

GROWTH AND SEXUAL MATURITY OF THE KNOBBED WHELK, *Busycon carica* (GMELIN, 1791), FROM A COMMERCIALY HARVESTED POPULATION IN COASTAL GEORGIA

**OCCASIONAL PAPERS OF THE
UNIVERSITY OF GEORGIA MARINE EXTENSION SERVICE
Vol. 4, 2009**

By Alan J. Power, Christina J. Sellers*, and Randal L. Walker
Marine Extension Service, University of Georgia, Shellfish Research Laboratory,
20 Ocean Science Circle, Savannah, GA 31411-1011.



* Marine Sciences Program, Savannah State University, Savannah, GA 31404.

Acknowledgments

This work was funded in part by the National Sea Grant Program through funds provided to Savannah State University under a grant through the Minority Serving Institute Program, which supported an Aquaculture course taught at Savannah State University. Ms. Sellers summer internship in Aquaculture was supported by funds from the Skidaway Science Foundation and the Marine Extension Service. Special thanks to Dr. E. Reitz, Georgia Museum of Natural History for the loan of the Buehler Isocut low speed saw. Thanks to Ms. Carolyn Belcher for performing the statistical analyses. Thanks also to Mr. Pat Geer and Ms. Julie Califf of the Georgia Department of Natural Resources for providing information and data on the Georgia whelk fishery. The authors wish to thank Mr. George Davidson for his editorial comments and final printing of the material.

The authors would also like to thank the crew of the University of Georgia’s R/V GEORGIA BULLDOG for obtaining the animals needed for this work.



Table of Contents

Acknowledgments	ii
List of Figures	iv
List of Tables	iv
Abstract.....	v
Introduction	1
Materials & Methods.....	4
Results	7
Discussion.....	8
References	22

List of Figures

Figure 1. Shell measurements of the knobbed whelk (SL = shell length from siphonal channel to shell apex and SW = shell width from across the shoulder including spines).
12

Figure 2. Annual growth rings on the inner surface of an operculum from a knobbed whelk (N = nucleus, R1-R4 = rings 1-4).12

Figure 3. Shell length (mm) histogram of male and female knobbed whelks, <i>Busycon carica</i> , collected in St Simons Sound, GA.....	13
Figure 4. Shell width (mm) histogram of male and female knobbed whelks, <i>Busycon carica</i> , collected in St Simons Sound, GA.....	14
Figure 5. Shell weight (g) histogram of male and female knobbed whelks, <i>Busycon carica</i> , collected in St Simons Sound, GA	15
Figure 6. Age frequency distribution of male and female whelks as determined from operculum examination of annual rings.	16
Figure 7. The von Bertalanffy growth curves calculated for female and male knobbed whelks from St Simons Island through opercular analysis.	17
Figure 8. The relationship between male gonadal weight (g) and shell length (mm) for whelks collected from St Simons Sound, GA.....	18
Figure 9. The relationship between female gonadal weight (g) and shell length (mm) for whelks collected from St Simons Sound, GA.....	19
Figure 10. The length of the penis (mm) versus shell length (mm) in male knobbed whelks collected from St Simons Sound, GA.	20
Figure 11. The weight of the pallial oviduct (g) versus shell length (mm) in female knobbed whelks collected from St Simons Sound, GA.....	21

List of Tables

Table 1. Whelks, <i>Busycon</i> and <i>Busycotypus</i> species, production in kilograms of meat landed from 1882 to 2007 in Georgia. Data from the Georgia Department of Natural Resources and the National Marine Fisheries Service.	3
Table 2. Size of male and female whelks found mating at various locations in Wassaw Sound, Georgia in March/April 2003.	6

Abstract

The knobbed whelk, *Busycon carica* (Gmelin, 1791), is an important commercial gastropod species in Georgia. This paper examines its growth rate, age, and size at sexual maturity to assist the Georgia Department of Natural Resources in the development of a management plan to ensure the sustainability of this resource. Female whelks (N = 397, range 32 to 167 mm shell length) grew larger in size than males (N = 310, range 30 to 128 mm). Females were aged to 8 years, while males were aged to 11 years; however, the sample was biased as larger whelks (N = 347) were removed from the original sample at the time of collection. The results indicate that males and females have very

different growth rates with females attaining a larger size in a shorter period of time. The sex ratio (1.00 F: 0.78 M) of the biased sample was significantly different from parity (Chi-square = 10.7). Males reach sexual maturity at 85 to 90 mm in shell length and at an age of approximately 4 years, while females achieve sexual maturity at 100 mm and an age of approximately 6 years. The implications of this information on the imposition of size limits on the fishery are discussed.

v

Introduction

The knobbed whelk, *Busycon carica* (Gmelin, 1791); the lightning whelk, *Busycon sinistrum* (Hollister, 1958); the pearwhelk, *Busycotypus spiratus* (Lamarck, 1816); and the channeled whelk, *Busycotypus canaliculatus* (Linnaeus, 1758), are all commercially important prosobranch species of the Family Melongenidae. *B. carica* and *B. canaliculatus* occur along the western Atlantic coast, from Cape Cod, Massachusetts to central Florida (Abbott, 1974). *B. sinistrum* is found from New Jersey to Florida and into the Gulf States; whereas, *B. spiratus* occurs from North Carolina to both sides of Florida (Abbott, 1974). *B. spiratus* is uncommon in Georgia; whereas, the other whelk species are common in occurrence (Walker, 1988; Walker *et al.*, 2008). All species are commercially harvested throughout the southeastern U.S. where they are used in salads, chowders, fritters, as scungilli (pasta), and they are also canned or frozen for national and international distribution.

The Georgia Department of Natural Resources (GA DNR) first authorized the commercial harvesting of whelks in Georgia in 1980. Initially, whelks were landed as by-catch of the winter crab trawl fishery and were managed under existing crab trawl regulations from 1980-1997 (Belcher *et al.*, 2001). Statutory authority to independently regulate the whelk fishery was officially given to the GA DNR in 1998. Currently, the fishing season is open in Georgia's nearshore waters from approximately January/February through April. Whelk harvesting season opens only after the penaeid shrimp season closes. Smaller numbers of whelks are also harvested as by-catch of the inshore blue crab, *Callinectes sapidus* (Rathbun, 1896), trap fishery and are also gathered intertidally by commercial oystermen, clammers, and/or sport fishermen (Walker, 1988).

Most whelks are harvested from offshore areas by the shrimp trawl industry. The recurrence of poor shrimp harvest in Georgia, coincident with favorable market conditions and the recognition of abundant whelk populations offshore, led to an intensification of effort and a dramatic increase in landings of whelks during the late 80's and early 90's (Table 1). Whelks are presently landed mostly from offshore areas by the shrimp trawl industry using modified heavy-duty otter trawls with 4-inch stretched-mesh webbing. Once the Georgia shrimp trawl fisheries closes in December or January, some boats change gear and fish for whelks during winter. On average 15-to-

20 shrimp vessels fished for whelks each year. The introduction of new regulations requiring all nets to be equipped with Turtle Excluder Devices (TEDs) (Belcher *et al.* 2001) are thought to have

1

contributed to recent low landings; however, it appears that the offshore fishery has collapsed due to overfishing.

On the other hand, low levels of blue crab and shrimp production in the last few years, coupled with the a closure of the shrimp fishery in the federal waters off Georgia and South Carolina have led to mounting interest in opening a year-round whelk fishery and developing an inshore whelk fishery. Blue crab processing plants also process whelk meat. With the collapse of the blue crab industry in Georgia presumably due to drought conditions (1999-2003) and the occurrence of the epizootic *Hematodinium* in the crab population, blue crab processing facilities wish to process whelk year around. The additional pressure of a longer fishing season in offshore areas, as well as, an intensification of harvesting of inshore stocks could be detrimental to the whelk resource propagation if stocks are presently fished beyond their maximum sustainable yield.

There is little information on the population dynamics of whelks found along the coast of Georgia to allow for sound management decisions regarding the sustainability of the fishery. Whelk fishery practices include the retention of all whelks, regardless of size, which is conducive to over-harvesting. This study seeks to address the lack of information on growth rates and the size at sexual maturity in a commercially harvested area, which will be important in considering size limits to conserve future stocks.

2

Table 1. Whelks, *Busycon* and *Busycotypus* species, production in kilograms of meat landed from 1882 to 2007 in Georgia. Data from the Georgia Department of Natural Resources and the National Marine Fisheries Service.

Year	Kilograms of Meat	Value (\$)	\$/kg
1881-1979	0	0	0
1980	83	120	1.44
1981	3,106	4,337	1.40
1982	38,810	42,076	1.08
1983	91,163	88,579	0.97
1984	253,848	263,558	1.04
1985	92,126	95,692	1.04
1986	56,217	52,346	0.93
1987	423,671	519,091	1.23
1988	455,345	403,949	0.89

1989	230,530	257,426	1.12
1990	462,204	507,718	1.10
1991	399,748	464,121	1.16
1992	206,943	247,566	1.20
1993	179,659	242,049	1.35
1994	305,099	377,323	1.24
1995	252,714	336,654	1.33
1996	193,022	254,717	1.32
1997	281,790	389,437	1.38
1998	266,497	408,942	1.53
1999	257,766	401,195	1.56
2000	191,076	277,482	1.45
2001	147,765	245,330	1.66
2002	28,842	49,621	1.72
2003	40,901	69,393	1.70
2004	1,624	3,693	2.27
2005	1,157	2,544	2.20
2006	2,148	5,729	2.67
2007	487	1,315	2.70
2008*	1,424	4,086	2.87

* Preliminary data for January and February 2008.

Materials & Methods

In April 2000, knobbed whelks ($N = 1,055$) were collected by the crew of the R/V GEORGIA BULLDOG from the south shipping channel of St. Simons Sound, Georgia. Whelks were captured with a 45-foot two-seam balloon trawl net with four-inch stretched-mesh webbing. The original purpose of this trawl was to gather whelks for a mark-recapture study. From the original sample, a biased selection ($N = 708$) of smaller-sized whelks (30 to 167 mm in shell length) was retained for an examination of the size and age at sexual maturity. The sample was taken around the spawning season to ensure that individuals would be reproductively ripe.

Specimens were preserved by deep-freezing at -20°C in the laboratory. Each whelk was numbered and measured for shell length (siphonal channel to shell apex) and width (across the shoulder) (Fig. 1) to the nearest millimeter using a measuring board and/or Vernier calipers. The total weight (body and shell) to the nearest 0.01 gram was also measured for each individual. Whelk meat was subsequently extracted from shells by repeated freezing and thawing. The sex was

determined according to the presence/absence of a penis. Finally the operculum was removed from the foot and labeled according to the individual from which it was taken.

Knobbed whelks have growth marks on the inner surface of the operculum (Figure 2). Previous research studies have validated the occurrence of annual growth rings on several whelk species including *Buccinum undatum* (Santarelli and Gros, 1985; Kideys, 1996), *Babylonia japonica* (Kubo and Kondo, 1953), *Neptunea antiqua* (Power, 2000), and *Busycon carica* (Kraeuter *et al.*, 1989). Two methods were used in determining the number of rings on each specimen's operculum. The first and easiest way to observe the growth lines on the inner surface is by tilting the operculum back and forth in front of a light source under a dissecting microscope. Sometimes the rings are not consistent, particularly in older animals when growth rates have slowed down causing some of the rings to overlap, resulting in a "bubbling effect." In other instances the operculum appeared to have two or three nuclei. This effect may also result from unsuccessful attacks by predators, and even by rings forming around foreign objects on the inner opercular surface. Ninety-eight whelks had operculae that were unreadable using this approach. An alternative technique consisted of embedding each operculum into an epicure resin. The embedded operculum was sectioned from the nucleus to the upper margin by a Buehler Isocut low speed saw. The rings

4

were then counted by looking at the cross section of each embedded operculum. This more labor intensive method was employed to examine the accuracy of the previous more convenient technique. The number of rings determined for each specimen was then plotted against its respective sex and size. This data was then used to construct a von Bertalanffy growth equation (von Bertalanffy,

1938) for each sex. The von Bertalanffy equation is: $L = L_{\max} (1 - e$

$-K(t-t_0)$ where L = shell length in

mm, L_{\max} = length at infinity, K = instantaneous growth rate, and t_0 = age at zero length.

In April 2001, a scallop trawl net (10-foot opening, width with 1.5-inch stretched-mesh webbing) was used to gather additional whelks from the south shipping channel of St. Simons Sound. Two-hundred and forty-six whelks were captured the majority of which (83%) was knobbed whelks. The specimens were kept in a deep freezer at -20° Celsius for approximately two months until thawed and processed to examine size at maturity. All whelks were measured, weighed and meat was extracted as previously described. Once knobbed whelk meat was removed from the shell, they were separated into males ($N = 100$) and females ($N = 105$) by the presence/absence of a penis. A total wet weight of whelk meat per individual was determined by weighing on a top loading balance to

the nearest 0.01 gram. For the male whelks, the penis was removed and measured to the nearest mm and then weighed to the nearest 0.01 gram. For the female specimens, the oviduct was removed and weighed. For both male and female whelks, the gonads, if present, were removed and weighed. Reproductive organ sizes were plotted against shell length and the size range at which sexual maturity (i.e., a sudden increase in organ size) was attained in each sex was visually determined. Size ranges were then applied to the von Bertalanffy growth curves and ages at maturity were derived.

To complement our data on size at maturity based on reproductive organ size, we also undertook field trips during the spring 2003 breeding season to observe the sizes of mating whelks on the intertidal mud flats around Wassaw Island, Georgia. In some instances more than one male was found mating with a single female (Table 2).

Table 2. Size of male and female whelks found mating at various locations in Wassaw Sound, Georgia in March/April 2003.

Location

Female Shell Length (mm)	Male Shell Length (mm)		
	No. 1	No. 2	No. 3
Little Tybee Island	156	102	
	224	140	
	164	94	
	170	123	
	158	123	119
	178	115	
	151	107	
	172	83	
	149	98	69
South Cabbage	196	110	
	159	104	
	175	110	
	162	83	86
	155	75	81
	121	95	
Mud Island	191	114	78
	179	86	
Pa Cooper	184	86	
Wassaw Island	111	94	
	148	107	
	144	107	
	161	83	
	163	109	
	144	90	
	182	79	

135	81		
148	86		
133	82		
183	90		
188	94		
185	93		
94	89		
178	97		
165	88	94	
153	111		
148	95		
130	109	108	99
142	84	95	
151	92		
154	97		
107	91		

Results

Figures 3, 4, and 5 present the size frequency distributions for the shell length, shell width, and total wet weight, respectively, of all whelks that were used in the opercular analysis (N = 708). There was no statistically significant difference between the results obtained from reading the operculae surfaces and sections at the 95% level. Males (N= 310) ranged from 30-to-128 mm in length (mean \pm S.E. = 89.4 ± 0.84 mm), from 14-to-93 mm in width (64.6 ± 0.7 mm), and from 2.2- to-284 g (102 ± 2.7 g) in weight. Females (N = 397) attained a larger size in all parameters ranging from 32-to-167 mm in length (101.2 ± 1.01 mm), from 15-to-124 mm in width (75.5 ± 0.84 mm), and from 2.1-to-510.3 g in weight (153.9 ± 4.4 g). The sex ratio (1.00F:0.78M) was significantly different from parity (Chi-square = 10.7). It should be noted that this was a biased sample as 347 larger specimens were removed from the original sample.

The age frequency distribution of male and female whelks is presented in Figure 6. Females were aged to 8 years, while males were aged to 11 years. The growth rates of females and males are presented in Figure 7. It should be noted that while females in the sample did not attain the same age as males, they were larger in size. The growth parameters for each sex are as follows: $L_{\max} = 213.19$, $K = -0.1172$, and $t_0 = 0.2016$ for females; $L_{\max} = 105.37$, $K = -0.6311$, and $t_0 = 1.4470$ for males.

Gonadal weight in relation to shell length is illustrated in Figures 8 and 9. Gonadal material was observed in males as small as 74 mm and in females as small as 85 mm in shell length. Of the 100 males that ranged in size from 74-to-128 mm in shell length, all but two individuals (78 mm & 98 mm individual) had gonads present. In general, the larger the male, the larger the penis observed (Figure 10). Although a penis was present in all male specimens, male gonadal weight did not

appreciatively increase in mass until animals were in the 85-to-90 mm size range. Even in larger male size classes, some males had small amounts of gonadal material. In the field, fifty males were observed mating with 78% being greater than 85 mm in length (Table 2). The remaining ten whelks ranged from a minimum of 69 mm, to three at 83 mm. Of the 105 females ranging in shell length from 76-to-148 mm, no female less than 85 mm (N=10) had gonads present (Figure 9). Female gonads were absent in 21 individual ranging from 76-to-118 mm in shell length. For females, oviduct weights

7

remained low until a size of 100 mm in length was attained (Figure 11), approximately the same size at which female gonadal weights began to increase. As with males, many females exhibited low gonadal and oviduct weights within larger size classes. In the field, all copulating females (N=41) were greater in size than 100 mm, with the notable exception of one individual (94 mm). The approximate ages at which males and females achieve sexual maturity according to Figure 7 is 4 and 6 years, respectively.

Discussion

Important biological information concerning the life history of the knobbed whelk in coastal Georgia was revealed by this study. Based on an analysis of reproductive organ size and field observations on copulation, sexual maturity is attained at approximately 85 mm or four years of age in male whelks, and 100 mm or six years in females. In most dioecious prosobranchs, males mature prior to females (Runham, 1993). Females must invest greater energy in spawning, producing eggs, nutrition, and casings for their offspring, presumably resulting in a delayed size at maturity. Female *Buccinum undatum* (Linnaeus, 1758) are reported to expend almost fifteen times the energy in reproduction as males (Kideys *et al.*, 1993). In Virginia, knobbed whelks mature as males at nine years of age (130 mm) and females at twelve years (172 mm) (Castagna and Kraeuter 1994). While this follows the same pattern as in Georgia, the size and age at maturity there is much greater. It should be noted that the latter study was based on laboratory-reared whelks; however, differing sizes at sexual maturity with geographical location have also been observed for *Buccinum undatum* (Martel *et al.*, 1986, Kideys *et al.*, 1993; Kenchington & Glass, 1998). Reasons may include genetics, fishing pressure (Martel *et al.*, 1986) or long-term selective pressure from natural predation (Gendron, 1992). The Georgia population in the St Simons Sound area has been heavily fished for years, however the Wassaw Sound population has not. Temperature regimes are very different between these states, which may lead to different developmental rates. In Georgia, hatchling whelks emerge from egg strings after approximately six weeks (Power *et al.*, 2002a) as compared with six months in Virginia (Castagna & Kraeuter, 1994).

Female knobbed whelks were also observed to grow to a larger size than males. Typically in prosobranchs showing size dimorphism the female is larger, and this has indeed been previously reported for the knobbed, channeled, and lightning whelks (Magalhaes, 1948; Weinheimer, 1982;

8

Anderson *et al.*, 1989; Sisson & Wood, 1988; Dicosimo, 1988, Shalack 2007; Walker *et al.*, 2008). Whelks were aged to a maximum of eleven years, but the sample was biased, since larger and presumably older individuals were removed. Castagna and Kreauter (1994) report that knobbed whelks occur in Virginia in the 21-to-23 year age class. The predominance of large-sized females led to the popular theory that these whelks were sequential protandrous hermaphrodites. However, recent genetic evidence has proved that sex reversal does not occur naturally (Avisé *et al.*, 2004). Size dimorphism is more likely a result of distinct growth and mortality rates.

For both sexes, many large individuals exhibited little signs of gonadal development (Figure 8 & 9). This in itself is not surprising. From field observations (Walker, 1988; Power *et al.*, 2002a; Walker *et al.*, 2008), we know that the knobbed whelk population in Georgia spawns twice per year, once in the fall and again in the spring. What we do not know is whether a single female spawns twice per year. It may be that some individuals spawn in the fall and do not have the energy reserves stored to spawn again in the spring. We are also certain that knobbed whelks in offshore areas bury themselves during the winter months (Power *et al.*, in preparation). This is in agreement with tagging studies of knobbed whelks which were released in January on an intertidal flat in Georgia. Whelks were buried in January, and few moved more than approximately 3 meters by February. All were moving by March once water temperatures reached 13°C (Walker *et al.*, 2004). Thus, females that spawned in fall probably are not feeding sufficiently over winter to generate the energy reserves needed to spawn again in the spring. For the common whelk, *Buccinum undatum*, 20-to-40 percent of females do not reproduce within a given year (Martel *et al.*, 1986). Given the high energy demand for reproduction, it is reasonable to assume that female whelks in Georgia probably only spawn once a year, if that often.

An unequal sex ratio (1 F: 0.78 M) was observed in our biased sample. In an eighteen-month study of offshore knobbed whelks (N = 7,022) from the same area, a similar ratio of 1 F: 0.89 M was determined (Power *et al.*, in preparation). We also know that there is an equal sex ratio of embryos within individual egg capsules along the egg string (Avisé *et al.*, 2004). This contrasts with whelk population studies from intertidal areas of coastal Georgia (Walker, 1988; Power *et al.*, 2002b; Walker *et al.*, 2008) and Virginia (Castagna and Kreauter, 1994), where females dominate. Highest abundances in the intertidal zone occur in the spring and the fall around the breeding seasons (Walker, 1988). Out of 2,908 whelks hand picked from the intertidal zone in Wassaw

Sound, 89.72% were female. It may be that due to energy requirements females are forced to migrate here at these times to feed on the abundant supplies of oysters [*Crassostrea virginica* (Gmelin, 1791)] and hard clams [*Mercentaria mercenaria* (Linnaeus, 1758)] that generally only occur intertidally in Georgia (Harris, 1980; Walker and Rawson, 1985).

Whelks are very vulnerable to overfishing; they are a slow-moving, slow-growing, long-lived species with an entirely benthic reproductive strategy that limits their recovery in heavily exploited areas. Whelks also occur in high-density aggregations prior to spawning. Whelk fisheries worldwide have followed the same “boom and bust” development pattern, with catch and effort dramatically increasing until resources are overfished. In Europe, the most substantial whelk fishery is for the common whelk, *Buccinum undatum*. In Ireland, rapid expansion of a baited-pot based whelk fishery in the 1990s led to a pronounced Lee effect in heavily fished areas of the Irish Sea. A minimum size limit was introduced in 1994, but this has failed as a conservation measure, and the future of the fishery is not favorable (Power, 2000). One of the oldest whelk fisheries in Europe was in the Netherlands. This was a trawl-based fishery that dates back to the latter half of the nineteenth century. Fishing effort intensified after World War II until landings plummeted to practically zero in 1970, which ended the fishery. There has been no recovery since, and in fact the whelk is now extinct in the Dutch Wadden Sea (Cadee *et al.*, 1995). A similar pattern occurred in Germany where whelks were dredged from the Ems estuary. A steady increase in landings through the 1970s led to an increase in the number of small whelks being captured, which in turn led to the fishery being discontinued in 1983 (see European whelk fishery review by MacKenzie *et al.*, 1997). A seasonal trawl-based fishery for knobbed whelk commenced in South Carolina in the 1970s. The fishery has since been cyclical, going through periods of intensive harvesting followed by periods where stocks collapse (Anderson *et al.*, 1985). The state originally established a size limit of 5 inch (127 mm), which was subsequently reduced to 4.5 inches and finally 4 inch (101.6 mm) at the request of commercial fishermen (Eversole *et al.*, 2008). Many lessons can be learned from these experiences. Accordingly, conservative measures are critical to the sustainability of this fishery in Georgia.

Since larger whelks are more economical in terms of processing, it seems likely that sexually mature female whelks are most desirable to fishermen. The imposition of size limits on the fishery is questionable. A minimum size limit is designed to allow a commercial species to

spawn at least once before it is harvested. In the case of the knobbed whelk, this becomes difficult since establishing a minimum size limit of say 110-120 mm based on female size at maturity data would prohibit the catch of almost all males and sexually immature females. The long-term effect

of the removal of one sex from a whelk population in equilibrium is unknown. In reality, some fishermen are already practicing voluntary size culling both dockside and at sea, and in doing so are returning these components of the population. In order to reduce physiological stress and increase the survival rate of smaller whelks, all grading should be performed at sea and sub-sized individuals returned as quickly as possible. With the mandatory requirement that all trawls in Georgia waters have TEDs equipped with 4 inch spaced bars, a size limit may have been introduced indirectly.

Restrictions on the intertidal hand-picking of whelks may also need to be considered. Currently, there are no restrictions in terms of size limits or quantities. All that is required is a recreational fishing license. However, hand collectors have been observed locally, collecting several bushels to supply local seafood dealers. Shalack *et al.*, (in preparation) showed that hand gathering of whelks in the intertidal zone quickly depleted stocks. Given the fact that these intertidal whelks are typically very large females that are coming ashore to feed either prior to or just after spawning, harvesting in these areas should be restricted at least until after all egg strings have been laid. In many whelk species, the larger the adult, the greater the fecundity (Miloslavich & Dufresne, 1994; Spight & Emlen, 1976). Would it therefore be better to catch medium-sized whelk of both sexes and leave the larger-sized ones as breeders? In this situation a minimum and a maximum size limit would be appropriate.

11

SL

SW

Figure 1



Figure 1. Shell measurements of the knobbed whelk (SL = shell length from siphonal channel to shell apex and SW = shell width from across the shoulder including spines).

R4

R3

R2

R1

N

Figure 2

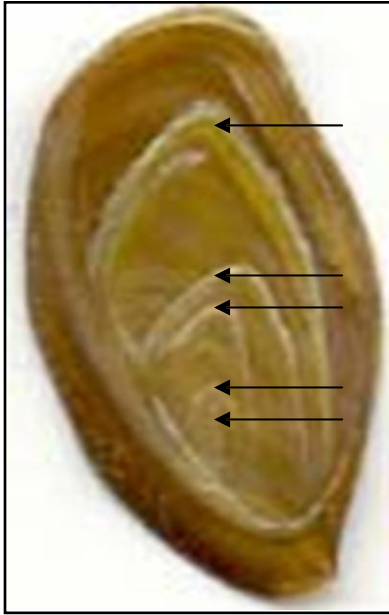
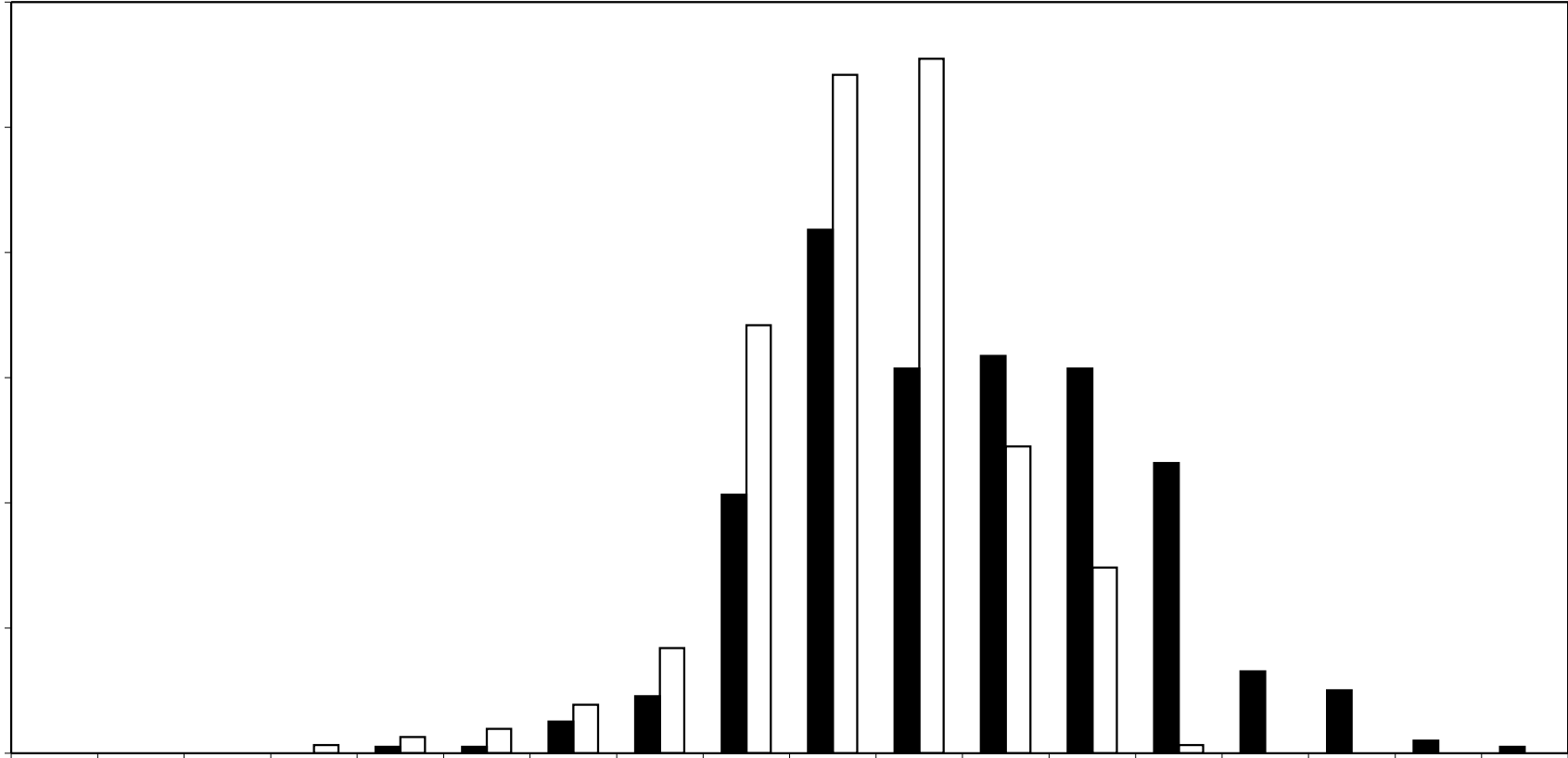


Figure 2. Annual growth rings on the inner surface of an operculum from a knobbed whelk (N = nucleus, R1-R4 = rings 1-4).



Female (N=397)
Male (N=310)



25
20
15
10

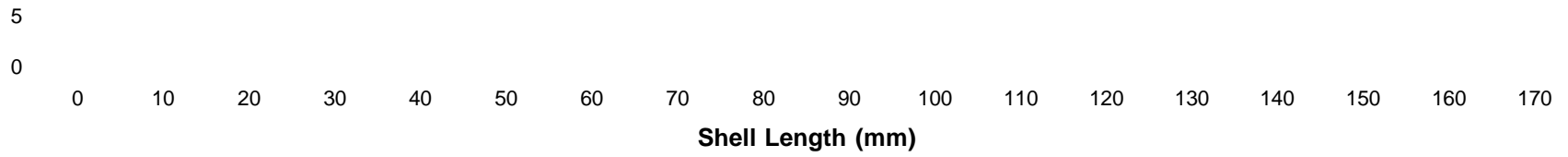
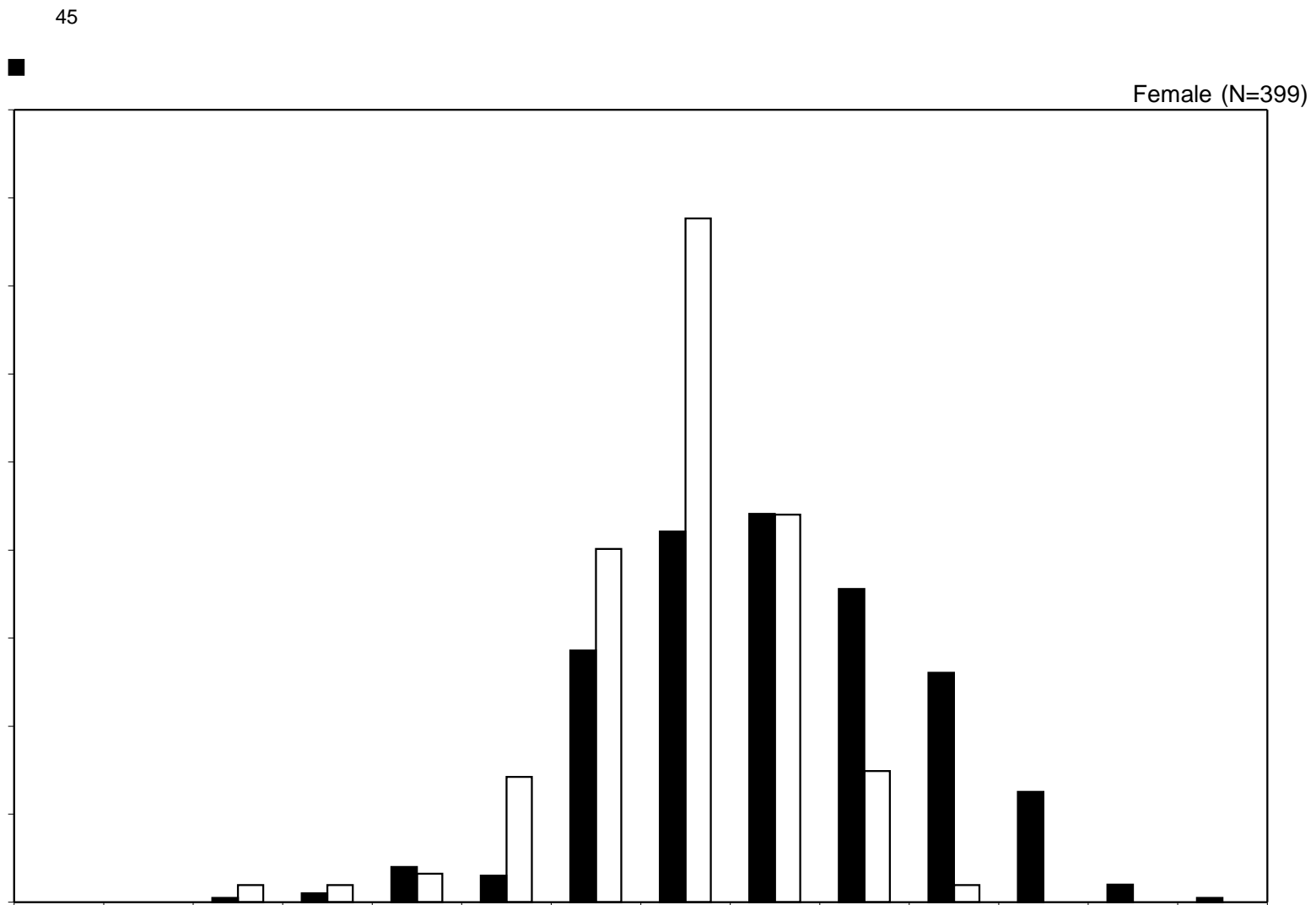


Figure 3. Shell length (mm) histogram of male and female knobbed whelks, *Busycon carica*, collected in St Simons Sound, GA

13



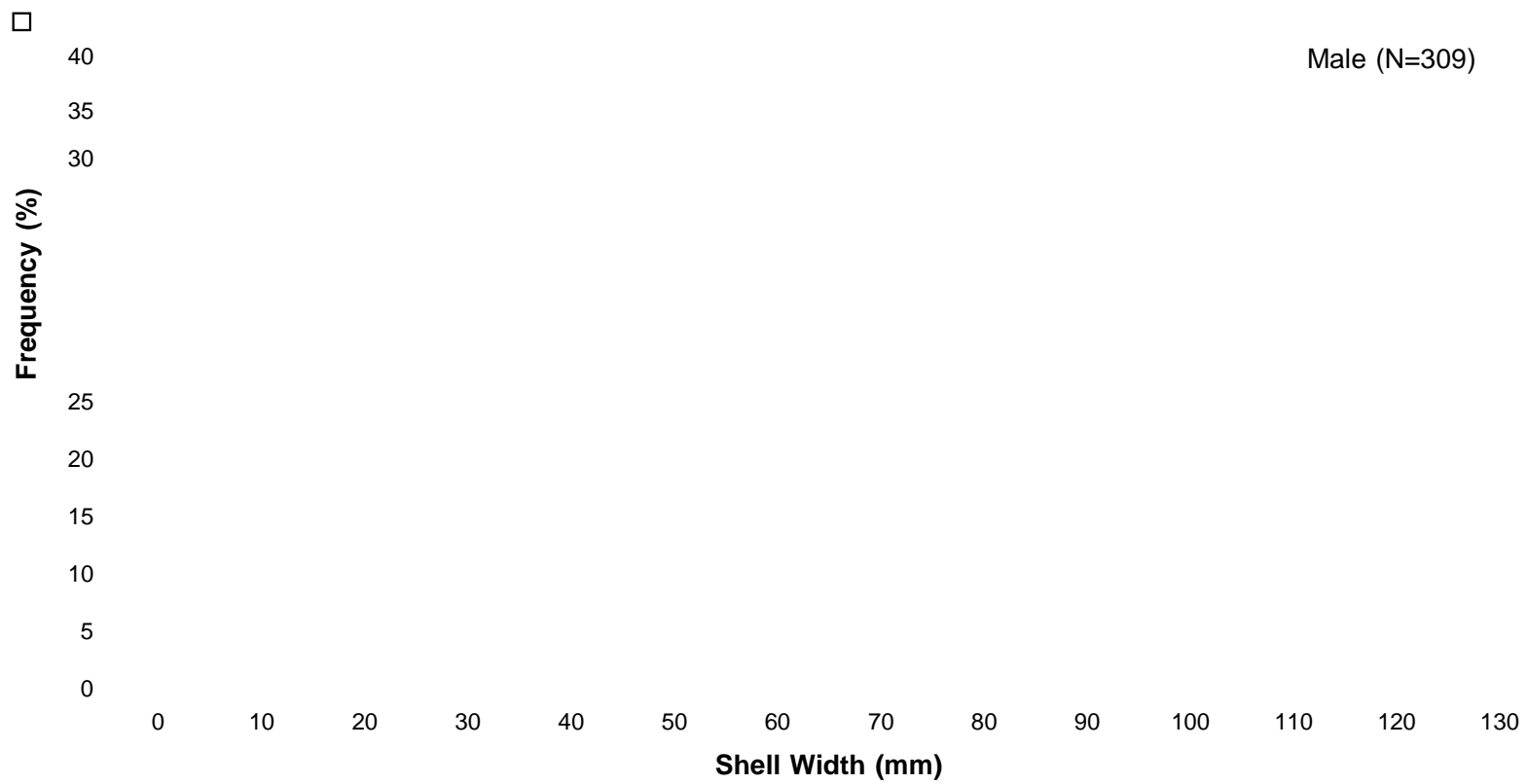
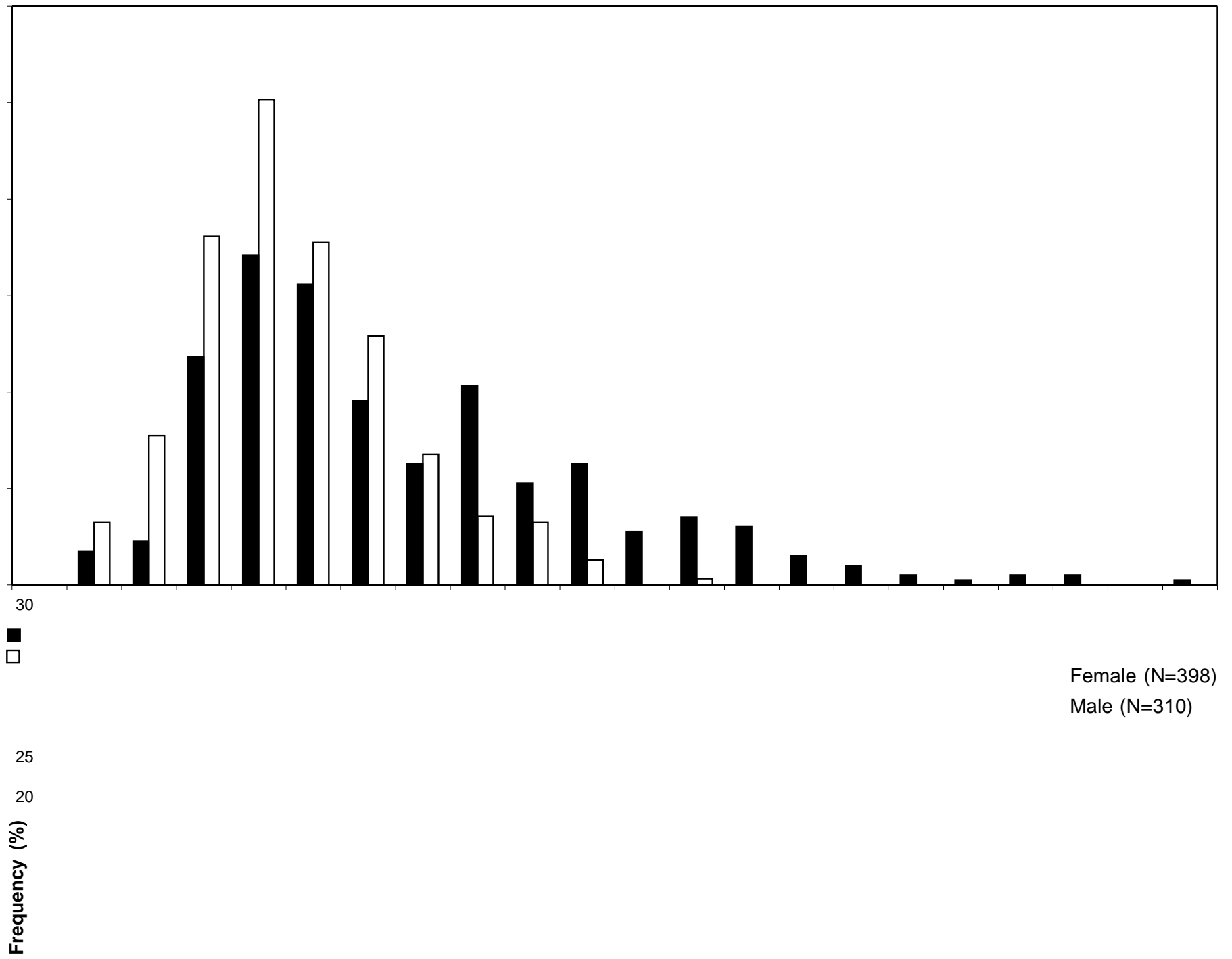


Figure 4. Shell width (mm) histogram of male and female knobbed whelks, *Busycon carica*, collected in St Simons Sound, GA



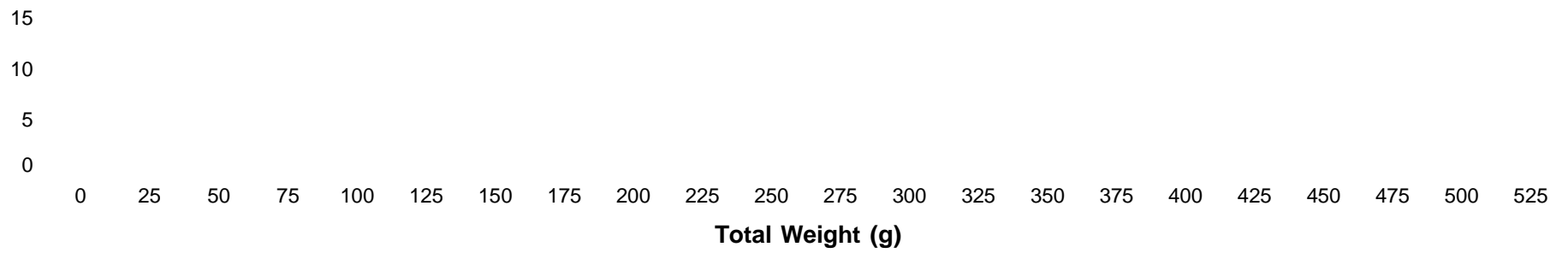
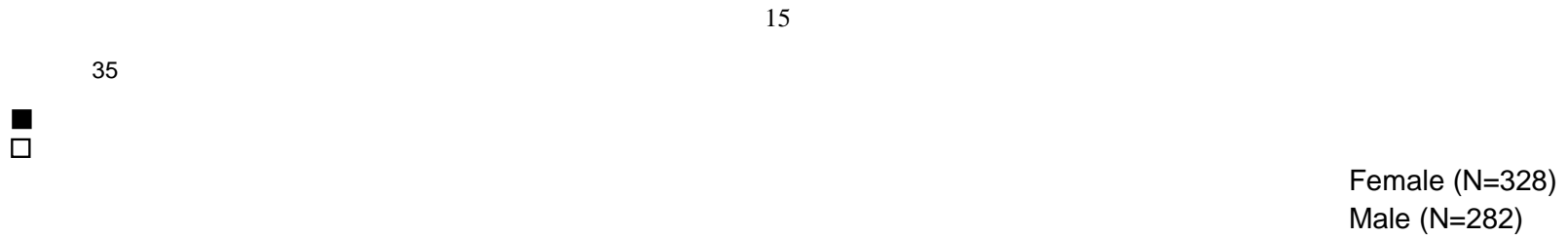
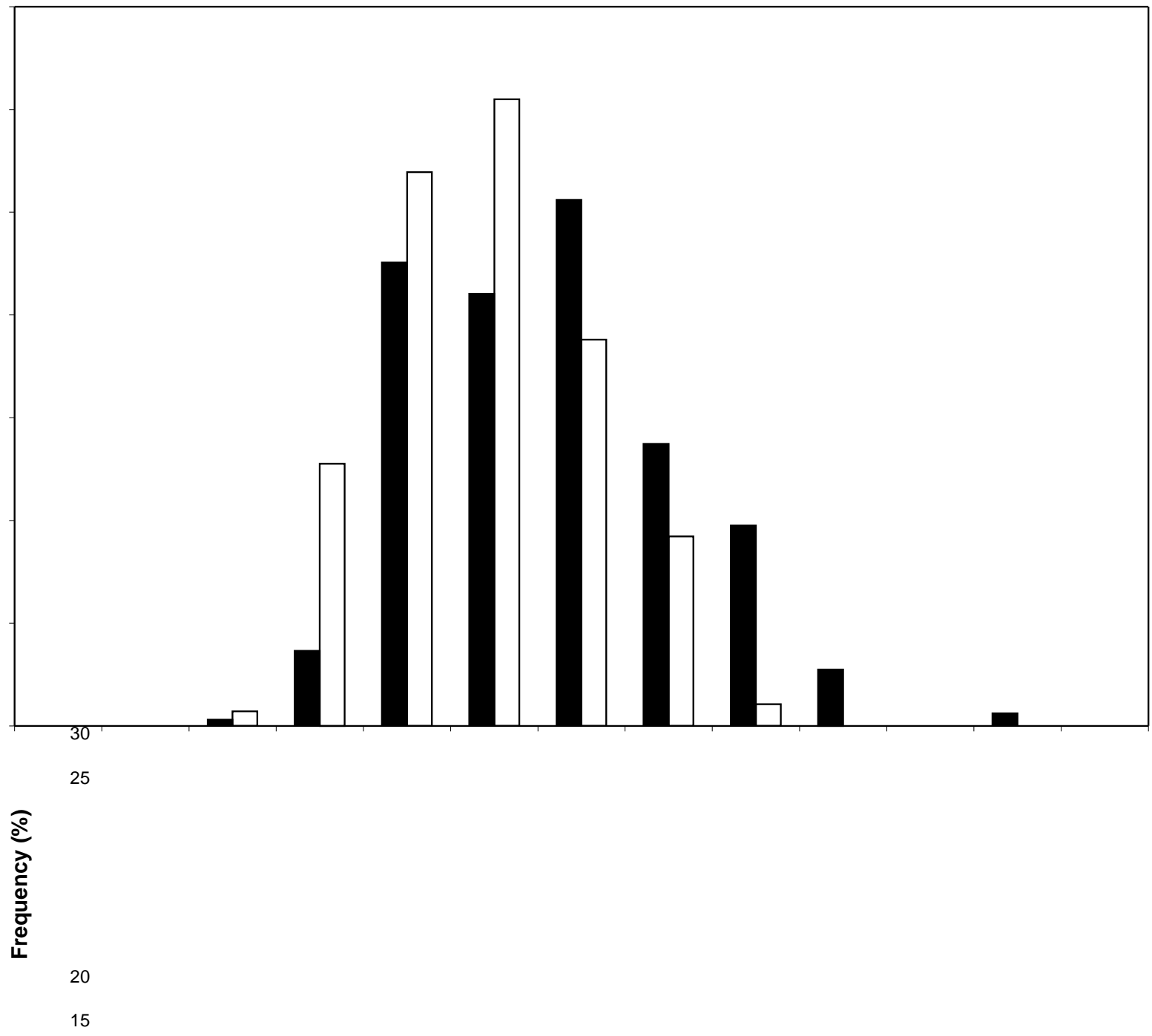


Figure 5. Shell weight (g) histogram of male and female knobbed whelks, *Busycon carica*, collected in St Simons Sound, GA





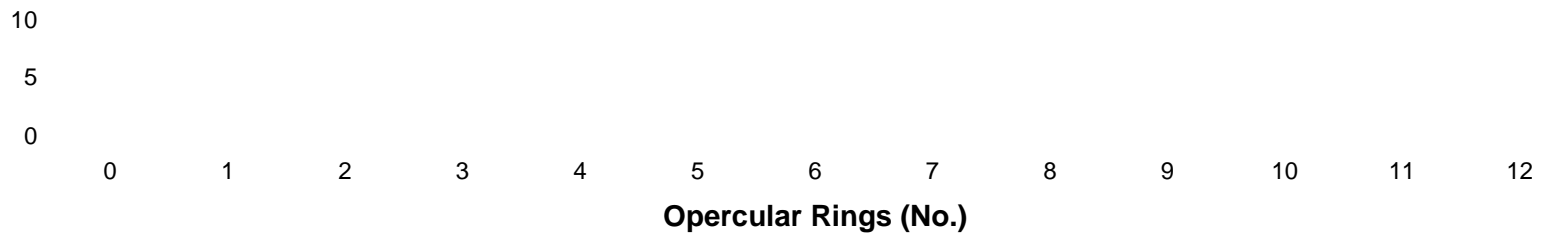
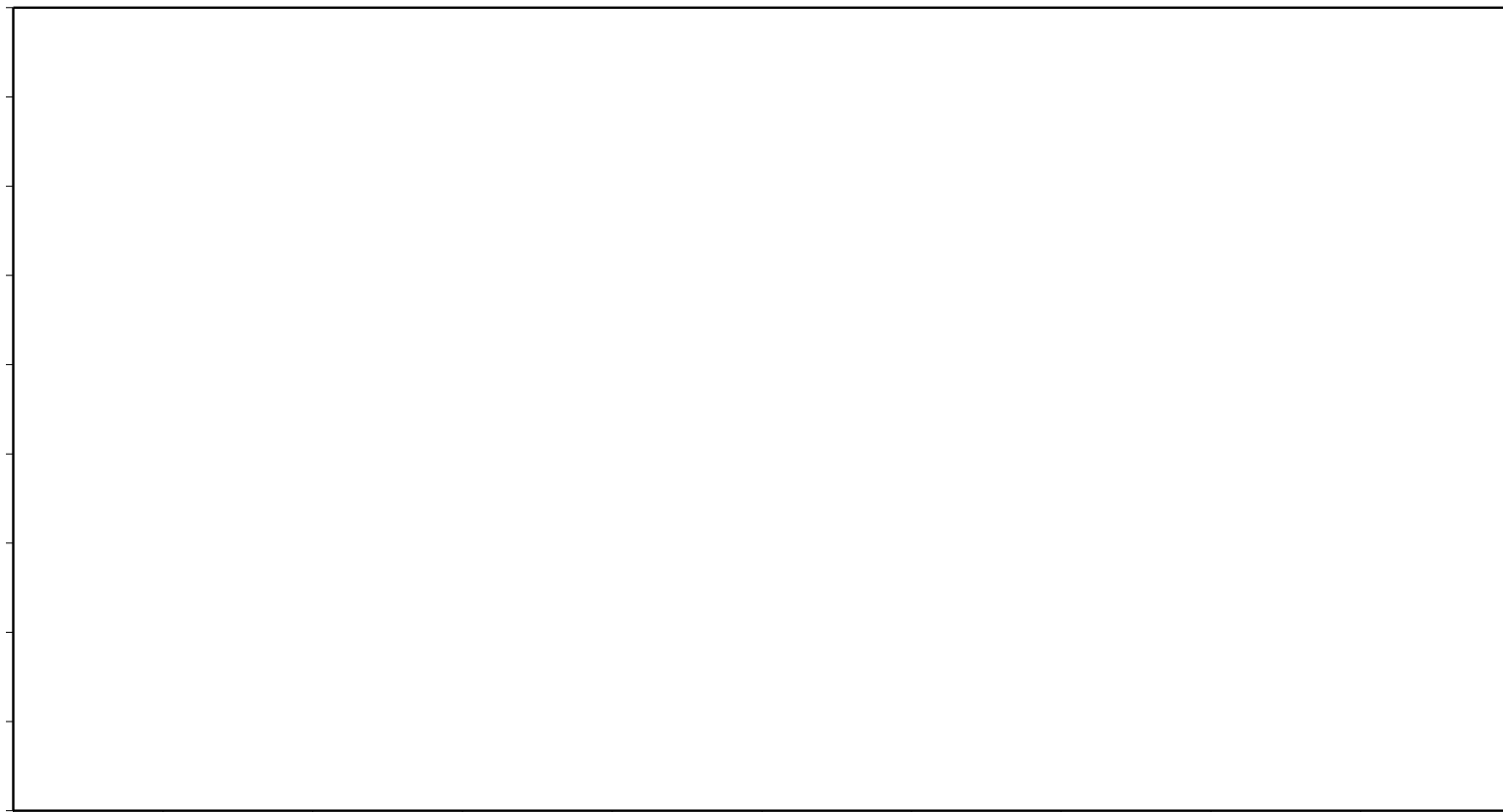


Figure 6. Age frequency distribution of male and female whelks as determined from operculum examination of annual rings.

16

von Bertalanffy Growth Function for Male & Female Whelks



180

•
—
160

Male

Female

140

Shell Length (mm)

120

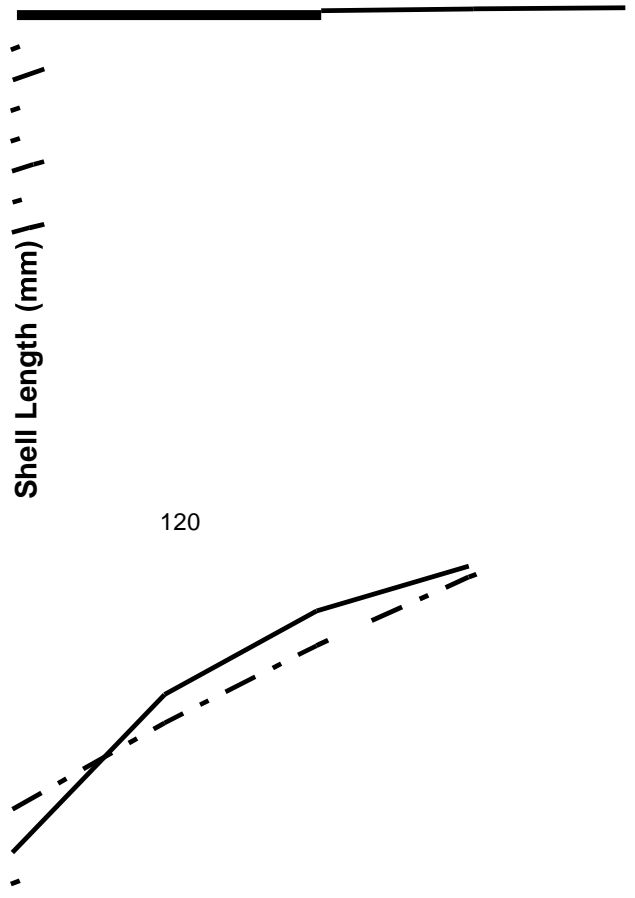
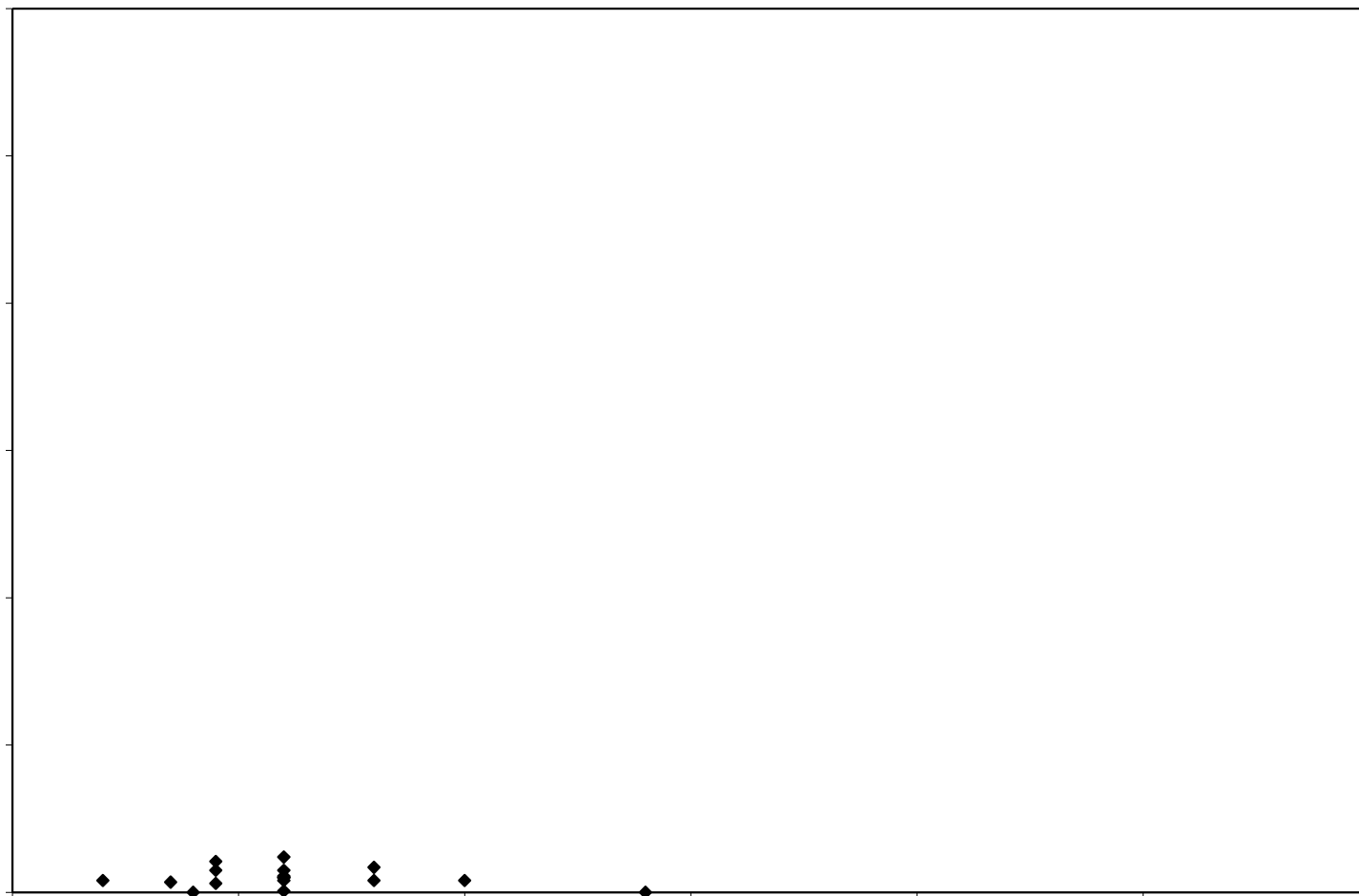




Figure 7. The von Bertalanffy growth curves calculated for female and male knobbed whelks from St Simons Island through opercular analysis.



0.6

N = 100

- ◆
- ◆
- ◆
- ◆

0.5

0.4

Gonad Weight (g)

0.3

0.2



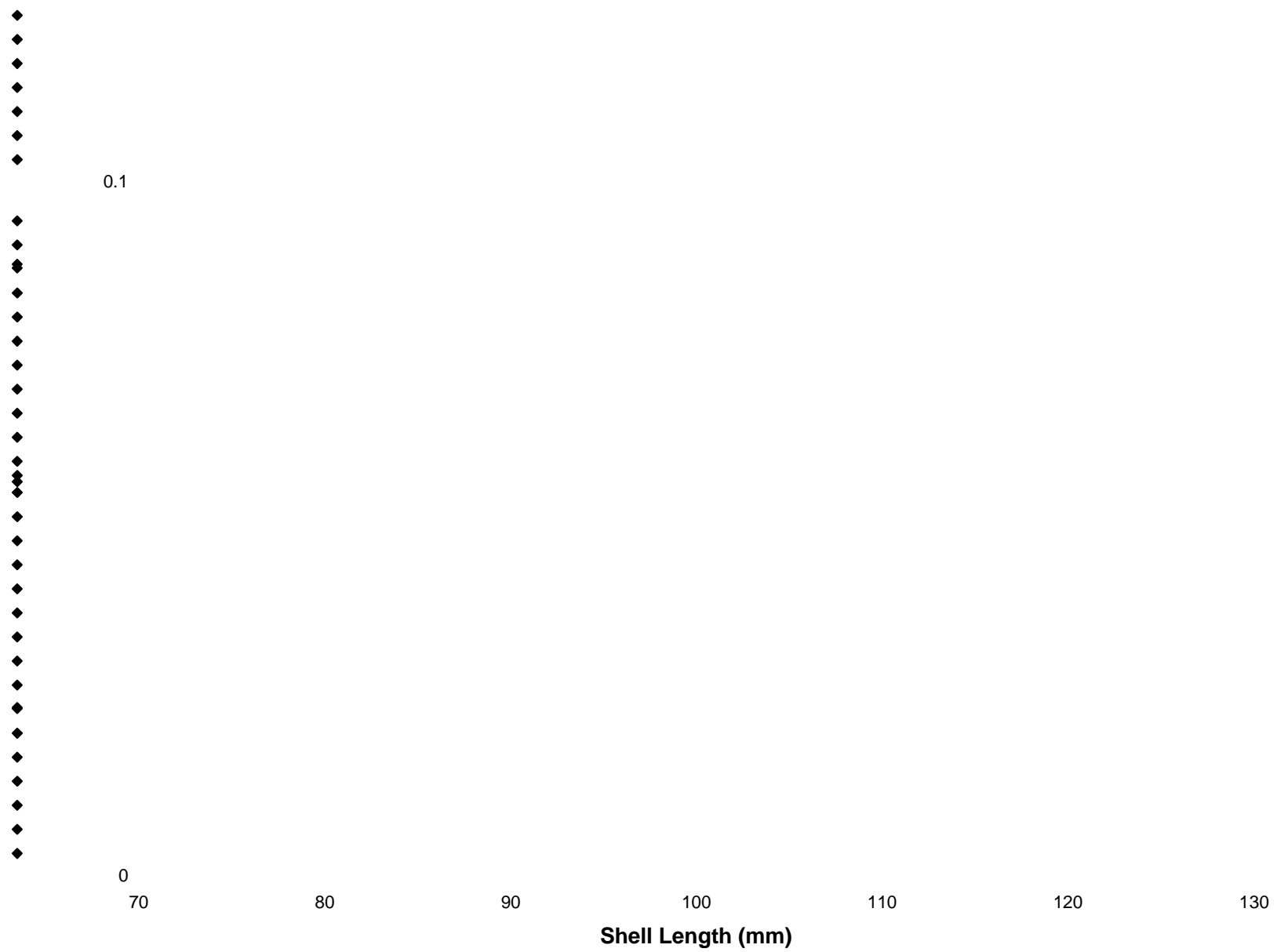
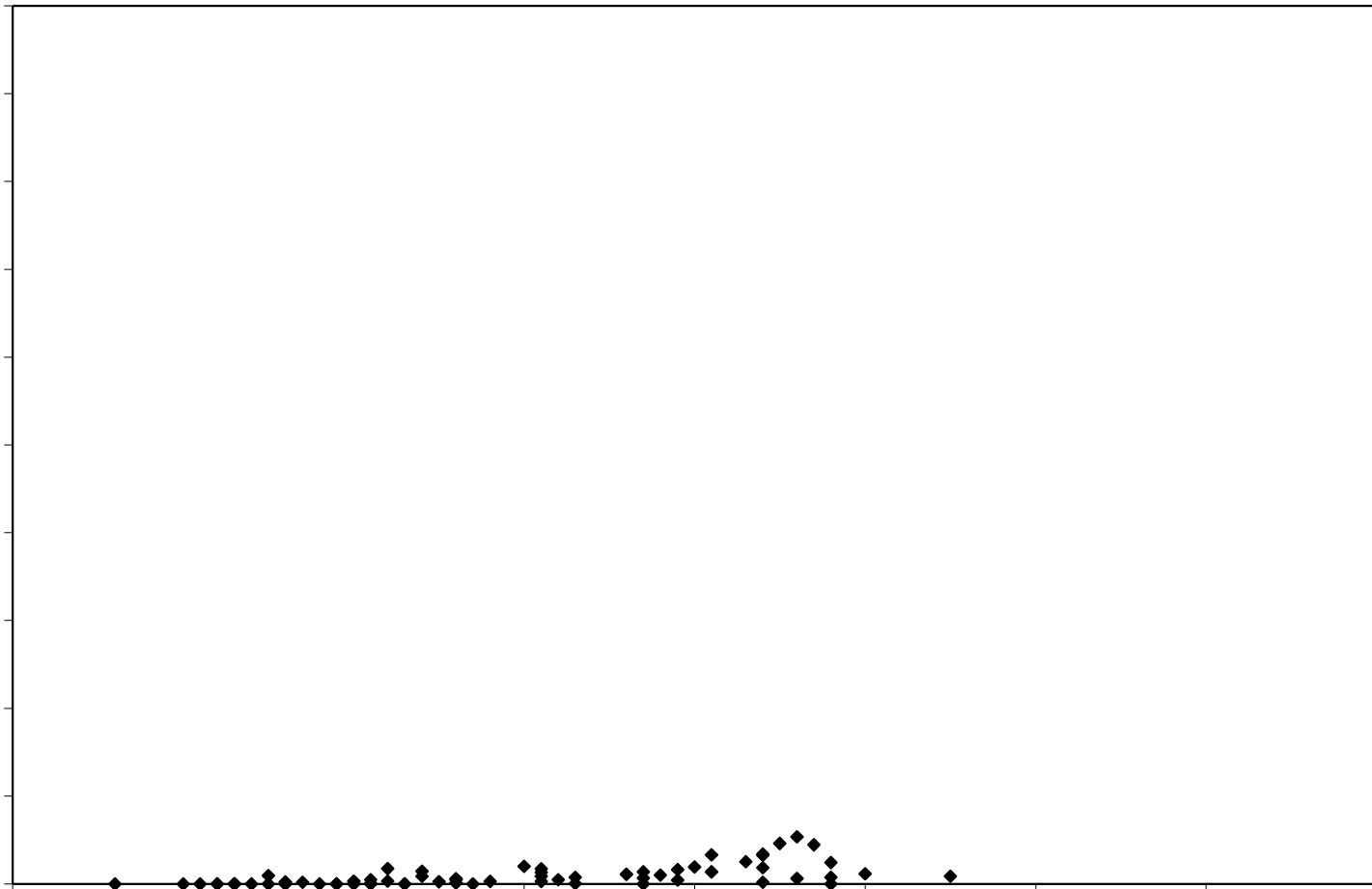


Figure 8. The relationship between male gonadal weight (g) and shell length (mm) for whelks collected from St Simons Sound, GA.



5

◆
4.5

◆
N = 105

4

3.5

◆

Gonad Weight (g)

3
2.5
2
1.5
1
0.5
0

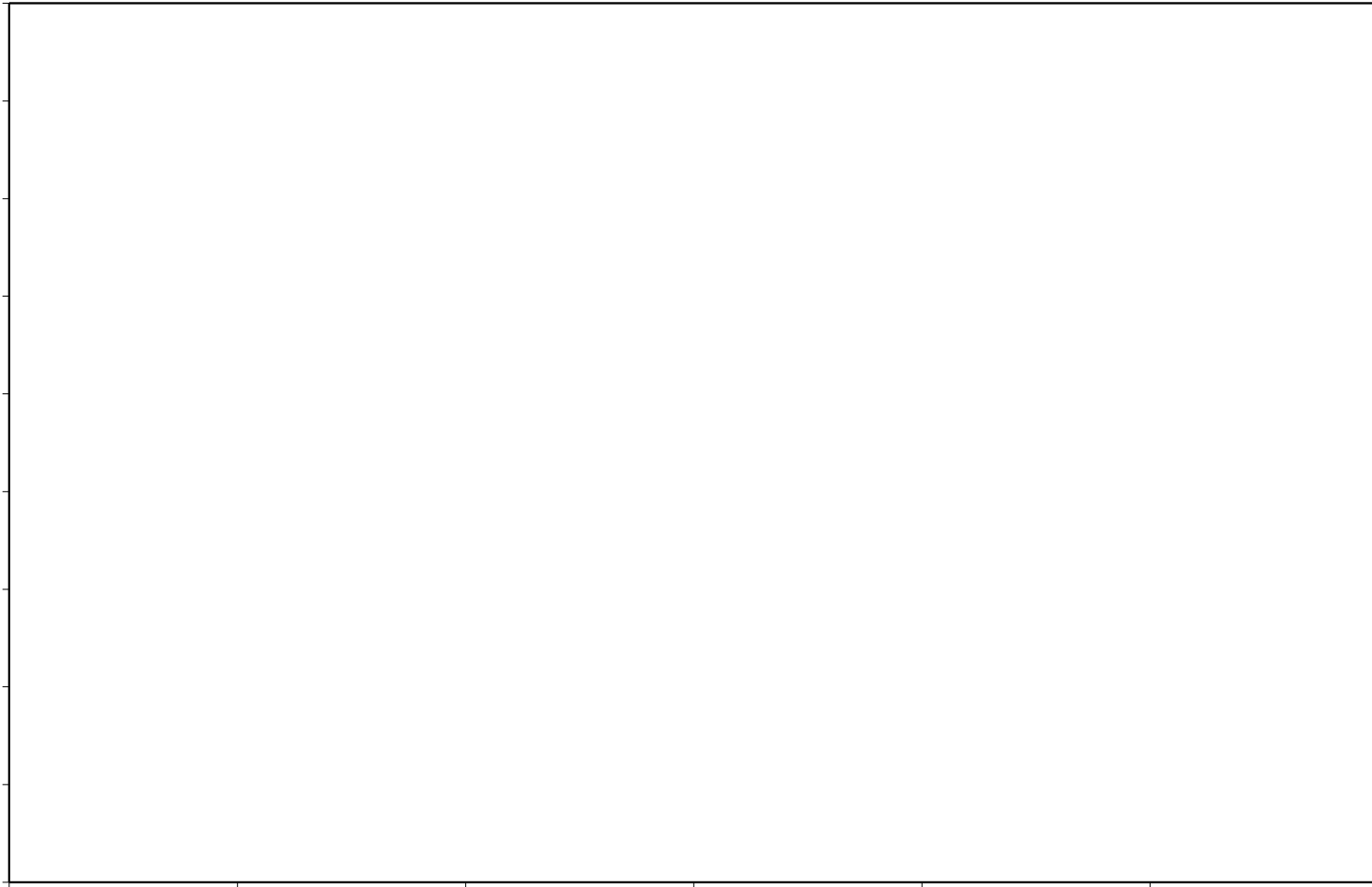
70 80 90 100 110 120 130 140 150



Shell Length (mm)

Figure 9. The relationship between female gonadal weight (g) and shell length (mm) for whelks collected from St Simons Sound, GA.

19



90

◆
◆◆
◆
◆

N=100



70

60

50

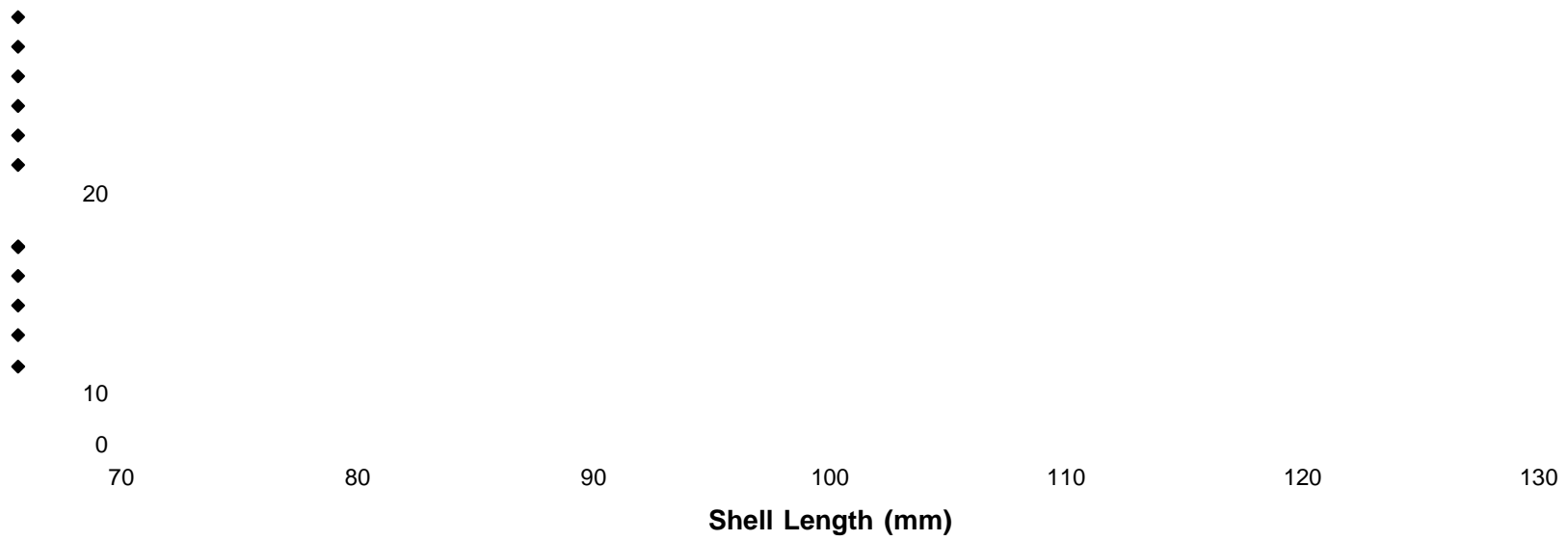
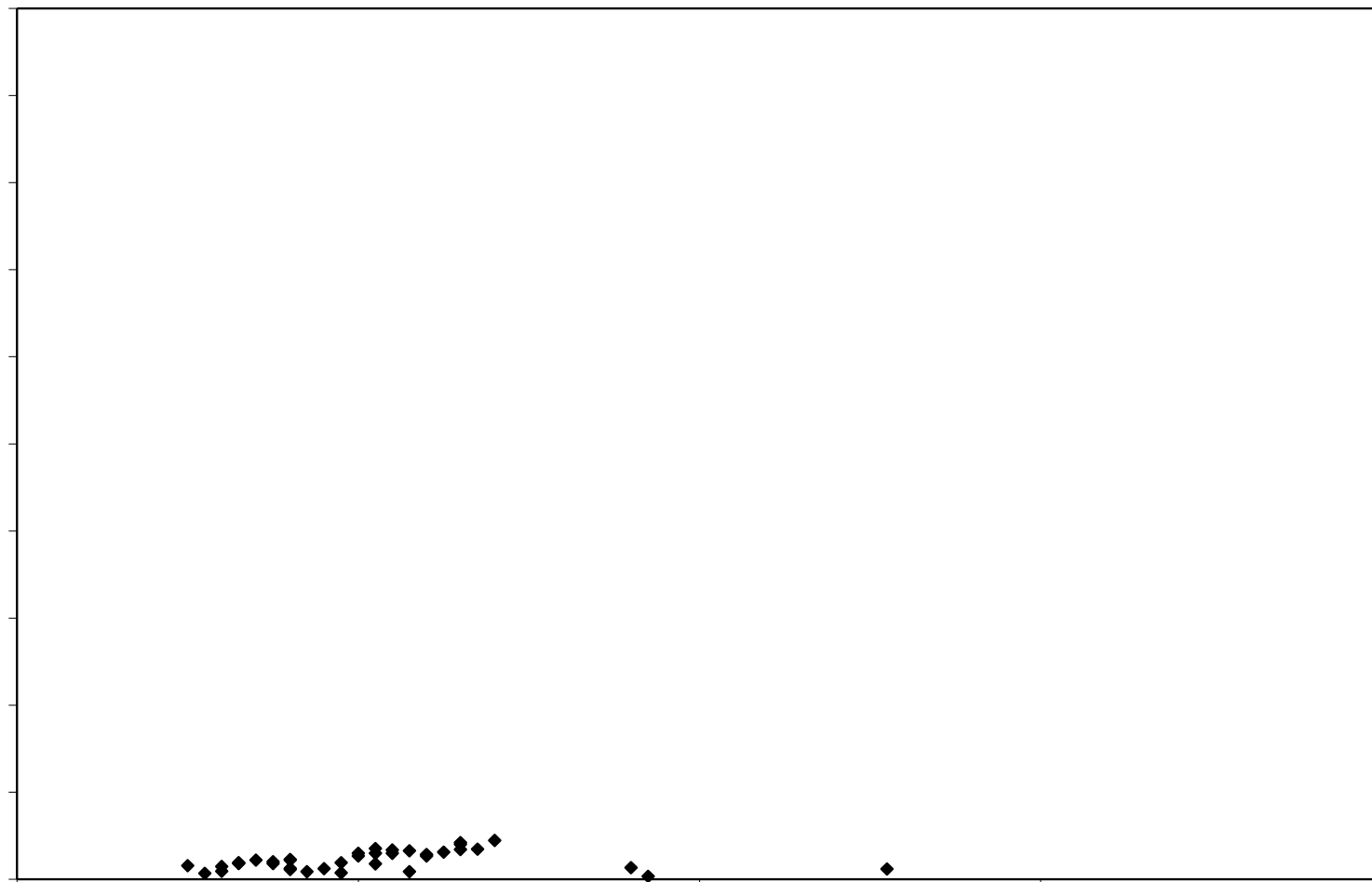


Figure 10. The length of the penis (mm) versus shell length (mm) in male knobbed whelks collected from St Simons Sound, GA.



20

◆

18

16

◆

◆

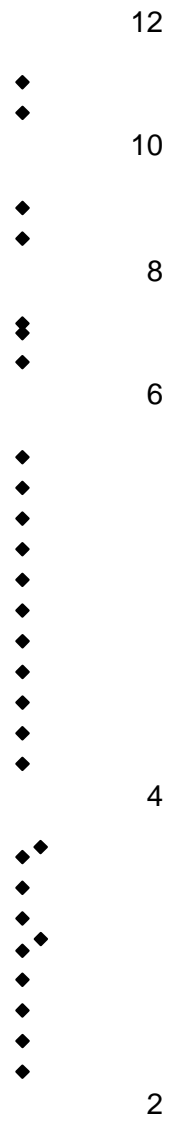
◆

14

◆

N=105

Oviduct Weight (g)



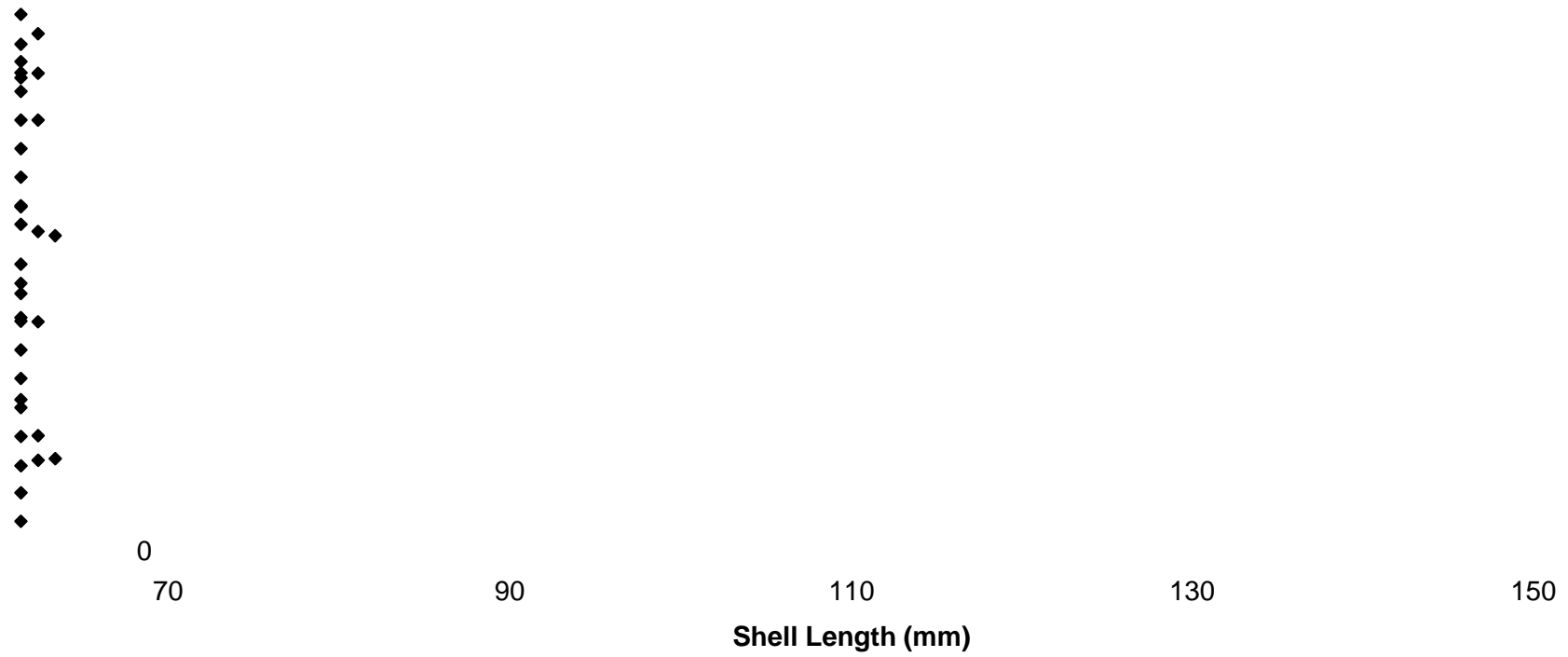


Figure 11. The weight of the pallial oviduct (g) versus shell length (mm) in female knobbed whelks collected from St Simons Sound, GA

References

- Abbott R.T. (1974) *American Seashells*, 2nd edition. Van Nostrand Company, Inc. New York. p. 222.
- Anderson W.D., Eversole A.G., Anderson B.A. and Van Sant K.B. (1985) A biological evaluation of the knobbed whelk fishery in South Carolina. Final Completion Project # 2-392-R. S.C. Wildlife and Marine Resources Department, Marine Resources Division, Charleston, S.C.
- Anderson B.A., Eversole A.G. & Anderson W.D. (1989) Variations in shell and radula morphologies of knobbed whelks. *Journal of Shellfish Research* **8**, 213-218.
- Avisé J.C., Power A.J. & Walker D. (2004) Genetic sex determination, gender identification, and pseudohermaphroditism in the knobbed whelk, *Busycon carica* (Mollusca: Melongenidae). Proceedings of the Royal Society of London, Series B 271: 641-646.
- Belcher, C., Vendetti R. Gaddis G. and Parker L. (2001). Results of Gear Testing to Reduce Turtle Capture in the Whelk Trawl Fishery. University of Georgia Marine Extension Service Bulletin Number 23, 27 p.
- Cadee G.C., Boon J.P., Fisher C.V., Mensink B.P. & Ten Hallers-Tjabbes C.C. (1995). Why the whelk *Buccinum undatum* has become extinct in the Dutch Wadden Sea. *Netherlands Journal of Sea Research* 34, 337-339.
- Castagna M. & Kraeuter J. N. (1994). Age, growth rate, sexual dimorphism, and fecundity of knobbed whelk *Busycon carica* (Gremlin 1791) in Virginia. *Journal of Shellfish Research* 13, 581-586.
- Dicosimo J. (1988) Commercial fisheries analysis of *Busycon* whelks in Virginia. *Journal of Shellfish Research* 7, 155.
- Eversole A.G., Anderson W.D., and Isley J.J. (2008). Age and growth of the knobbed whelk *Busycon carica* (Gmelin 1791) in South Carolina subtidal waters. *Journal of Shellfish Research* 27:423-426.
- Gendron L. (1992). Determination of the size at sexual maturity of the waved whelk *Buccinum undatum* in the Gulf of St. Lawrence as a basis for the establishment of a minimum catchable size. *Journal of Shellfish Research* 11, 1-7.
- Harris D.C. (1980). Survey of the intertidal and subtidal oyster resources of the Georgia coast. Georgia Department of Natural Resources, Coastal Resources Division, (Final Completion Report, Project no. 2-234-R). Brunswick, GA 44 pp.

- Kennington E. & Glass A. (1998). Local adaptations and sexual dimorphism in the waved whelk (*Buccinum undatum*) in Atlantic Nova Scotia with applications to fisheries management. *Canadian Technical Report of Fisheries and Aquatic Sciences*. No. 2237.
- Kideys A.E. (1996). Determination of age and growth of *Buccinum undatum* (Gastropoda) off Douglas, Isle of Man. Institute of Marine Sciences, Middle East Technical University, Turkey. *Helgolander Meeresunters.* 50, 353-368.
- Kideys A.E., Nash R.D.M. & Hartnoll R.G. (1993). Reproductive cycle and energetic cost of reproduction of the neogastropod *Buccinum undatum* in the Irish Sea. *Journal of Marine Biological Association of the United Kingdom* 73, 391-403.
- Kraeuter J.N., Castagna M.A. & Bisker R. (1989). Growth rate estimates for *Busycon carica* (Gmelin 1791) in Virginia. *Journal of Shellfish Research* 8, 219-225.
- Kubo I. & Kondo K. (1953) Age determination of the *Babylonia japonica* (Reeve), an edible marine gastropod, basing on the operculum. *Journal of the Tokyo University Fisheries* 39, 199-207.
- MacKenzie C.L., Burrell V.G., Rosenfield A. & Hobart W.L. (1997). The history, present condition, and future of the molluscan fisheries of North and Central America and Europe. Volume 3, Europe. US Dep. Commer. NOAA Tech. Rep. 129, 240pp.
- Magalhaes H. (1948). An ecological study of snails of the genus *Busycon* at Beaufort, North Carolina. *Ecological Monographs* 18, 377-409.
- Martel A., Larrivée D.H., Klein K.R. & Himmelman J. (1986). Reproductive cycle and seasonal feeding activity of the neogastropod *Buccinum undatum*. *Marine Biology* 92, 211-221.
- Miloslavich P. & Dufresne L. (1994). Development and effect of female size on egg and juvenile production in the neogastropod *Buccinum cyaneum* from the Saguenay Fjord. *Canadian Journal of Fisheries and Aquatic Science* 51, 2866-2872.
- Power A.J. (2000). Aspects of the biology and ecology of the red whelk, *Neptunea antiqua* (Mollusca: Prosobranchia) in the Irish Sea. Dissertation, National University of Ireland, Galway.
- Power A.J., Covington E., Recicar T., Walker R.L. & Eller N. (2002a). Observations on the egg capsules and hatchlings of the knobbed whelk, *Busycon carica* (Gmelin, 1791) in coastal Georgia. *Journal of Shellfish Research* 21, 769-775.
- Power A.J., Sweeney-Reeves M., Recicar T., Thompson D. & Walker R.L. (2002b). Population biology of melongenid whelks in the intertidal zone in Wassaw Sound, Georgia. *Journal of Shellfish Research* 21, 437.
- Runham D.W. (1993). Reproductive biology of invertebrates. In : Adiyodi, K.G. & R.G.

- Adiyodi (eds.). *Asexual propagation and reproductive strategies*. Volume VI, Part A: 311-384. John Wiley & Sons.
- Santarelli L. & Gros P. (1985). Détermination de l'âge et de la croissance de *Buccinum undatum* L. (Gasteropoda: Prosobranchia) à l'aide des isotopes stables de la coquille et de l'ornementation operculaire. *Oceanologica Acta* **8**, 221-229.
- Shalack J. (2007) Movement and behavior of whelks (Family Melongenidae) in Georgia Coastal Waters. University of Georgia, School of Marine Programs, Master Thesis, Athens
- Shalack J., Power, A.J., Walker, R.L. in preparation. Intertidal whelk (Family Melongenidae) hand harvesting in coastal Georgia: Day and Night. *American Malacologist Bulletin*
- Sisson R.T. & Wood R.S. (1988). Observations on some life history aspects of a commercially exploited population of *Busycon canaliculatum* (L.) in Narragansett Bay, Rhode Island. *Journal of Shellfish Research* **7**, 176.
- Spight T.M. & Emlen J. (1976). Clutch sizes of two marine snails with a changing food supply. *Ecology* **57**, 1162-1178.
- Von Bertalanffy C. (1938). A quantitative theory of organic growth (Inquiries on growth laws, II). *Human Biology* **10**, 181-213.
- Walker R.L. (1988). Observations on intertidal whelk (*Busycon* and *Busycotypus*) populations in Wassaw Sound, Georgia. *Journal of Shellfish Research* **7**, 473-478.
- Walker R.L. & Rawson M.V. (1985) Subtidal hard clam, *Mercenaria mercenaria* (Linne), resources in coastal Georgia. *Georgia Marine Science Center Technical Report Series*, No. 85-1, 164 pp.
- Walker R.L., Power A.J., Sweeney-Reeves M., Covington E., Mitchell M. and Recicar T. (2008) Growth, migration, population structure, and sex ratio of four species of whelks (Family Melongenidae) within Wassaw Sound, Georgia. *Occasional Papers of the University of Georgia Marine Extension Service*, Vol. 1, 46 pp.
- Walker R.L., Smith J.H. and Power A.J. (2004). Movement and behavioral patterns of whelks on intertidal flats in Wassaw Sound, Georgia. *University of Georgia Marine Extension Bulletin* Number 29, 18 pp.
- Weinheimer D.A. (1982). Aspects of the biology of *Busycon carica* (Gremlin, 1791) in waters off South Carolina with emphasis on reproductive periodicity. Masters Thesis, College of Charleston, Charleston, S.C., 92p, 1982.