middle of the distribution. These findings suggest that all species were robust and likely have somewhat similar abilities to swim and capture food. The shape of the swimbladder was similar in all species, and sonic muscle dimensions were not different between sexes although I say this with caution due to the small sample size of females.

Some specimens had been dissected previously or damaged during preservation. I kept these because of the small sample sizes for most species.

Swimbladder

The swimbladder has a single chamber covered with a white tunica externa in all species (Fig. 1). It is located below the third through fourteenth vertebrae and is attached to the ventral sides of vertebrae 3 through 12 on the dorsal midline where the swimbladder is rigid and slightly concave. It is also closely attached to the dorsolateral ribs. The dorsal edge is straight until it curves to a blunt tip at the rostral and caudal ends. The anterior surface of the swimbladder is blunt and rounded. The swimbladder is widest at the anterior region and tapers posteriorly. It is elliptical in cross section, and the lumen is wider than high. Each species has three long retia maribila of varying length that occur in pairs; they start on the anterior ventral surface and extend caudally to the approximate midpoint of the bladder. Marshall (1960) stated that retia length varies from 7 to 13 mm in fish from 140 to 2300 m in depth.

Swimbladders of all species increased in length, width, and weight with fish size (Table 3, 4, 5; Fig. 4, 5, 7, 8, 9, 10). Swimbladders were not obviously sexually dimorphic, and their dimensions co-scattered on graphs.

Sonic Muscle

The sonic muscles of the six species appear similar and do not exhibit sexual differences (Table 3, 4, 5; Fig. 4, 6, 7, 8, 9, 10). The pair of sonic muscles is intrinsic and attaches to the dorsal and dorsolateral region of the anterior swimbladder (Fig. 1). Parallel

muscle fibers travel in the anterior to posterior direction. Muscles exhibited a reddish color.

Coelorhincus carminatus

Since there were only two females, we did not compare regressions of males and females although they appear to overlap. Swimbladder length and width increased linearly with HL, and swimbladder weight increased linearly with fish weight (Fig. 4). Similarly, sonic muscle dimensions increased linearly with fish size (Fig. 4).

Nezumia bairdii

Swim bladder length (SBL) and swim bladder width (SBW), increased linearly with HL, and swim bladder weight (SBWt) increased with fish weight in both males and females (Fig. 5). An analysis of covariance for both season and sex indicated no significant difference in either parameter (Table 3). A combined regression line is therefore presented (Fig. 5).

Data for males and females overlapped between sexes and between summer and winter samples (ANCOVA: $p > 0.05$). Sonic muscle length (SML) did not change in specimens between 11 and 40 mm HL and then increased rapidly in larger fish. Therefore the two regions were fit with a separate linear regression. Sonic muscle width (SMW) increased with HL although the increase leveled off somewhat in fish above 30 mm HL. Sonic muscle weight (SMWt) continued to increase at a linear rate with fish weight perhaps because of rapidly increasing sonic muscle length and more slowly increasing width (Fig. 6).

Gonad weight (GWt) increased with fish size although the increase leveled off somewhat in fish reaching 35 mm. A linear increase in larger fish began around 40 mm fish weight (FW) which corresponds with the increase of SML in larger individuals (Fig. 6).

Coryphaenoides rupestris

SBW increased linearly with HL (Fig. 7), and SBWt increased linearly with fish weight in both males and females (Fig. 7); data for both sexes were combined. An analysis of covariance for season determined no significant difference in SBW and SBWt (Table 4). SBL increased linearly with HL and showed a significant difference between sexes (Fig. 7).

SML, SMW, and SMWt were larger in females than in males (Fig. 7). However, although female sonic muscles weighed more than in males, the regression slope was lower (Fig. 7).

Nezumia equalis

SBL and SBW increased linearly with HL, and SBWt increased with fish weight in both males and females (Fig. 8). Data for males and females overlapped between sexes and between summer and winter samples. An analysis of covariance for both season and sex determined no significant difference in either parameter (Table 5). A combined regression lines is therefore presented (Fig. 8).

SML increased linearly with HL in males. Similarly SMW increased in males, but did not in the four larger females. SMWt was larger in females and had a significantly

higher elevation than males ($F_{1,8} = 0.09927$, $p < 0.0001$) (Fig. 8). An analysis of covariance determined that SMW and SMWt showed a difference between males and females (Table 5). SMW of females was higher than in males and explains the low r^2 for SMWt (Fig. 8).

Coryphaenoides armatus

SBL and SBW increased linearly with HL in males, and SBWt increased linearly with fish weight. SML and SMW also increased linearly with HL and SMWt with fish weight (Fig. 9).

Coryphaenoides carpinus

SBL and SBW increased linearly with HL, and SBWt increased linearly with fish weight. SML and SMW also showed a linear increase with HL, and SMWt with FW (Fig. 10).

Somatic Indexes

Swimbladder somatic index showed a suggestive, but not statistically significant, increase in swimbladder weight per total weight (Fig. 14) as depth increased ($F_{5,12} = 0.09$, $p = 0.0965$). Sonic muscle somatic indexes showed a linear increase for all species (Fig. 11). An analysis of variance exhibited no difference among species (Fig. 15). No differences were found between sexes of each species except for *C. rupestris* (Fig. 19).

Gonasomatic indices increased linearly for all species and both sexes (Fig. 12, 13). Note there were only two individual females for *C. carminatus*. An analysis of variance showed no significant difference among species (Fig. 16).

Discussion

Macrourids are present in all oceans from subarctic to antarctic regions and make up one of the most important deep-sea fish families (Marshall & Iwamoto 1973). Of the approximately 300 species, 90% populate the continental slope zones between depths of 200 and 3000 m (Marshall 1965). While much of its distribution and biology has been examined (McLellan 1977, Geistdoerfer 1978, 1978–1979, Mauchline & Gordon 1984, 1985, 1986, Gordon & Duncan 1987, Merrett 1987, Gordon & Mauchline 1990), nothing is known about its sound production beyond Marshall's description of sonic muscles. (Marshall 1967) suggested they function in sound production, but development of sonic muscles had not been measured. To my knowledge, this study identifies sonic muscles in females for the first time suggesting that they likely are equally capable of sound production.

The macrourid swimbladder is an oblong oval shaped vessel which is covered with a tunica externa. A long anterior retia maribila on the ventral surface extends to the middle of the bladder. The swimbladder has a semicircular anterior end, the dorsal edge is straight and ventrally the bladder tapers to a blunt posterior tip. It attached dorsally to the spine from the third to twelfth rib in all species examined.

Body proportions were somewhat similar (Fig. 2, 3). Swimbladder length, width, and weight increased linearly in all species. Data suggest that swimbladders may increase in size with depth. Deep-sea macrourids exhibit zones of predation averaging 200 – 400 m that are segregated by depth and overlap during times of limited food availability.

Individuals were shown to invade predation boundaries of competing species when slope-fish biomass and production are maximal. They are opportunistic euryphagic consumers that navigate the water column hundreds of meters food allocation (Laptikhovsky, 2005; Carrasson, 2002) which explain the increased swimbladder weight of deeper individuals. Similar body proportions and a well developed swimbladder suggest that all species, regardless of depth, are active swimmers.

Despite limited food availability, macrourids' sonic muscles did not decrease with depth nor were they larger in males. Sonic muscles were similar in all species by sex, season, and depth except for *C. rupestris*. They are intrinsic and attach to the anterior dorsolateral end of the swimbladder. Fibers travel in the anterior to posterior direction.

Although hypothesized, no sexual dimorphism existed in any species except *C. rupestris*. Dimensions of the swimbladder, sonic muscle, and gonad were similar for both sexes. Male specimens dominated each collection for unknown reasons.

The lack of obvious decrease in swimbladder and sonic muscle development with depth suggests that deeper species are active foragers (Laptikhovsky, 2005; Carrasson, 2002) and that sound production likely plays an important role in social and reproductive behavior of these species at depths to 3,000 m despite restricted food availability on the lower continental slope.

Results Figures

Table 1. Table listing the head length, fish weight, and sex ratio.

Species	HL, mm	Weight, g	males	females
<i>Coelorhincus carminatus</i>	43.1 – 70.6	16.1 – 85.4	10	2
<i>Nezumia bairdii</i>	12.3 – 50.8	1.2 – 59.5	55	6
<i>Coryphaenoides rupestris</i>	52.3 – 98.1	57.7 – 240.7	14	4
<i>Nezumia equalis</i>	32.2 – 48.5	17.7 – 33.5	6	5
<i>Coryphaenoides armatus</i>	25.8 – 62.0	5.4 – 64.8	11	0
<i>Coryphaenoides carapinus</i>	40.9 – 56.7	26.8 – 65.2	4	0

Table 2. Table listing the location, date of collection, coordinates, and depth of macrourid species.

Species	Location	Date of Collection	Latitude	Longitude	Depth Collected
<i>Coelorhincus carminatus</i>	Mid Atlantic Bight	8-May-80	36.32.5 N	74.40.1W	338-343 m
	Blake Plateau	22-Sept-80	29.10.1 N	75.59.4 W	424 m
<i>Nezumia bairdii</i>	Scotian Shelf	24-Jul-70	58.37.5 N	43.55.8 W	340-360 m
	Mid Atlantic Bight	3-Nov-91	39.50.86 N	71-25-10 W	560-591 m
	Mid Atlantic Bight	22-Aug-90	38.58 N	72-48 W	458-631 m
<i>Coryphaenoides rupestris</i>	-	15-Aug-69	39.27.12 N	71.54 W	810-1400m
<i>Nezumia equalis</i>	-	7-Sept-75	33.33.4 N	76.03.8 W	980-1000 m
<i>Coryphaenoides armatus</i>	Mid Atlantic Bight	25-Aug-91	38.22.07 N	72.52.69 W	2505-2540m
<i>Coryphaenoides carapinus</i>	Norfolk Canyon	13-Jul-79	36.37.8	74.05.5 W	3000 m

Table 3. Regression equations comparing swimbladder sonic structures against fish weight (Wt) and TL, coefficients of determination, and analysis of covariance in *Nezumia bairdii* SBL, swimbladder length; SBW, swimbladder width; SBWt, swimbladder weight; SML, sonic muscle length; SMW, sonic muscle width; SMWt, sonic muscle weight; GWt, gonad weight.

	Reg. eqn.	r^2	Slopes		Intercepts	
			F	P	F	P
SBL	$Y = -11.60 + 1.042X$	0.9460	$F_{1,51} = 1.8738$	0.177	$F_{1,52} = 1.5055$	0.2254
SBW	$Y = -2.054 + 0.2991X$	0.8504	$F_{1,51} = 0.0089$	0.9249	$F_{1,52} = 0.1106$	0.7408
SBWt	$Y = 31.87 + 1.662X$	0.9228	$F_{1,51} = 1.0262$	0.3158	$F_{1,52} = 1.1947$	0.2794
SML	$Y = 2.201 + 0.1141X$	0.2628	$F_{1,51} = 1.5759$	0.2151	$F_{1,51} = 9.7131$	0.00298
SMW	$Y = 0.5767 + 0.04957X$	0.9264	$F_{1,51} = 3.4757$	0.0680	$F_{1,52} = 0.6268$	0.4321
SMWt	$Y = 10.36 + 0.866X$	0.8801	$F_{1,50} = 1.6154E-4$	0.9899	$F_{1,51} = 0.5082$	0.4792
GWt	$Y = -6.022 + 1.998X$	0.9306	$F_{1,50} = 0.1649$	0.6864	$F_{1,51} = 6.3674$	0.01478

Table 4. Regression equations comparing swimbladder sonic structures against Wt and TL, coefficients of determination, and analysis of covariance in *Coryphaenoides rupestris* SBL, SBW, SBWt, SML, SMW, SMWt, and GWt.

Male	Reg. eqn.	r^2	Slopes		Intercepts	
			F	P	F	P
SBL	$Y=-1.141+0.0929X$	0.9149	$F_{1,18}=9.2940$	0.006	-	-
SBW	$Y=-0.4083+0.078X$	0.6763	$F_{1,17}=0.0728$	0.7906	$F_{1,18}=1.0614$	0.3165
SBWt	$Y=1.341+0.1788X$	0.8241	$F_{1,15}=0.1103$	0.7444	$F_{1,16}=1.3341$	0.2650
SML	$Y=0.0928+0.0270X$	0.4758	$F_{1,16}=3.5469$	0.0779	$F_{1,17}=83.076$	<0.001
SMW	$Y=0.3130+0.0257X$	0.9136	$F_{1,17}=7.6011$	0.0135	-	-
SMWt	$Y=0.0744+0.0083X$	0.8693	$F_{1,14}=5.1629$	0.0394	-	-
GWt	$Y=-0.1403+0.035X$	0.3757	$F_{1,18}=15.460$	0.0009	-	-

Table 5. Regression equations comparing swimbladder sonic structures against Wt and TL, coefficients of determination, and analysis of covariance in *Nezumia equalis* SBL, SBW, SBWt, SML, SMW, SMWt, and GWt.

Male	Reg. eqn.	r^2	Slopes		Intercepts	
			F	P	F	P
SBL	$Y=-0.7282+0.066X$	0.9661	$F_{2,16}=0.8758$	0.4356	$F_{2,18}=0.3210$	0.7232
SBW	$Y=-1.604+0.5206X$	0.7036	$F_{2,17}=0.4586$	0.4586	$F_{2,19}=0.9540$	0.4029
SBWt	$Y=1.468+0.3257X$	0.8355	$F_{2,16}=0.3859$	0.686	$F_{2,18}=3.4788$	0.0528
SML	$Y=1.855+0.2913X$	0.9103	$F_{2,16}=0.0096$	0.9905	$F_{2,18}=0.0286$	0.9718
SMW	$Y=1.262+0.2338X$	0.8794	$F_{2,7}=6.3658$	0.0396	-	-
SMWt	$Y=0.3293+0.2798X$	0.2572	$F_{1,7}=0.3981$	0.3981	$F_{1,8}=69.540$	<0.001
GWt	$Y=05900+0.1365X$	0.8236	$F_{1,7}=2.1293$	0.1879	$F_{1,8}=70.015$	<0.001

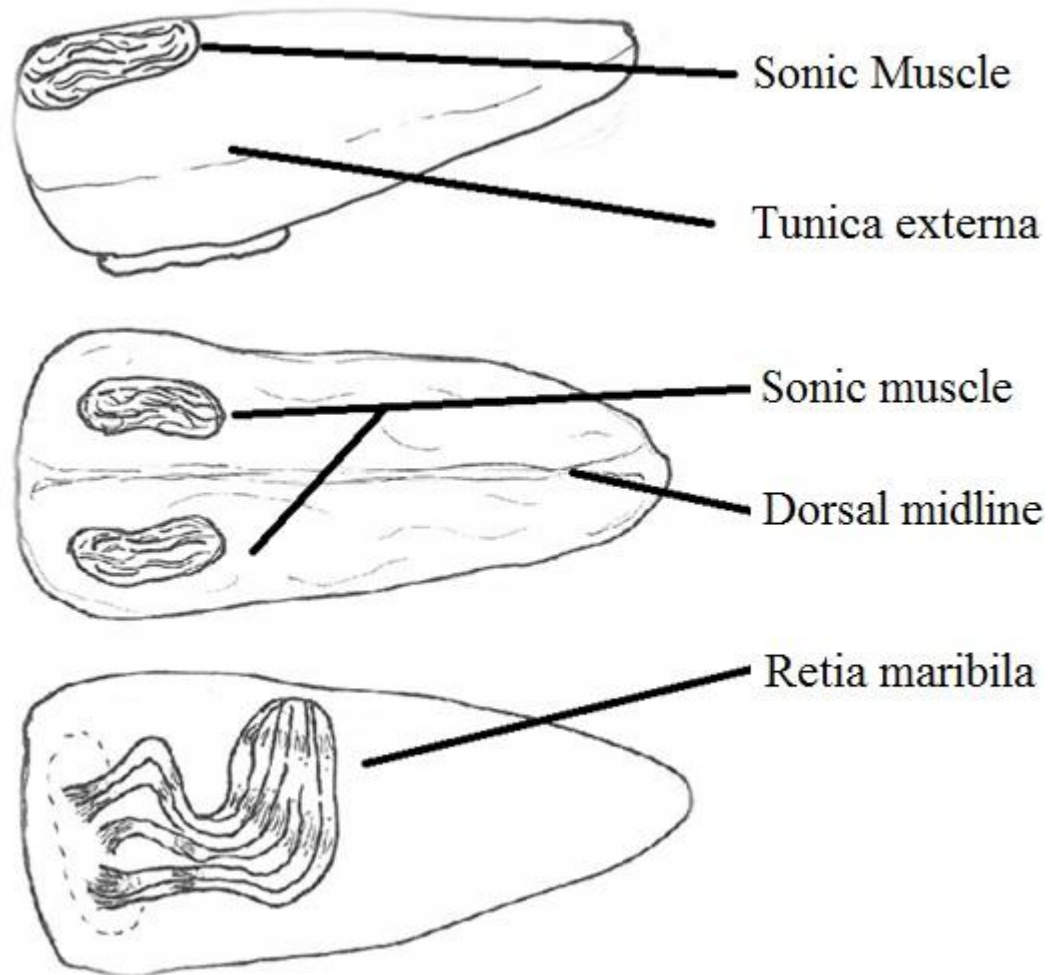


Figure 1. Lateral, dorsal, and ventral views of the swimbladder, sonic muscle, tunica externa, and retia maribila for all species.

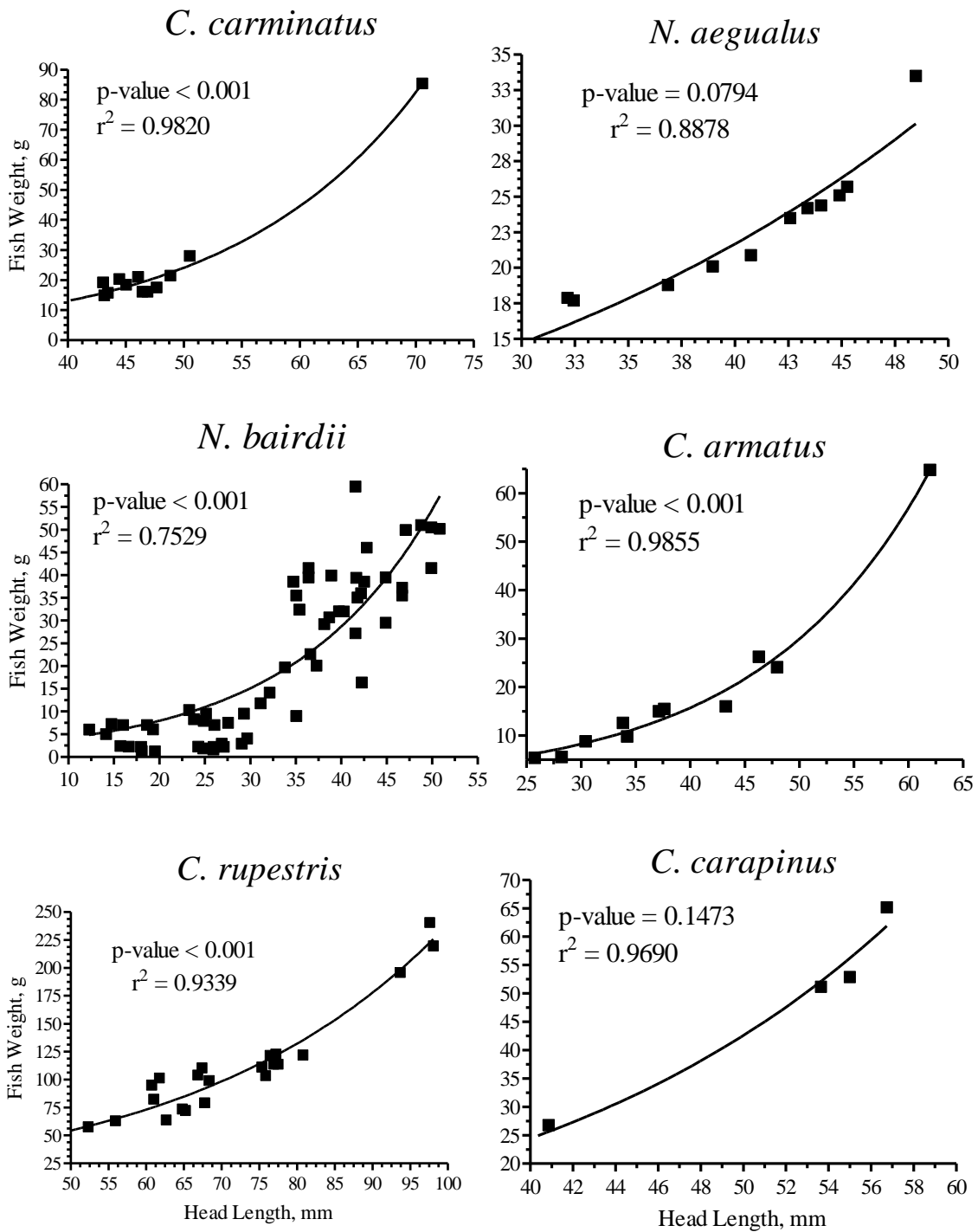


Figure 2. Relationship of fish weight and head length of all species.

Length-Weight Regression of all Species by Depth

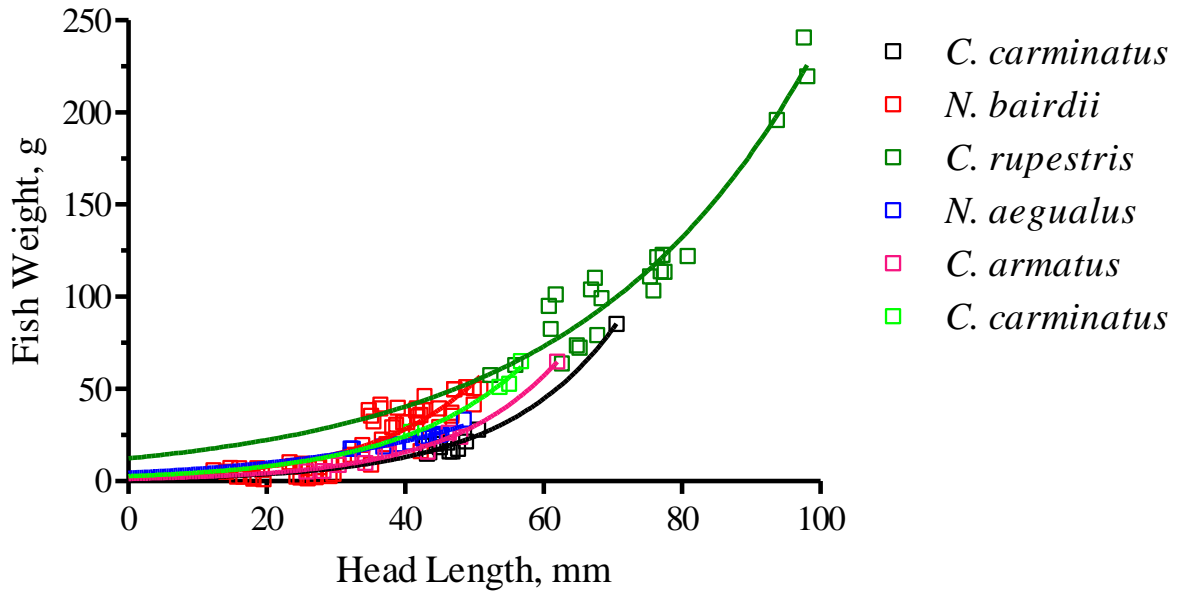


Figure 3. Relationship of head length and fish weight of all species.

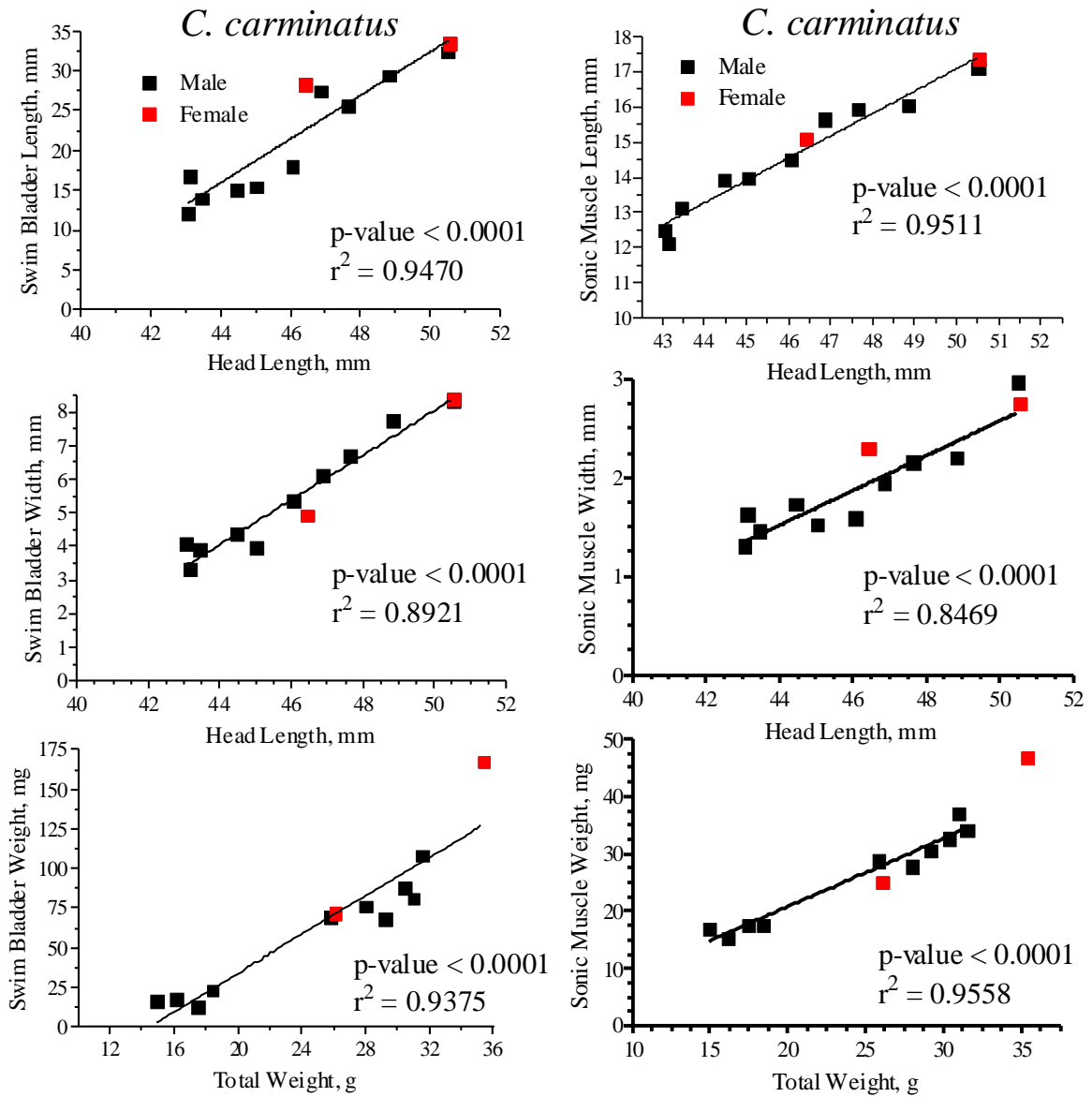


Figure 4. Relationship of SBL and SBW to HL , SBWt to Wt, SML and SBW to HL, and SMWt to Wt of *Coelorhincus. carminatus*.

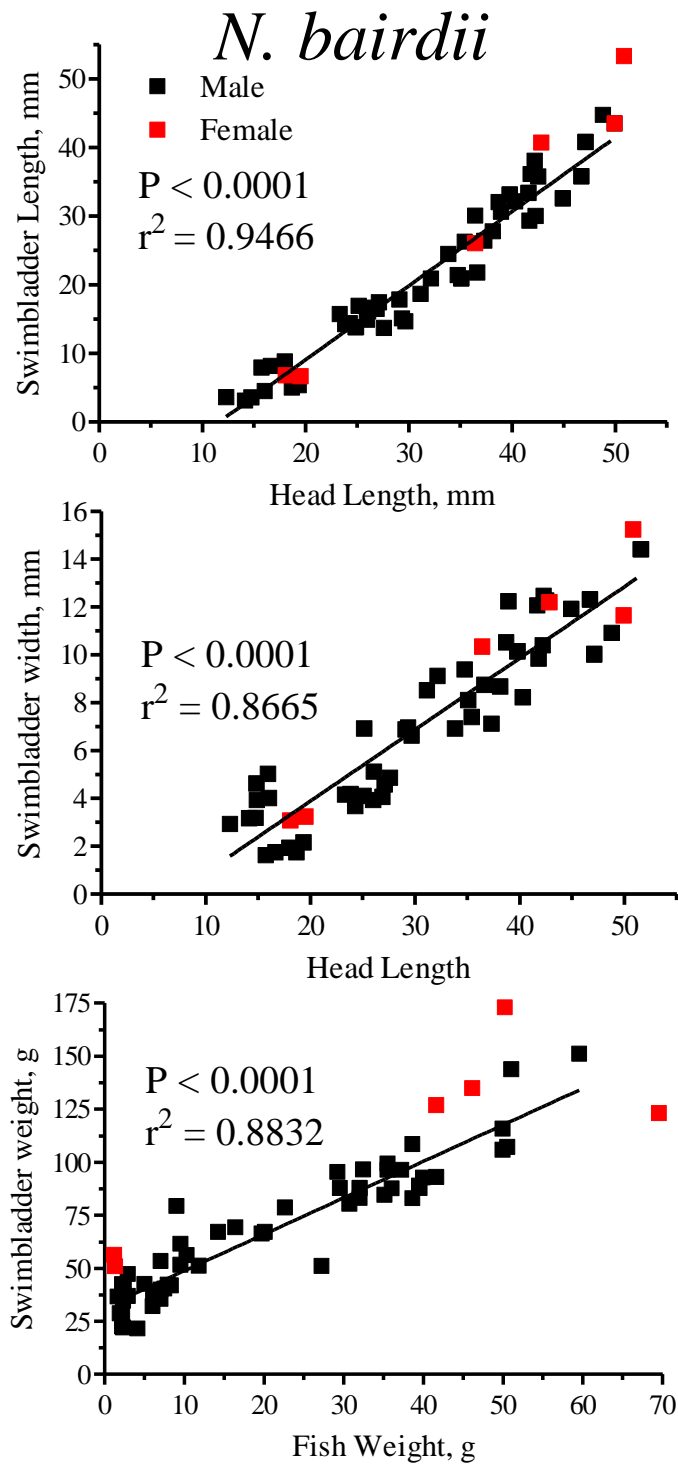


Figure 5. Relationship of SBL and SBW to HL, and SBWt to Wt of *Nezumia bairdii*.

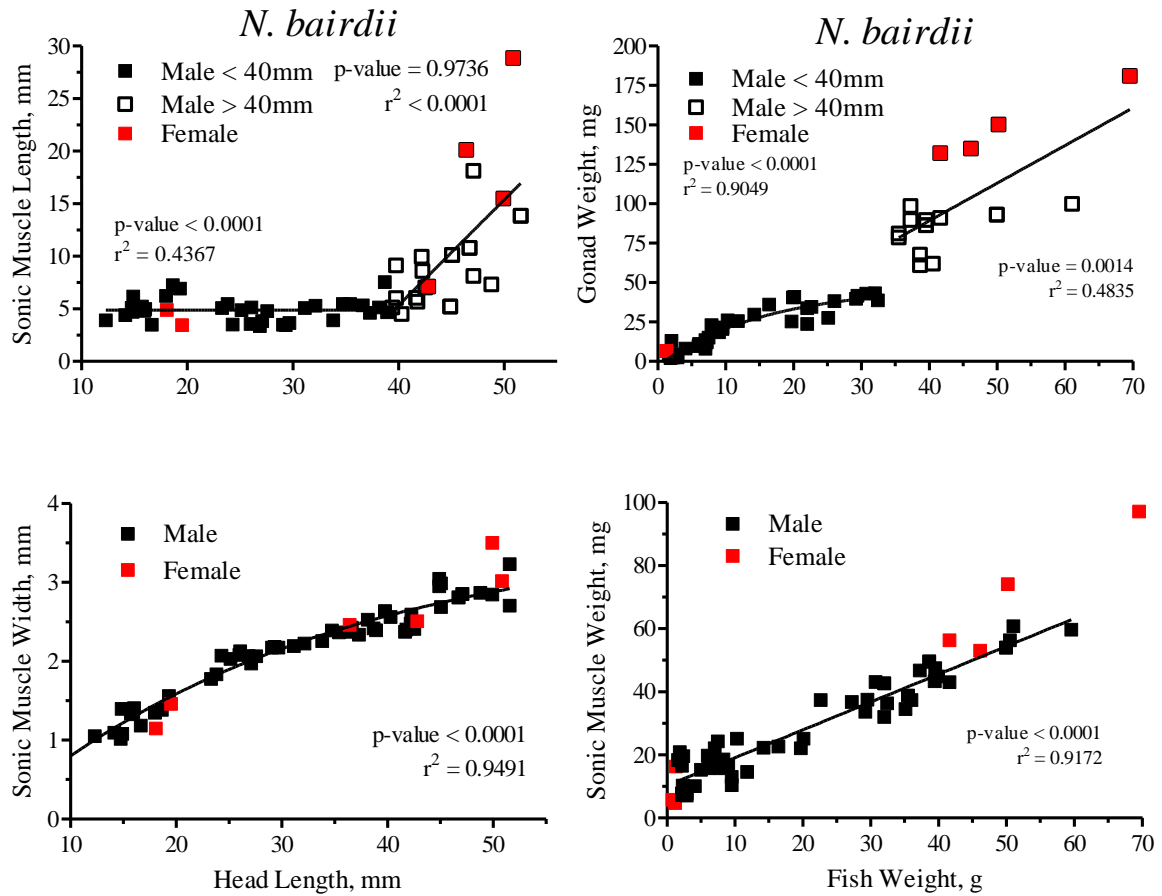


Figure 6. Relationship of SML and SMW to HL of *N. bairdii*. Relationship of SMWt and Gwt to Wt of *Nezumia bairdii*.

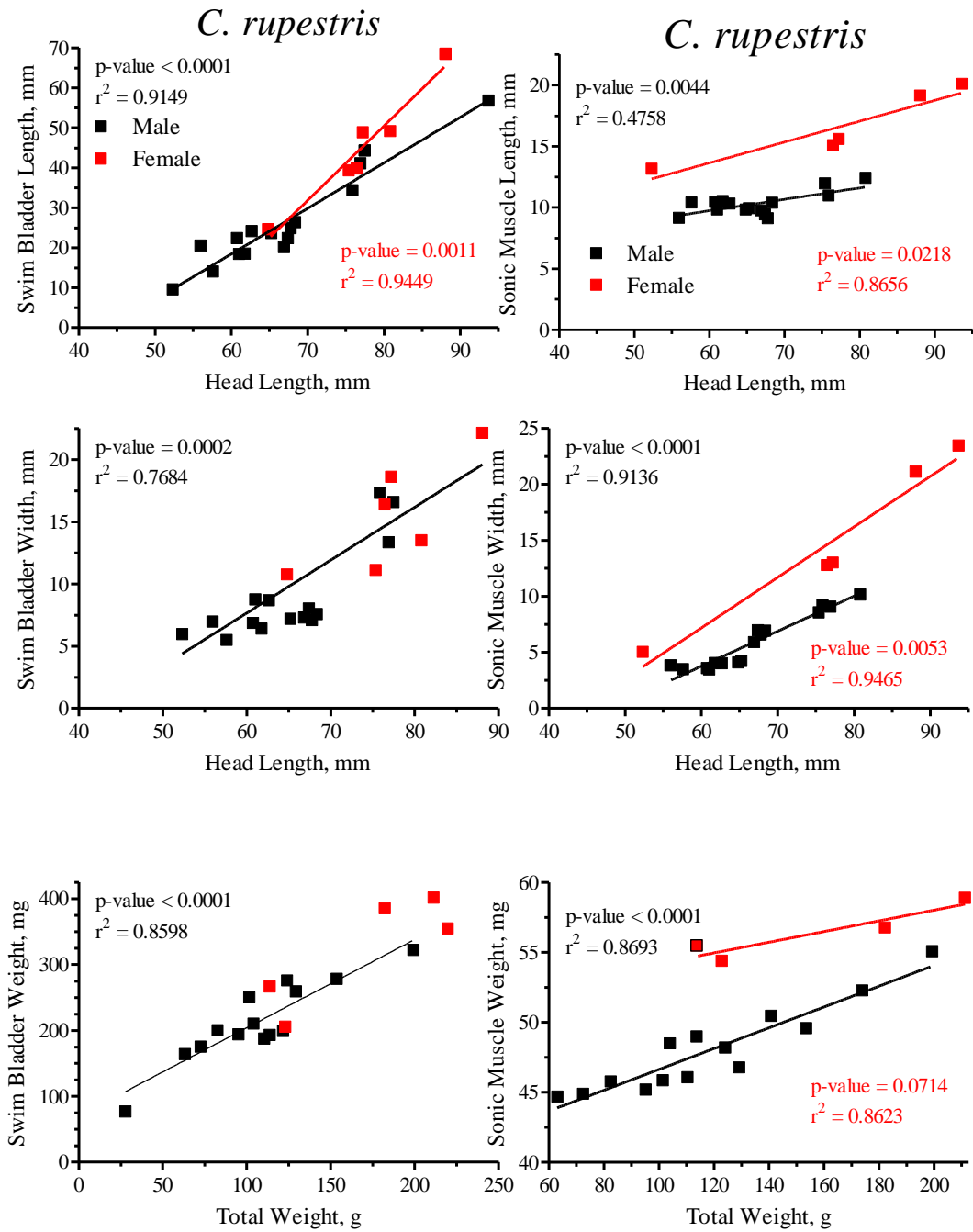


Figure 7. Relationship of SBL and SBW to HL, SBWt to Wt, SML and SBW to HL, and SMWt to Wt of *Coryphaenoides rupestris*.

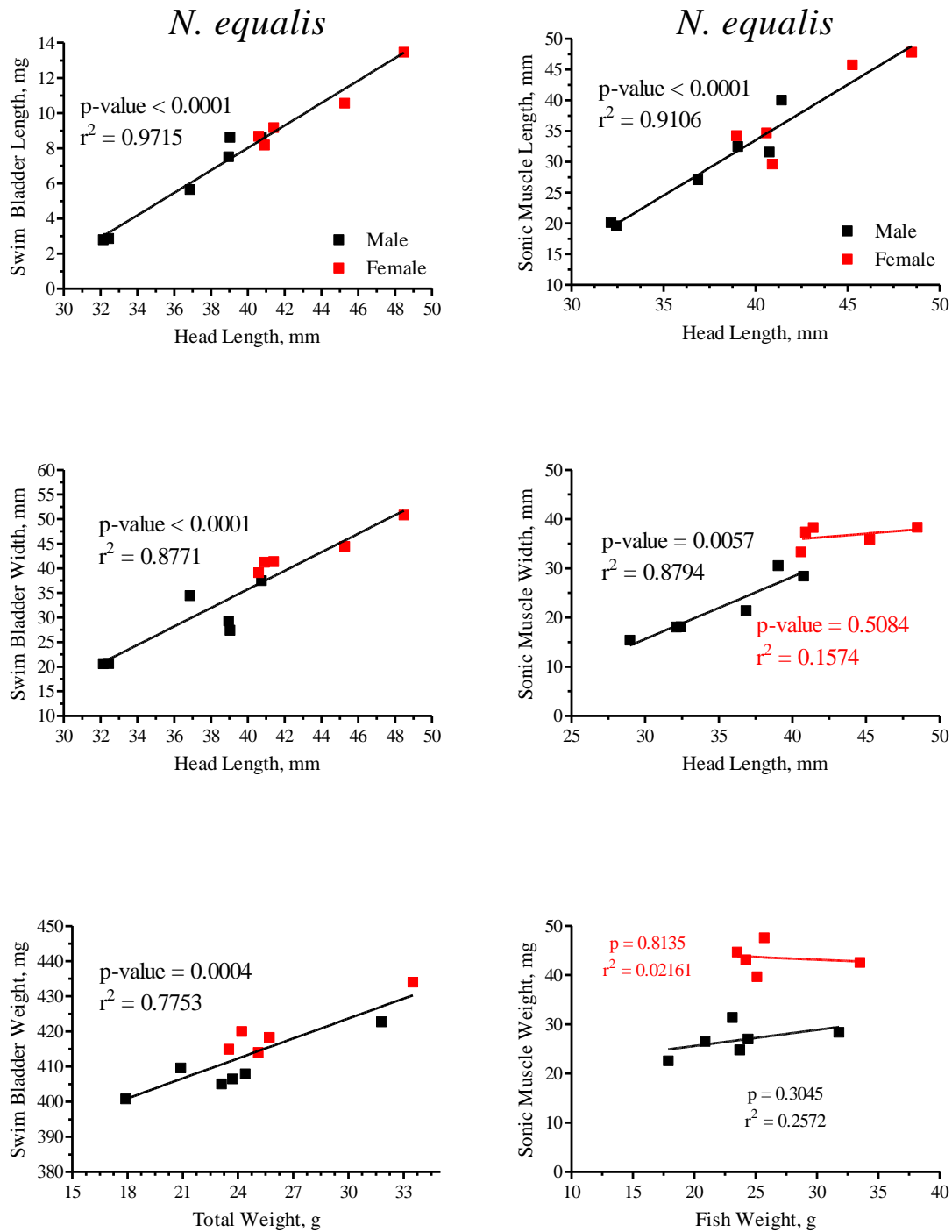


Figure 8. Relationship of SBL and SBW to HL, SBWt to Wt, SML and SBW to HL, and SMWt to Wt of *Nezumia equalis*.

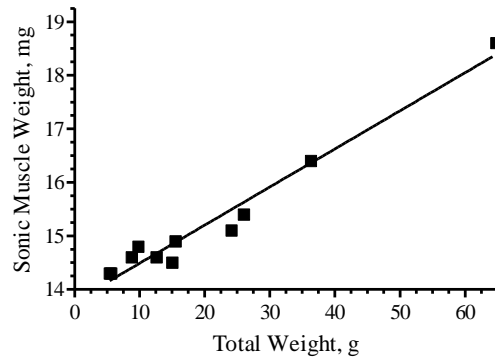
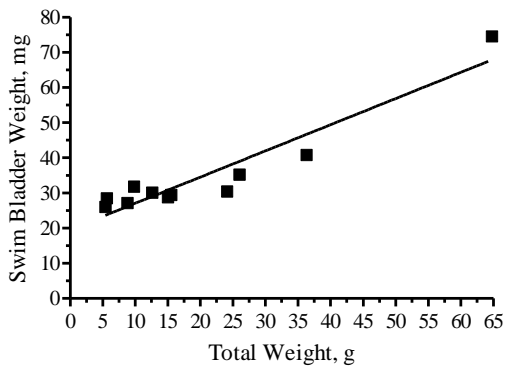
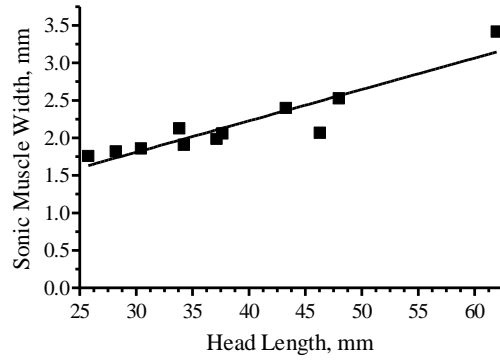
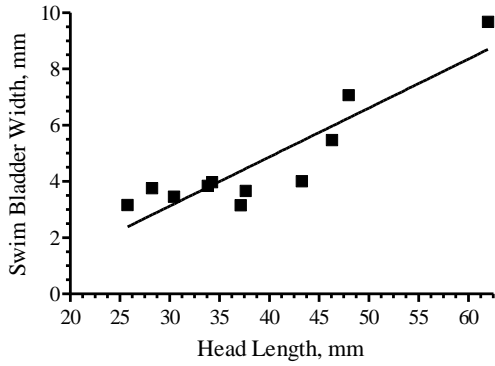
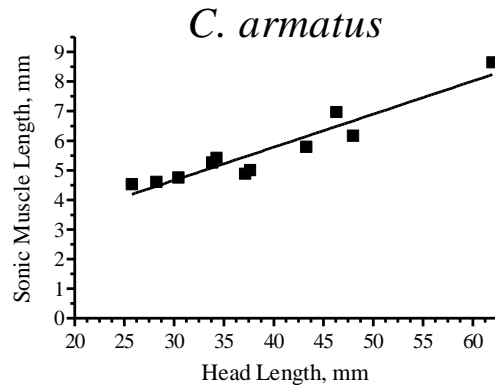
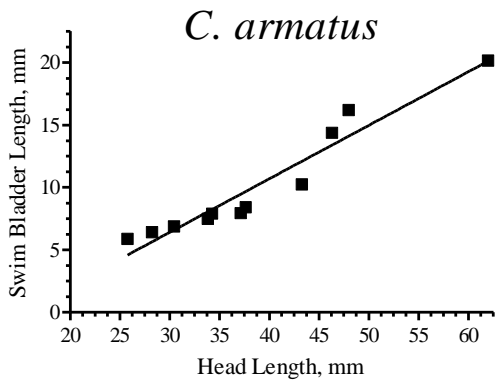


Figure 910. Relationship of SBL and SBW to HL, SBWt to Wt, SML and SBW to HL, and SMWt to Wt of male *Coryphaenoides armatus*.

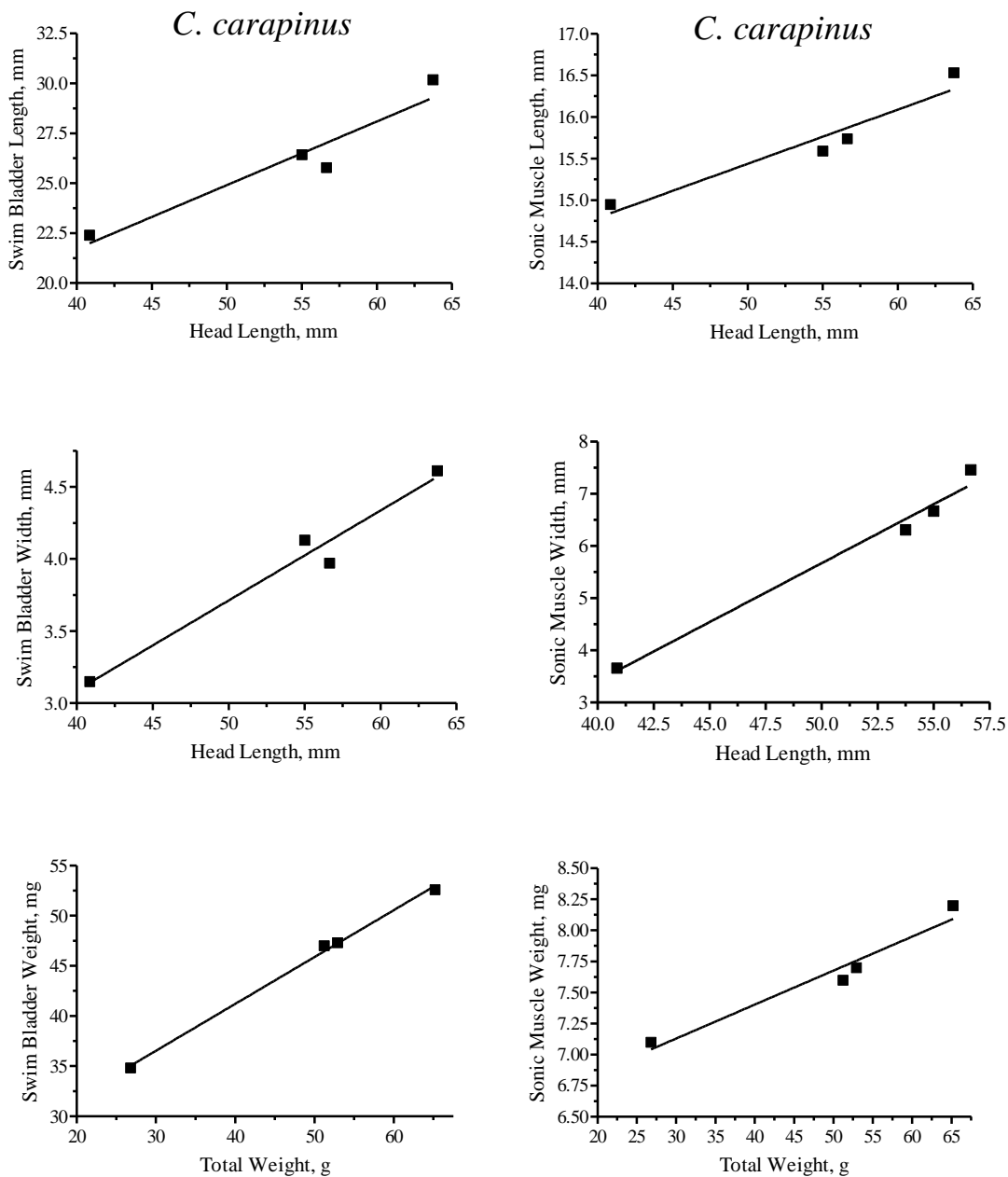


Figure 10. Relationship of SBL and SBW to HL, SBWt to Wt, SML and SBW to HL, and SMWt to Wt of male *Coryphaenoides carapinus*.

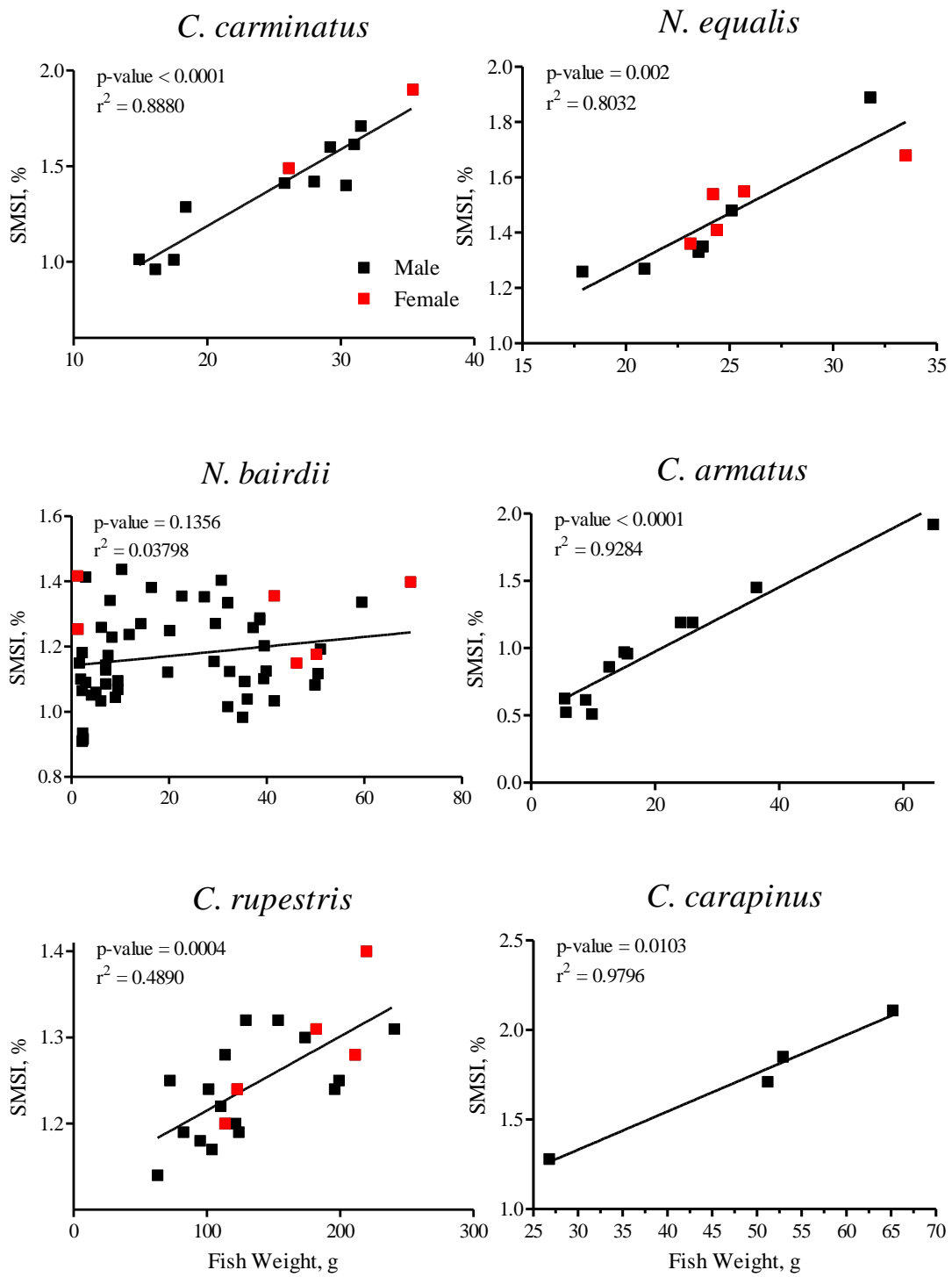


Figure 11. Sonic muscle somatic Indexes (SMSI) for all species.

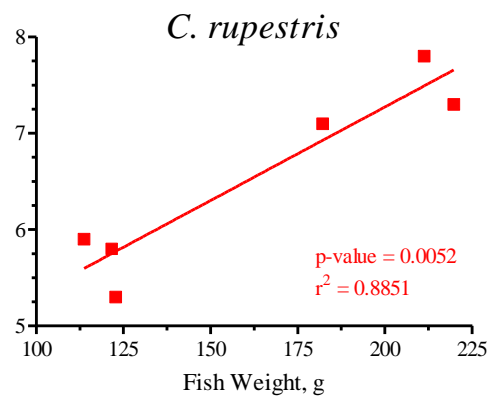
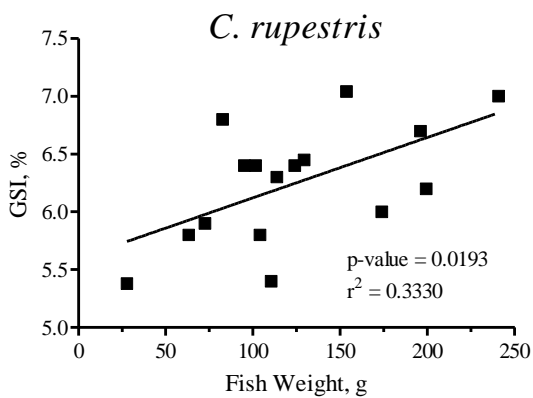
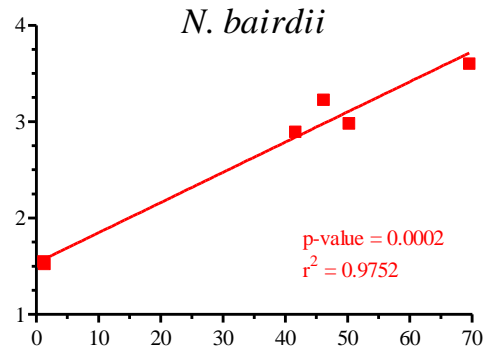
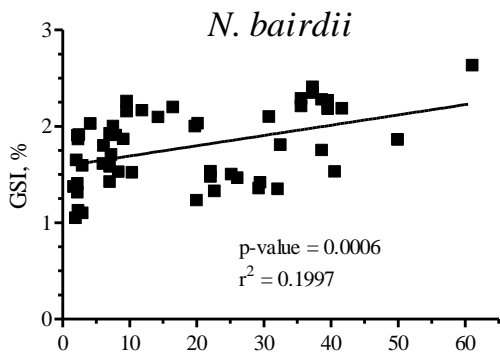
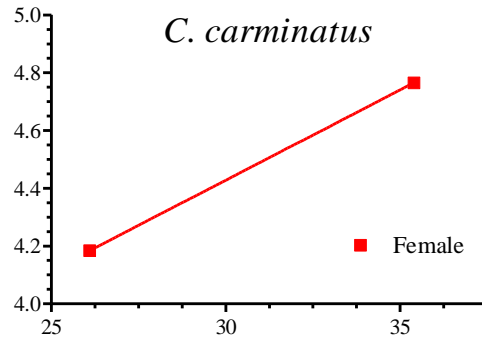
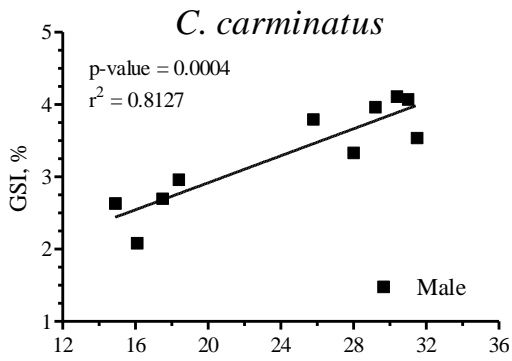


Figure 12. Gonasomatic Indexes (GSI) for males and females of *Coelorhincus carminatus*, *Nezumia bairdii* and *Coryphaenoides rupestris*.

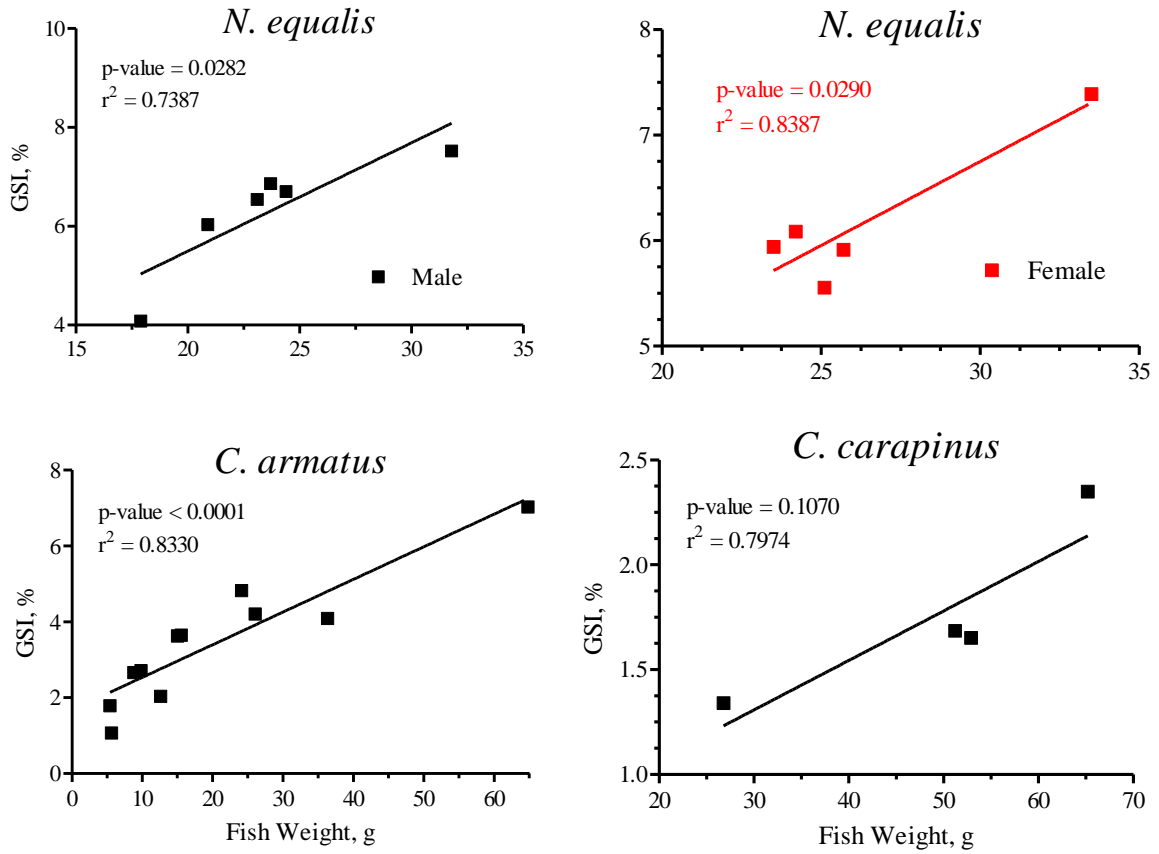


Figure 13. GSI for males and females of *Nezumia equalis*, and males of *Coryphaenoides armatus* and *Coryphaenoides carapinus*.

Swimbladder Somatic Index

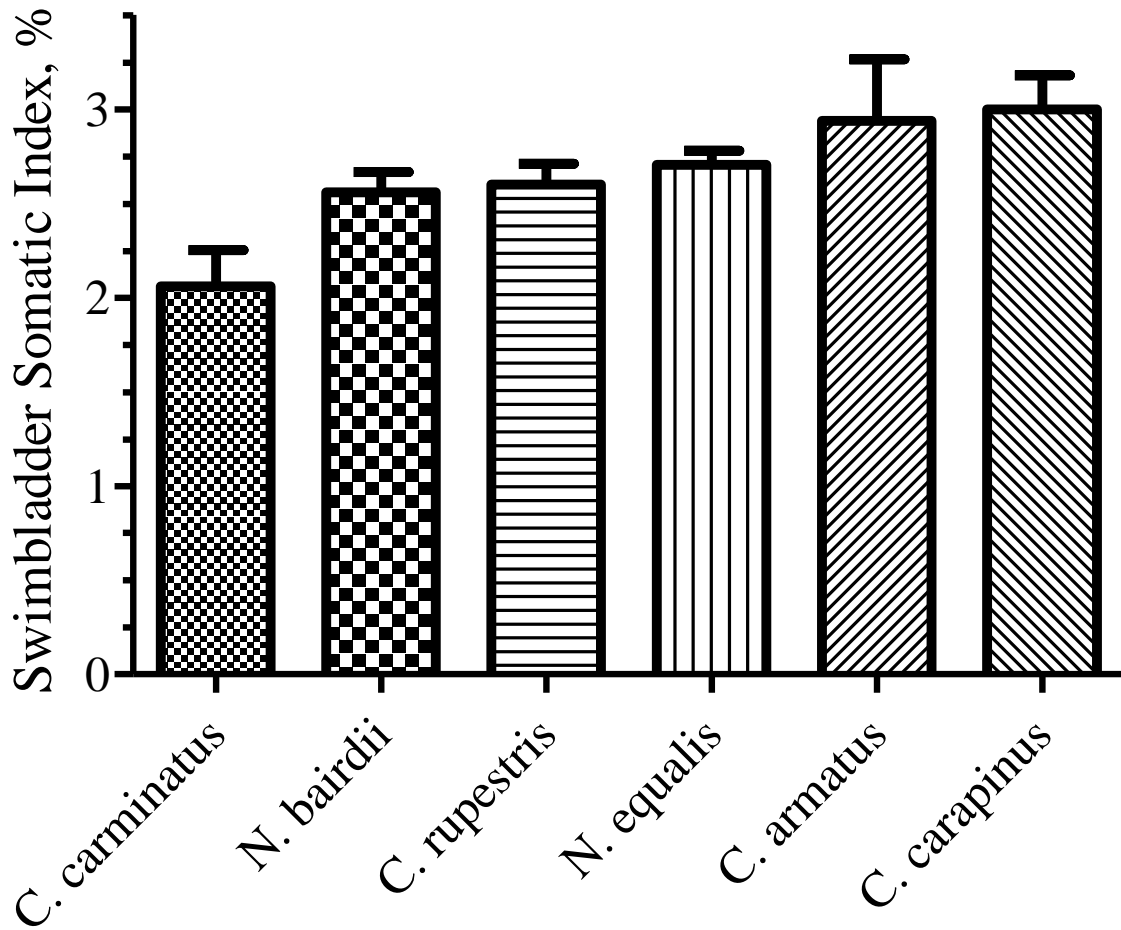
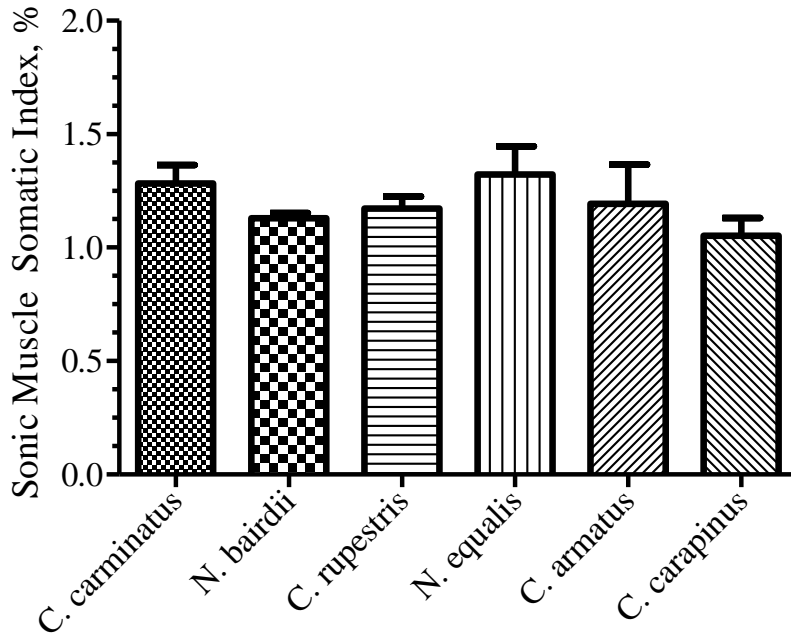


Figure 14. Swimbladder Somatic Index (SBSI) for all species.

Sonic Muscle Somatic Index for all Male Species



Sonic Muscle Somatic Index for all Female Species

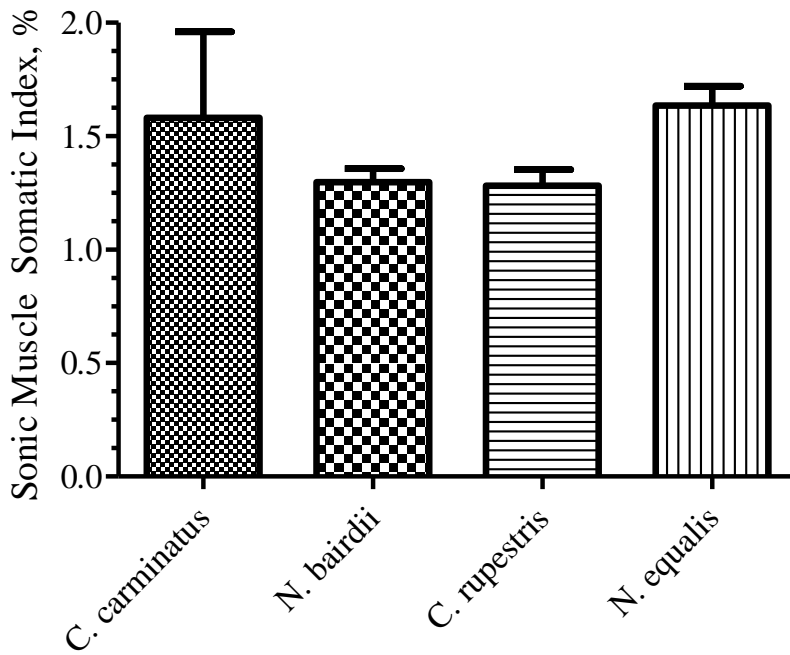


Figure 15. ANCOVA results of SMSI for males and females of all species.

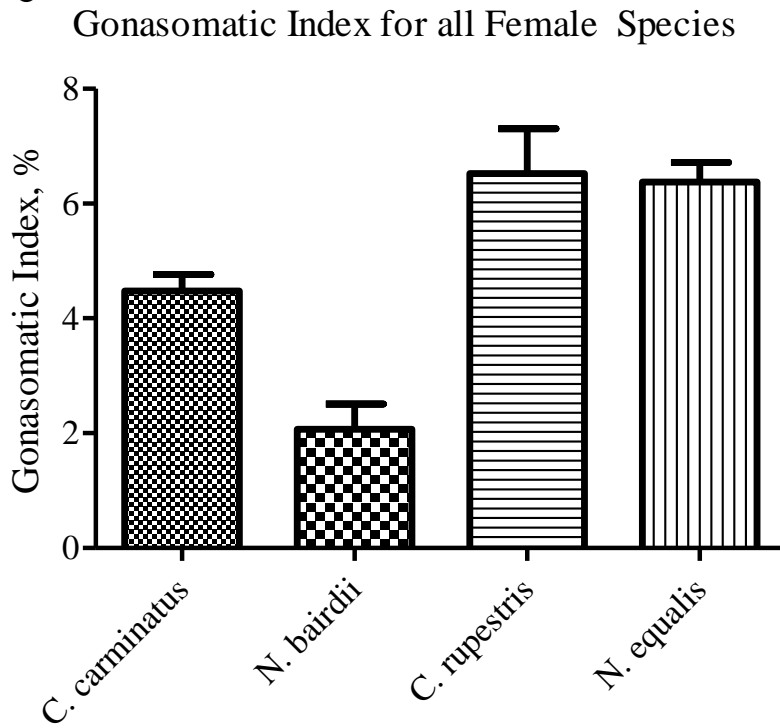
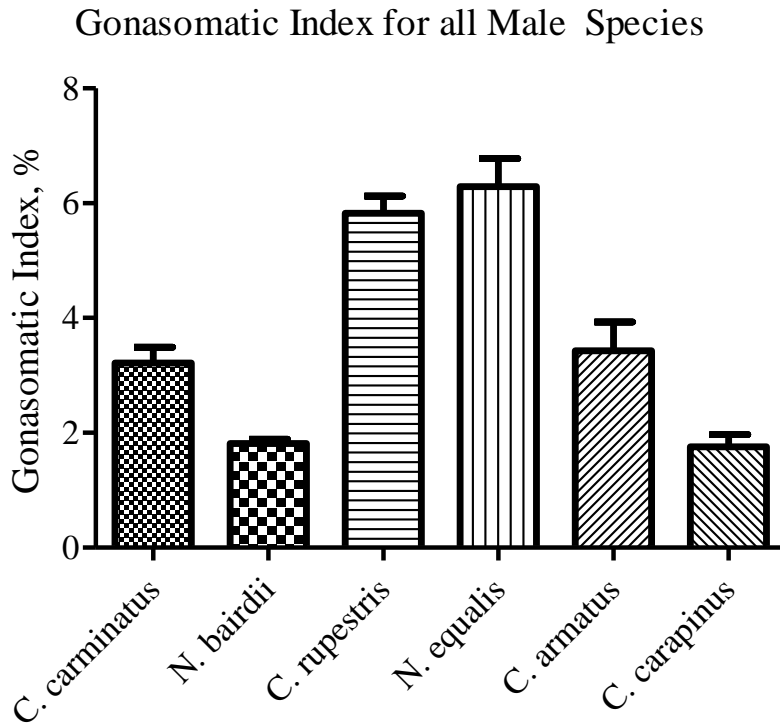


Figure 16. ANCOVA results of GSI for males and females of all species.

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VITA

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