Age, growth rate, sexual dimorphism and fecundity of knobbed whelk Busycon carica (Gmelin, 1791) in a western mid-Atlantic lagoon system, Virginia

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AGE, GROWTH RATE, SEXUAL DIMORPHISM AND FECUNDITY OF KNOBBED WHELK *BUSYCON CARICA* (GMELIN, 1791) IN A WESTERN MID-ATLANTIC LAGOON SYSTEM, VIRGINIA

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ABSTRACT Growth, onset of sexual maturity, and sexual reversal in laboratory-reared *Busycon carica* have been examined. Animals first matured at 9 years of age. The first sign of maturity in all animals we reared was the presence of the penis. At 12.4 years of age, one of the animals laid an egg case that did not contain embryos. This animal, and all others, still retained a penis. At 13.5 years, three egg cases were laid and over half the animals had undergone sex reversal (loss of the penis). Field studies have shown that egg strings are laid in the fall on tidal and intertidal flats and over winter to hatch in the spring. Organisms that require a relatively long time to mature, that lay few eggs per spawning season, and that are vulnerable for a long time are difficult to manage for a sustained yield fishery.

KEY WORDS: *Busycon carica*, whelk, age, growth, sex reversal, sexual dimorphism, fecundity

INTRODUCTION

Busycon carica is a large, predacious gastropod that is commercially harvested along the east coast of the United States and marketed as conchs or, more properly, as whelks. Over 200,000 lbs were landed in Virginia in 1986. The frozen meats are used in salads and chowders or sold in ethnic markets as squingelli (DiCosimo 1986, Kaplan and Boyer 1992).

There are few published data on growth rates, age of onset of sexual dimorphism, or sex ratios of busyconine whelks (Frank 1969, Powell and Cummings 1985, Kraeuter et al. 1989), and no information on the age at which females become sexually mature. Although there are relatively large numbers of studies on epifaunal snails, other than growth rates, little information is available on size at age or the age of sexual maturity of long-lived predaceous infaunal gastropods. Growth information is available for *Polinices duplicatus* (Say 1822) (Edwards and Huebner 1977). Gendron (1992) reported growth rate and the size of sexually mature *Buccinum undatum* (Linne 1758), whereas Santarelli and Gros (1985) examined age structure in *B. undatum* on the basis of opercular striae. Heller (1990) compared longevity throughout the entire mollusca phylum to reveal common patterns of reproduction. This was based on data gleaned from the existing literature on the life durations of 547 species from marine, freshwater, or terrestrial habitats. Gastropods are the second most long-lived of mollusks, after bivalves. Short-lived mode of life is often correlated with: lack of external shell or an external shell that is semitransparent, dwelling in a harsh microenvironment that is exposed to high solar radiation and high temperatures, dwelling in an environment in which reproduction occurs at least once a year, and very minute size. Powell and Cummings (1985) compiled data on longevity of bivalves and gastropods and found that a higher-than-average number of long life spans coincide with periods of long-term cycles in marine communities. These cycles could affect longevity in one of two ways: cyclic phenomena that produce environmental changes beyond the species tolerance limit or cycles that might affect recruitment success and thereby exert selective pressure for longevities longer than the cycle affecting recruitment. Interest in culture of queen conch, *Strombus gigas* (Linne 1758), has provided substantial information on the growth, size-specific mortality, and ecology of that species (Wefer and Killingley 1980, Appeldorn 1988).

Magalhaes (1948) studied *B. carica* growth rate in the field near Beaufort, North Carolina, and Sisson (1972) measured growth of *Busycotypus* (*Busycon*) *canaliculatus* (Linne 1758) in Narragansett Bay, Rhode Island. The general ecology of whelks is best known from Magalhaes (1948), Peterson (1982) in North Carolina, and from Menzel and Nichy (1958), Paine (1962 and 1963), and subsequent studies by Kent (1983) in Florida. Davis and Sisson (1988) have increased the available information on whelks in Rhode Island, Massachusetts, and Georgia (Walker 1988). The work of Magalhaes (1948) remains the most complete ecological study of *B. carica* to date. She reports egg laying in Beaufort, North Carolina, from May to June and again from September to November. Numbers of egg capsules per string ranged from 9 to 156 (mean, 80), and the total numbers of egg per string ranged from 4,000 to 6,000 (Magalhaes, 1948). Ram (1977) found that an extract from the nervous system would cause mature animals to lay egg capsules.

We report on the continuation of a 14 year study of growth rates in which *B. carica* were reared in the laboratory from hatching to sexual maturity to egg laying. Kraeuter et al. (1989) examined the growth rate of a *B. carica* population in Virginia, using three methods: (1) measurement of individuals marked and recaptured in the field; (2) examination of growth lines in the operculum; and (3) measurement of laboratory-reared individuals. Most whelks that were marked and recaptured were larger than 170 mm. The smallest individual tagged and recaptured grew from 138 to 151 mm (0.098 mm/day^{-1}). Growth rates for males were not calculated because too few were obtained to make accurate estimates. Most of the males were in the 170 to 209 mm size classes. Two series of marked individuals were released into the field.

Males were 7.8% (N = 23) of the 190 individuals in the first group and 9.0% (N = 167) of the 1,859 individuals of the second group. No indications of sex reversal were noted in the field studies. Information on numbers of eggs per capsule, numbers of capsules per string, seasonal changes in gonad and nidamental gland precursor (precapsulin; see Goldsmith et al. 1978), and time of hatching for a Virginia population of *B. carica* is presented in this article.

METHODS

Sexual Maturity and Growth at Age

B. carica were hatched from egg cases collected from an intertidal sand flat behind Cedar Island, Virginia, in the winter of 1976 to 1977. Nine egg strings were returned to the Virginia Institute of Marine Science Laboratory in Wachapreague, Virginia, and maintained in a running seawater system. Seawater is drawn from a nearby channel where salinity ranges from 25 to 32 ppt, with short excursions below 20 ppt after extreme rain storms. Hatching from the strings was complete by May 1977. Attempts to keep newly hatched whelks in glass dishes, plastic trays, or shallow trays filled with sand from the intertidal flat failed because the animals continually climbed out of the water and desiccated. Some individuals were hatched in a 2.4 × 0.6 m fiberglass flowing seawater tray in which a miniature sand beach had been made. Some newly hatched individuals from several egg strings were reared inside a polypropylene filter bag that received flowing ambient seawater. When the animals reached approximately 20 mm shell length, they were transferred to the running seawater trays with beach sand substrate and supplied with small, live juvenile clams (*Mulinia lateralis, Mercenaria mercenaria,* or *Mya arenaria*). As the *B. carica* grew, larger size clams were furnished. *M. mercenaria* was the most commonly fed species and was used exclusively after the third year. Dietary supplements may have entered with the flowing seawater.

Length measurements were made on individual whelks removed from the substrate five times during the first year, then two or three times in subsequent years. Measurements were made on a minimum of 25 individuals per sampling period, until 1985, when the number was reduced to 20.

Initially, over 2,000 individuals were maintained but these were reduced to 261 through attrition and sacrifice for other studies by the fall of 1977. Mortality had reduced the total numbers being maintained to 93 after 5 years (February 1982). In the fall of 1989, the remaining whelks were divided into groups of six and placed in four sand-filled 0.6 × 0.6 m boxes with a standpipe supplied with ambient flowing seawater. The organisms were maintained in these boxes until April 1990, when a number of individuals had developed a boring sponge (*Cliona*) infestation in their shells. All individuals were given a 10 second dip in a saturated salt solution and air dried for 1 hour before being returned to flowing seawater. These same individuals were used for the sexual maturation studies.

The cultured whelks were sexed by observing the presence or absence of a penis. The observations were made in three ways. Animals were placed in a shallow plastic tray containing 1 to 3 cm of flowing ambient seawater until they were firmly affixed to the bottom (about 1 hour). The penis, a C-shaped organ, could be observed by gently tilting the shell clockwise. In another method, the whelks' shells were attached dorsal side down and held in place with a small ball of clay or with malleable lead wire. The tray was left in a partially darkened room for 0.5 to 2 hours, allowing time for the animals to attempt to right themselves by extending their foot. The extension of the foot exposed the penal area. A third method was sometimes used for older intractable specimens. With a 1 ml syringe and a 23 gauge needle, 0.4 ml of 2 mM serotonin (5-hydroxytryptamine, creatinine sulfate complex; Sigma Chemical Co., St. Louis, MO) was injected into the foot just posterior to the operculum. The animals reacted within 2 hours by extending the foot and rolling the operculum away from the aperture, exposing the phallus.

Gonadal Analysis

About 10 specimens were randomly collected in 1976 to 1977 at approximately 11 monthly intervals (Σ N = 105) from the study site behind Cedar Island, returned to the laboratory, and frozen. Shell length and width were measured before the removal of the flesh. The animal was extracted from the shell, sexed (presence or absence of eggs or a penis), and weighed to the nearest 0.1 g. The tissue was dissected into four fractions: meat, viscera, nidamental gland (females only), and gonad, and each was weighed to the nearest 0.1 g.

Egg Strings and Egg Capsules

Several studies examined the timing of egg laying, numbers of capsules per egg string, and time and number of egg hatching. Egg laying and paired individuals (copulation) were recorded during mark recapture field studies (approximately monthly during 1976 and 1977). Numbers of egg capsules per egg string were recorded in the field, the location was noted, and the string was marked. These were followed on subsequent visits until hatching was recorded.

To determine hatching success, the shoreline was examined for old egg strings in the fall and winter of 1976 and these were removed. Any egg string that was found on the beach in the spring (late March to May 1977) was returned to the laboratory, and numbers of juveniles per capsule were determined. These data formed the basis for an estimate of the numbers of hatchlings per string and the percent mortality. For these estimates, the total number of eggs per string was estimated on the basis of the largest numbers of juveniles found in capsules from the midportion of the egg string.

A number of strings were returned to the laboratory for more detailed study of the number of embryos per capsule and the number of capsules per string. The number of capsules before the first egg-bearing capsule (anchoring part of string) was determined from these strings. Capsules were randomly removed from the length of the string and measured (height, diameter, and volume). The number of embryos per capsule was determined by removing the top of the capsule and counting the eggs or developing embryos.

Hatching studies were performed on capsules removed from the same strings as those used to determine the distribution of the number of embryos per capsule. Ten capsules from each of four egg strings were placed in baths containing water of three temperature regimens: cold (2 to 5°C) ambient (10 to 15°C), and warm (20 to 25°C). Capsules were examined daily, and the day of hatching for various capsules was recorded.

RESULTS

Sexual Maturity and Growth at Age

Growth rate for individuals maintained in the laboratory was highest in the first year, when the animals grew from 4 to 36.5 mm shell length. The average size after 10 years of growth was 144 mm, and by 14 years, the average size was 168.7 mm shell length (Fig. 1). All 20 cultured individuals in 1986 at 9 years of age were considered to be males, because 9 had a relatively large, well-developed penis and 11 had a smaller penis. By October 1987, all 20 had either a large (10) or a moderately developed (10) penis, and by April 1989, all had a well-developed penis.

On September 25, 1989, 12 years 5 months after hatching (ca. 13 years after eggs were laid), one whelk laid an egg case, but it contained no embryos. The animal producing the egg case was 172 mm long and 95 mm wide and had a 25 mm long penis in April 1989. By April 6, 1990, 5 animals were female with the penis reduced to a rounded protuberance, 10 were males, and 5 had died, including the original female.

By May 20, 1991, 9 of the remaining 15 individuals were females. Rounded protuberances remained, but the individuals that appeared to have most recently become female had a small, vestigial, flap-like penis. This flap was approximately 5 to 7 mm across the widest point. *Busycon* under 166 mm length had a larger, C-shaped penis and were considered to be males.

In September 1991, 3 of the remaining 14 *Busycon* laid egg cases containing viable embryos. Five whelks were now presumptive males (under 166 mm), 7 were definite females with round, button-like protuberances, and 2 were apparently transitional with neither a flap, a well-shaped button, or a C-shaped phallus.

The three egg cases were maintained in running seawater from September to April, while temperatures ranged from 9.2 to 14.5°C and salinity averaged 30 ppt. During the first 3 weeks in April most of the *B. carica* hatched from the egg cases. Some of the early hatchlings climbed out of the tank and died. The others were removed from the tray and grown in the laboratory for nearly 60 days, during which they approximately doubled in size before being released in early June on the sand flats where the egg strings were collected in 1976.

Gonadal Analysis

Of the 105 individuals used for gonadal analysis, only 8 were males (sex ratio = 0.082), so males were not included in the analysis. Females were collected on June 30, July 29, August 26, October 10, and November 11, 1976, and on January 11, 1977, and a second series was collected on April 15, May 11, June 12, July 7, and August 8, 1979. The range in gonadal weight was 0.3 to 27.4 g. Average gonadal wet weight ranged from 4.1 to 12.2 g and average nidamental gland weight ranged from 21.9 to 52.1 g. The percentage of gonad or nidamental gland to total weight and meat weight are given in Table 1. The data indicate a decrease in these percentages in October, the time of maximum observed egg laying in the field. Although the data suggest a spring spawning, no such spawning was seen in over 5 years of field observations.

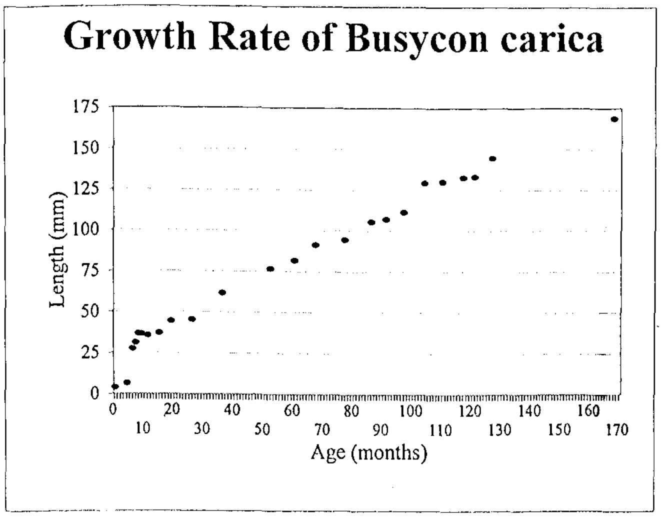

Figure 1. Growth rate of *B. carica*.

Egg Strings and Egg Capsules

The only months in which copulating individuals were observed on the intertidal flats were June and July. Eggs were laid in the field from mid-August to November, with most egg laying from mid-September to mid-October. The largest number of egg strings found on the intertidal flat was 66 in 1976. Capsules remained closed until spring, and hatching (on the basis of open capsules) was observed from mid-March through early May. A few of the earliest laid strings (late August) began hatching by the end of October. In general, strings were present on the intertidal flat throughout the winter, but by April or May, most had disappeared. Some of these egg strings washed ashore in those 2 months, and juveniles that had not hatched were dead.

Capsules per string ranged from 42 to 121. The average number of capsules above the anchor point per string was 99.7 (standard error [SE], 4.68; N = 16) in the winter of 1977 to 1978, 89.4 (SE, 2.44; N = 66) in the winter of 1978 to 1979, and 92.4 ± 4.93 in the spring of 1979. The number of capsules in the anchor portion of the string ranged from 8 to 22 (mean, 13.1; SE, 1.21; N = 16).

On the basis of the random selection of capsules along the length of four strings, the average number of eggs per capsule is less in the first and last 10% of egg-bearing capsules (Table 2). Seventeen egg strings were found washed up on the beach in April to May 1976. These cases were covered with fouling organisms (algae, *Illyanassa* eggs, *Corophium* tubes) and had apparently broken off from their anchor. One case had not hatched (escape plugs were intact); development had not occurred. The percent hatch (hatching success) ranged from 18 to 86% (Table 3). Thirteen of the 16 strings analyzed held hatching rates of more than 60%. Fouling by corophid amphipods or mud snail (*Illyanassa obtusata*) egg capsules may block the escape of whelks in the field.

Laboratory studies on hatching yielded a positive correlation of hatching with temperature. With increasing temperatures, hatching times were reduced: at 2 to 5°C, no hatching occurred; at 10 to 15°C, hatching began at 65 to 78 days, and at 20 to 25°C, it began at 22 to 30 days. One string was excluded because of a drop in water temperatures.

DISCUSSION

Sexual Maturity and Growth at Age

The growth rates and timing of the sex changes in these laboratory studies may not mimic those from the natural habitat; however, the whelks always had a surplus of clams of varied sizes, so food should not have been a limiting factor. The temperatures and salinities were typical of those in the field because of the continuously supplied ambient seawater. The containers in which the whelks were grown, although relatively uncrowded, would certainly not compare with the low-density habitats found in nature.

TABLE 1.

Seasonal gonadal indices (%) for female *B. carica* in Virginia. Indices are all wet weight

	Month and day										
Item measured[a]	J 30	J 29	A 26	O 10	N 11	J 11	A 15	M 11	J 12	J 7	A 8
G/TW	3.1	2.4	2.7	1.4	3.0	2.0	3.1	1.1	1.8	2.5	2.2
N/TW	12.9	10.3	12.3	8.1	12.7	11.3	11.1	7.3	8.6	12.5	11.2
G + N/TW	15.9	12.4	13.3	9.5	15.7	13.3	14.2	8.4	10.4	15.0	13.4
G/N	24.3	23.8	21.7	17.4	23.6	18.0	28.3	15.1	20.9	20.3	19.4
G + N/MW	22.1	16.8	20.5	12.8	21.7	18.2	20.6	11.3	15.1	22.0	19.1
G/MW	4.4	3.2	3.7	1.9	4.1	2.8	4.5	1.8	2.6	3.7	2.8
N/MW	17.7	13.6	16.8	10.9	17.6	15.4	16.0	9.5	12.5	18.3	16.4

[a] G, gonad; N, nidamental gland; TW, total weight; MW, meat weight.

Gonadal Analysis

The sex ratio (0.082) from this study is within the range 7.8 to 9.0% reported by Kraeuter et al. (1989) for whelks from this location and is almost identical to that reported for intertidal populations of *B. carica* in Georgia (Walker 1988). Magalhaes (1948) suggests that eggs are laid in the spring both at Beaufort, North Carolina, and in Connecticut, but her data from farther north are based on "fresh" capsules and not observed egg laying. On the basis of gonadal and nidamental gland data and the small amount of information available from the males, there appear to be two spawning seasons in Virginia. In over 5 years of field study, however, we did not find eggs being laid on an intertidal flat during the spring, although spawning might occur in deeper water.

Ram (1977) used categories of gonadal weights ranging from 0.0 to 0.9 g to >3.6 g. The gonads of his animals were significantly smaller than those on our animals; his largest class is smaller than the average weight in any month in our study and far less than our maximum of 27.4 g. It does not seem plausible that the large percent body weight reduction from egg laying could be recovered within a month, as our data suggest. The rapid recovery of the ratios after May and October could be the result of cohorts of snails moving on and off the intertidal flat. This rapid movement is consistent with mark-recapture studies done on animals from this same location (unpublished data). Similar rapid emigrations of marked snails were reported by Weil and Laughlin (1984) for tagged queen conchs on subtidal tropical grass flats. This explanation is further supported by the evidence that there was never a sample in which all females had spent gonads. It is possible that, in addition to fairly rapid immigration and emigration, not all of the females lay eggs every year.

TABLE 2.

Numbers of *B. carica* eggs per capsule along the length of strings collected from Cedar Island, Virginia, December 1976 to January 1977

Percent distance along string	No. of capsules sampled	Average no. of eggs	SE
0–10	6	20.0	8.53
11–30	5	37.4	5.98
31–60	8	51.5	4.20
61–90	9	37.5	3.64
91–100	5	10.2	3.08

Egg Strings and Egg Capsules

Magalhaes (1948) reported finding copulating individuals of *Busycon* in March, June, August, and September, but her article does not distinguish between *B. carica* and *B. canaliculata*. Kent (1983) found copulating *Busycon spiratum* and *Busycon contrarium* in October and January on tidal flats in northwest Florida. Walker (1988) found whelks mating in the spring and fall on Georgia intertidal flats. Our data fit the general pattern that copulation may be seasonal, but not necessarily at the same time as egg laying.

The range in numbers of egg capsules above the anchor from Beaufort, North Carolina (9 to 156) (Magalhaes 1948) spans the number found in Virginia. The mean number of capsules in North Carolina (80) is slightly less than the average number produced in 2 years on Cedar Island, VA. The numbers of individuals potentially hatching from a single string appear to range up to 5,000 to 6,000 in both North Carolina and Virginia, although 2,000 to 3,000 would be more typical.

The timing of egg laying (September) in the laboratory-reared animals matches that which we have observed in field studies on intertidal flats. Hatching in the laboratory in spring also mirrors what we have observed in both the field and from controlled-temperature laboratory studies. Egg strings washing ashore during winter storms or, more typically, during April and May, were destroyed along with unhatched juveniles. The mechanism that causes the egg strings to weaken and wash ashore around hatching time is not known.

Several factors of importance to management are apparent from this study. Clearly, the length of time required for maturity has far-reaching implications. The presence of a penis does not unambiguously define whether a particular individual is male or female, and thus, attempting to regulate harvests on the basis of sex or sex ratios would be difficult. The length of time before females ap-

TABLE 3.

Egg cases of *B. carica* washed up on the bay beach of Cedar Island, Virginia, in April and May 1977

Category	Range	No. of srings	Average	SE
Whelks/string	1,945–5,508	16	3770	206.50
Whelks/capsule	30–51	16	41.79	1.54
% Hatched	18–86	16		

peared in the cohort was very long (12 years), and their length (172 mm) was large. Harvest selection by size would probably be specific for females. Egg cases remain vulnerable to storms or other forms of bottom disturbance for 7 months before they hatch. This long development further restricts the amount of time an area could be exploited by dredges or other gear that disrupt the bottom. Most egg cases were concentrated in a relatively small portion of the flat. Hatching was controlled by temperature, and some factor also positively associated with temperature allows the egg strings to weaken so that they are more apt to wash away. Although we did not make estimates of posthatch mortality, the rapid loss of individuals in the laboratory suggests that field mortality of small individuals is significant. We were never able to discover small individuals in the field. Laboratory observations suggest that they remain buried most of the time (as do the adults).

This species, which requires a long time to mature, lays relatively few eggs per spawning season, has a low survival rate of its young, and appears to be extremely vulnerable to harvest pressure. Management for this resource for an optimal sustainable yield will be difficult.

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