Sex Differences in Growth of Channeled Whelks from Buzzards Bay, Massachusetts, during One or Two Years at Liberty

Authors: Stevens, Bradley G., and Peemoeller, Bhae-Jin

Source: Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science, 8(8) : 462-475

Published By: American Fisheries Society

URL: https://doi.org/10.1080/19425120.2016.1194918

Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science 8:462–475, 2016
Published with license by the American Fisheries Society
ISSN: 1942-5120 online
DOI: 10.1080/19425120.2016.1194918

ARTICLE

Sex Differences in Growth of Channeled Whelks from Buzzards Bay, Massachusetts, during One or Two Years at Liberty

Bradley G. Stevens* **and Bhae-Jin Peemoeller**
Living Marine Resources Cooperative Science Center, University of Maryland Eastern Shore, 1 College Backbone Road, Princess Anne, Maryland 21853, USA

Abstract
With the southern New England lobster fishery in distress, lobster fishers have focused more effort toward harvesting channeled whelks *Busycotypus canaliculatus*. Melongenid whelks generally grow slowly and mature late in life—characteristics that can make them vulnerable to overfishing as exploitation increases. However, minimal research has been conducted on the life history and growth rates of channeled whelks. We captured, marked, and released more than 8,700 whelks in Buzzards Bay, Massachusetts, during 2010 and 2011; 314 of the marked individuals were recovered after 1 or 2 years at liberty. Whelks that were recaptured in 2011 were measured and rereleased without determining sex, whereas whelks that were recovered in 2012 were dissected for sex determination. The unsexed animals were later classified by linear discriminant analysis using growth and morphometric variables. For both male and female whelks, growth increments decreased significantly with increasing size. Size-specific growth rates were significantly greater for females than for males, and females reached larger maximum sizes than males. Furthermore, rates of growth in shell length declined significantly with increasing time at liberty, whereas growth in shell width did not; this result may have been due to differential rates of shell damage versus repair. Increased fishing pressure on whelks—combined with their slow growth rates and inability to reproduce before being harvested—can easily constrain the long-term viability of the channeled whelk fishery in Massachusetts. Therefore, current whelk fishery management practices should be revised.

Whelks of the family Melongenidae have historically been the target of low-volume, low-value fisheries; one of these species is the channeled whelk *Busycotypus canaliculatus*, which belongs to the subfamily Busyconinae (Edwards and Harasewych 1988). Most of the fishing for channeled whelks in Massachusetts is conducted by fishers who also fish part-time for lobster, so whelk fishing typically constitutes only part of their economic activity. Channeled whelk landings in Massachusetts were less than 500 metric tons prior to 2000 but increased to about 1,400 metric tons in 2006 and have remained high since then (Glenn and Wilcox 2012). Increased effort after 2000 has led to decreases in the size frequency and average size of whelks in Massachusetts (Davis and Sisson 1988) and Delaware Bay (Bruce 2005). Since 2010, growing markets for live whelks have increased the ex-vessel value substantially. In 2013, the Atlantic States Marine Fisheries Commission enacted effort reductions for the southern

Subject editor: Debra J. Murie, University of Florida, Gainesville

*Corresponding author: bgstevens@umes.edu
Received April 3, 2015; accepted May 23, 2016

New England lobster fishery (ASMFC 2013), which has generated a shift in effort from lobster fishing to whelk fishing. Increased effort in the whelk fishery may lead to long-term population declines unless the fishery is managed to ensure sustainability. In 2010 (when we began this study), the minimum size limit for channeled whelks in Massachusetts was 69.9 mm (2.75 in) maximum shell width (MSW). However, this limit was set to accommodate industry preferences and market acceptability rather than biological criteria. Because information on whelk reproduction, size at maturity, and growth rates is limited, it is difficult to determine whether the minimum size limit is appropriate to ensure sustainability of the whelk fishery.

At least six species of *Busycon* whelk and three species of *Busycotypus* whelk exist along the U.S. East Coast (Turgeon et al. 1998). Whelks are typically slow growing and exhibit late maturity. There have been numerous studies on the biology of the knobbed whelk *Busycon carica* (Magalhaes 1948; Stevens 1976; Peterson 1982; Kent 1983; Edwards 1988; Walker 1988; Kraeuter et al. 1989; Castagna and Kraeuter 1994; Power et al. 2002, 2009; Walker et al. 2007; Avise et al. 2010), but remarkably few studies have focused on the channeled whelk (Davis and Sisson 1988; Peemoeller and Stevens 2013). Most of these studies have addressed the biology, demographics, or reproduction of whelks, but few have studied long-term growth. Growth of marked knobbed whelks was studied near Beaufort, North Carolina, by Magalhaes (1948) and near Wachapreague, Virginia, by Kraeuter et al. (1989). Results of both studies demonstrated that growth increased over time, declined with whelk size, and was highly episodic, with some individuals showing no growth for up to 2.5 years. We (Peemoeller and Stevens 2013) previously studied the reproductive biology, size, and age at maturity of channeled whelks in Buzzards Bay, Massachusetts, during 2010–2011 via dissection and histological examination of 473 individuals. Males had a maximum shell length (SL) of 175 mm, reached 50% sexual maturity (SM_{50}) at 115.5 mm SL or 6.9 years of age, and entered the fishery at 7.5 years of age. Female whelks had a maximum SL of 214.2 mm and reached SM_{50} at 155.3 mm SL or 8.6 years of age; however, females entered the fishery at 6.3 years of age, or approximately 2 years before attaining sexual maturity. These findings suggested that female whelks grew faster than males.

The goals of the present study were to (1) estimate growth rates in SL and shell width of channeled whelks over 1–2 years at liberty in their natural environment, and (2) determine how growth rates changed with whelk size. Furthermore, we desired to determine whether annual growth differed between sexes or during two consecutive years. For this purpose, we caught, measured, marked, and released more than 8,700 channeled whelks in Buzzards Bay, Massachusetts, during 2010 and 2011 and recovered 314 of them in 2011 and 2012 after 1–2 years of growth.

METHODS

Sampling.—Sampling was conducted in Buzzards Bay, a large, semi-enclosed estuary with depths of 10–15 m. Channeled whelks were captured in August 2010 and July 2011 with commercial wooden or wire-mesh conch traps that were set from a 13-m lobster boat and baited with Atlantic horseshoe crabs *Limulus polyphemus* or crushed green crabs *Carcinus maenas*. Traps were generally 50 × 50 × 30 cm and were set in strings of 10 or 20 traps at 10–15-m depths at 10–12 different sites in each year to maximize catches. Traps were allowed to soak for 1 week and then were retrieved weekly over a 4-week period in each year. Sites sampled in 2010 were mostly located in eastern Buzzards Bay, whereas those sampled in 2011 were mostly in the western portion of the bay (see Peemoeller and Stevens 2013 for descriptions of the ~30 capture locations). Whelks from different sites were pooled; therefore, water temperatures at individual sites were not measured, but we did examine seawater temperature data from National Oceanic and Atmospheric Administration (NOAA) data buoy station BZBM3 located at the NOAA Northeast Fisheries Science Center dock in Woods Hole, Massachusetts (Figure 1; NOAA station 8447930; www.ndbc.noaa.gov/station_history.php?station=bzbm3). During 2004–2014, water temperature averaged 22.0°C in July and 22.6°C in August, and salinity was almost uniformly 30‰ (Turner et al. 2009).

After capture, whelks were taken to a seawater laboratory in New Bedford, Massachusetts (School of Marine Science and Technology, University of Massachusetts Dartmouth) and were placed in shallow tanks with flow-through seawater at ambient temperature. Whelks were not sexed prior to measurement due to the difficulty in partially removing them from their shells without damaging them and the time required to do so. Whole wet weight (Wt, nearest 0.1 g; including shell and tissue) of each whelk was measured with an electronic balance. Using electronic calipers, the SL (nearest 0.1 mm) was measured as the straight-line distance from the apex (top whorl or protoconch) of the shell to the tip of the siphonal canal. The shell width (nearest 0.1 mm) was measured as the maximum distance across the upper edge of the largest whorl in a straight line across the apex; this measurement was defined as lip width (LW) because the edge (lip) of the shell was used to anchor the calipers. Maximum shell width (MSW) was also measured for 176 whelks because it is used by fishers and managers to determine minimum size limits; MSW for this subset of whelks ranged from 60 to 118 mm (2.35–4.66 in). However, channeled whelks have an asymmetrical shell structure that prevents accurate or repeatable width measurements; therefore, we used LW as our primary width measurement because it is more precise than MSW (see Peemoeller and Stevens 2013) and is similar to the “width without spines” measurement

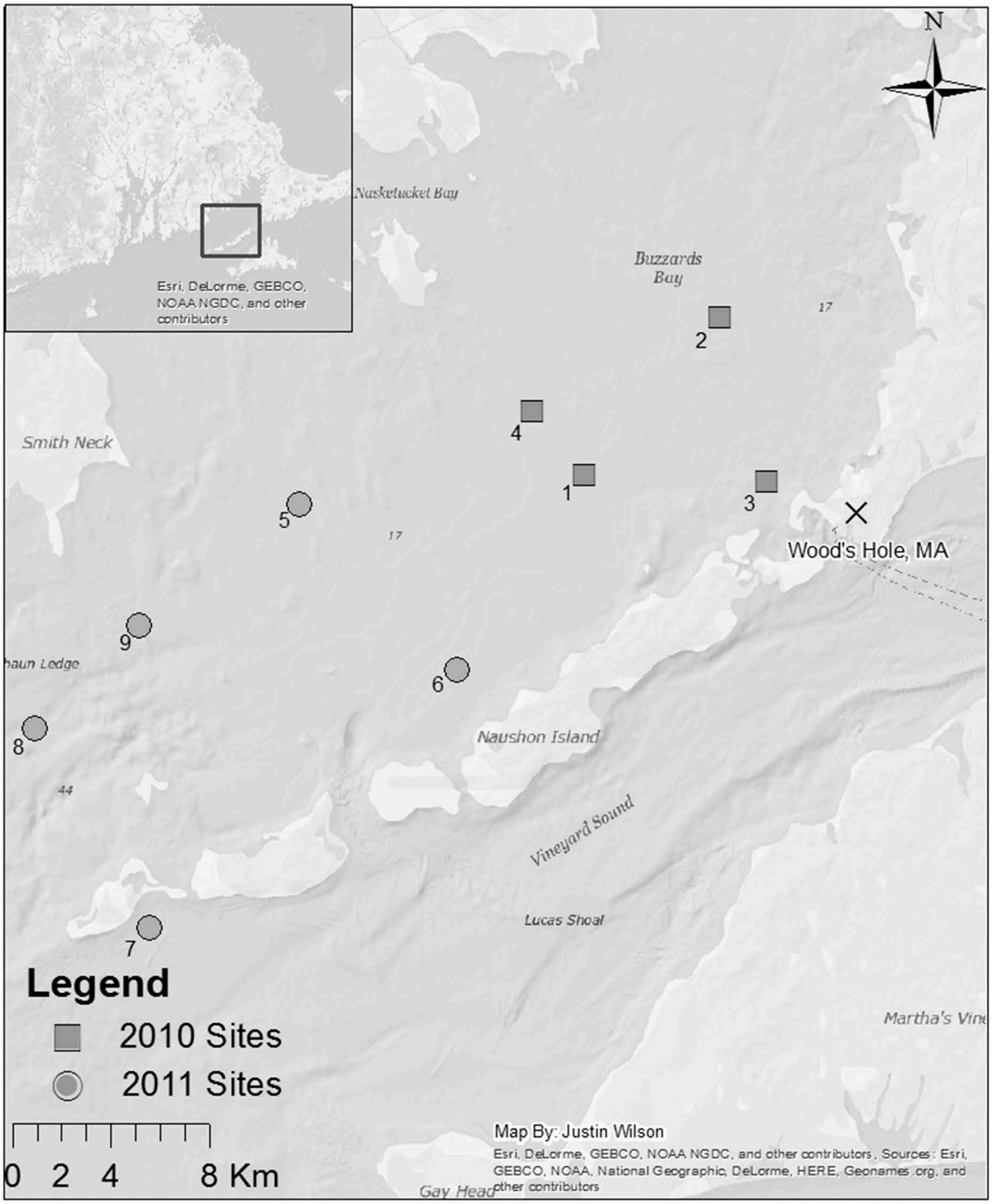

FIGURE 1. Map of Buzzards Bay, Massachusetts, showing sites where marked channeled whelks were released in 2010 (squares, 1–4) and 2011 (circles, 5–9). Whelks were recaptured at the same sites after being at liberty for either 1 year (sites 1–9) or 2 years (sites 1–4).

used by Magalhaes (1948) to evaluate the size of knobbed whelks.

Prior to marking, all whelks were cleaned with a rotating wire brush to remove the periostracum and the accumulated dirt from the outermost whorl. A rotary tool was then used to mark numbers on the top of the whorl between the suture line and the shoulder, as described by Magalhaes (1948). After the shell was cleaned with acetone, numbers were filled in with permanent marker, covered with two-part epoxy, and allowed to dry for 2–3 h before the whelks were returned to the tanks. Whelks that were marked in 2011 also received a small, numbered plastic tag that was glued onto the shell. Whelks were released within 1 week of capture at sites 1–4 in August 2010 and at sites 5–8 in July 2011 (Table 1; Figure 1). In addition, our charter boat captain occasionally caught marked whelks during the regular fishing season and released them at a separate location, which we designated as site 9.

Initially, we recovered whelks from fishers who had caught them during regular fishing activities; however, upon examination, we found that virtually all such whelks were shorter than originally recorded, which implied that their shells had been damaged. Fishers generally pack as many whelks as possible into deck totes, and stack them on top of each other, causing shell breakage (B.G.S., personal observation). Thus, for this study, we only used whelks that we recovered ourselves by using the same vessel and traps that were used for capture, and we placed the whelks in single layers within stacked deck totes. Whelks were recovered in October and November 2011 (from sites 1–4; Figure 1) and in November 2012 (from all sites) by setting strings of 10 traps at each of the release sites and letting them soak for 4–7 d. Thus, we defined four recapture groups (labeled by year of release and years at liberty). Groups 10-1a and 10-1b included whelks that were released in August 2010 and recaptured in October 2011 or November 2011, respectively, with a nominal time at liberty (TaL) of 1 year (actually 1.15–1.21 years) after release. None of the whelks in these groups was sexed because we released them all again at sites 1–4, hoping that we would recover some individuals more than once so as to obtain sequential annual growth measurements. Group 11-1 included whelks that were released in July 2011 and recaptured in November 2012, with a nominal TaL of 1 year (range = 1.25–1.31 years). Group 10-2 included whelks that were released in August 2010 and recaptured in November 2012, with a nominal TaL of 2 years (range = 2.20–2.26 years). All whelks that were recovered in 2012 (groups 10-2 and 11-1) were sexed by cracking the shells to determine the presence or absence of a penis or nidamental gland; none of those whelks was rereleased. All of the recovered whelks were remeasured for SL and LW, and their growth increments in SL (L_{inc}) or LW (W_{inc}) were calculated.

Data analysis.—Mean SLs of channeled whelks captured in 2010 and 2011 were compared by using *t*-tests; a nonparametric Kruskal–Wallis (K–W) test was used to compare cumulative length frequencies between years. Based on all measured whelks, we calculated regression equations for LW versus SL and for $\log_{10}$(Wt) versus $\log_{10}$(SL). Regression equations for LW versus MSW and vice versa were also calculated for conversion to conventional measurements. Mean sizes of male and female whelks that were caught and released in 2010 and 2011 were compared by use of *t*-tests, and values are expressed as means ± SD. Growth increments (L_{inc} and W_{inc}) for recaptured males and females were regressed separately against the original measurements (SL and LW, respectively) for the nominal TaL of 1 or 2 years. Covariance analysis was conducted to determine whether the intercepts and slopes of the regression equations for L_{inc} and W_{inc} differed between the sexes or based on TaL.

Because of large, obvious differences in growth rates between sexes, linear discriminant analysis (LDA) was conducted in order to utilize the unsexed whelks that were recovered during 2011. Three training sets using only known-sex whelks (from groups 11-1 and 10-2) were tested, including (1) all whelks of known sex, (2) only whelks with positive values for both L_{inc} and W_{inc}, and (3) only whelks with positive values for either L_{inc} or W_{inc}. Four variables measured after recapture (SL, LW, L_{inc}, and W_{inc}) were used, and all whelks were reclassified using the resulting discriminant equations. All combinations of the three training sets and four variables were tested to determine which combination provided the greatest discriminatory ability with the fewest variables. Unsexed whelks were then classified as either male or female by using the LDA results, and a combined data set was constructed with whelks of known sex and predicted sex. Using the combined data set, we reanalyzed the growth of whelks in terms of both L_{inc} and W_{inc}. Covariance analysis was conducted to determine whether the regression slopes and intercepts differed between known-sex whelks and individuals whose sex was predicted. Data analysis was conducted in R software (R Development Core Team 2011). Values are reported as means ± SD or SE as noted.

RESULTS

Seawater temperatures at Woods Hole (NOAA station 8447930) averaged 22.2 ± 0.7°C (mean ± SE) in August 2010 and 22.2 ± 0.6°C in July 2011 and were not significantly different. However, mean August temperature was 1.2°C greater in 2011 than in 2010. These temperatures are close to the average values at NOAA station 8447930 for July (22.0°C) and August (22.6°C) during 2004–2014, but we were unable to make inferences about temperature effects on growth due to differences in the locations and sex ratios of samples.

In total, 10,628 channeled whelks were caught in 2010 and 2011; 8,999 were measured and weighed, and 8,717 of those individuals were marked and released (Table 1). Shell lengths of all whelks captured in 2010 and 2011 were aggregated in 5-mm intervals for length frequency analysis (Figure 2). There was a significant difference in length frequency between years: more large whelks were caught in 2011 than in 2010 (K–W test: χ^2 = 137.1, P < 0.0001). Whelks that were captured and released in 2011 were significantly larger (142.1 ± 20.8 mm SL) than those that were captured and released in 2010 (137.2 ± 13.7 mm SL; t = 13.48, P < 0.0001). The LW–SL and $\log_{10}$(Wt)–$\log_{10}$ (SL) regressions were significant for all captured whelks,

TABLE 1. Dates, numbers, locations (see Figure 1), and time at liberty (TaL; mean ± SD) for channeled whelks that were caught, released, and recaptured in Buzzards Bay, Massachusetts, during 2010–2012, and summaries for all recapture groups.

Capture date	Number caught	Release date	Release site	Release site latitude	Release site longitude	Number released	Recapture group	Recapture date	Number recaptured	TaL (years)
Jul 30, 2010	979	Aug 4, 2010	1	41°35.215′N	70°45.730′W	867	10-1a	Oct 21, 2011	25	1.21
							10-1b	Nov 26, 2011	26	1.31
							10-2	Nov 5, 2012	10	2.26
Aug 4, 2010	1,251	Aug 13, 2010	2	41°34.800′N	70°42.783′W	1,005	10-1a	Oct 21, 2011	3	1.19
							10-1b	Nov 26, 2011	40	1.29
							10-2	Nov 5, 2012	13	2.23
Aug 13, 2010	1,340	Aug 20, 2010	3	41°32.117′N	70°41.733′W	989	10-1a	Oct 21, 2011	18	1.17
							10-1b	Nov 26, 2011	1	1.27
							10-2	Nov 5, 2012	0	2.21
Aug 20, 2010	1,392	Aug 26, 2010	4	41°33.267′N	70°46.867′W	1,048	10-1a	Nov 26, 2011	20	1.25
							10-1b	Nov 5, 2012	47	2.20
							10-2	Nov 5, 2012	2	2.20
Jul 8, 2011	1,385	Jul 15, 2011	5	41°31.733′N	70°52.000′W	1,175	11-1	Nov 5, 2012	11	1.31
Jul 15, 2011	1,468	Jul 22, 2011	6	41°29.000′N	70°48.533′W	1,342	11-1	Nov 5, 2012	4	1.29
Jul 22, 2011	1,535	Jul 29, 2011	7	41°24.783′N	70°55.267′W	1,407	11-1	Nov 5, 2012	74	1.27
Jul 29, 2011	1,278	Aug 5, 2011	8	41°28.050′N	70°57.767′W	884	11-1	Nov 5, 2012	15	1.25
Various (2011)	66	Various (2011)	9	41°29.733′N	70°55.483′W	66	11-1	Nov 5, 2012	2	0.94
							10-1a	Oct 21, 2011	66	1.18 ± 0.025
							10-1b	Nov 26, 2011	111	1.28 ± 0.023
							10-2	Nov 5, 2012	29	2.28 ± 0.029
							11-1	Nov 5, 2012	108	1.28 ± 0.015
Total	10,628					8,717			314	

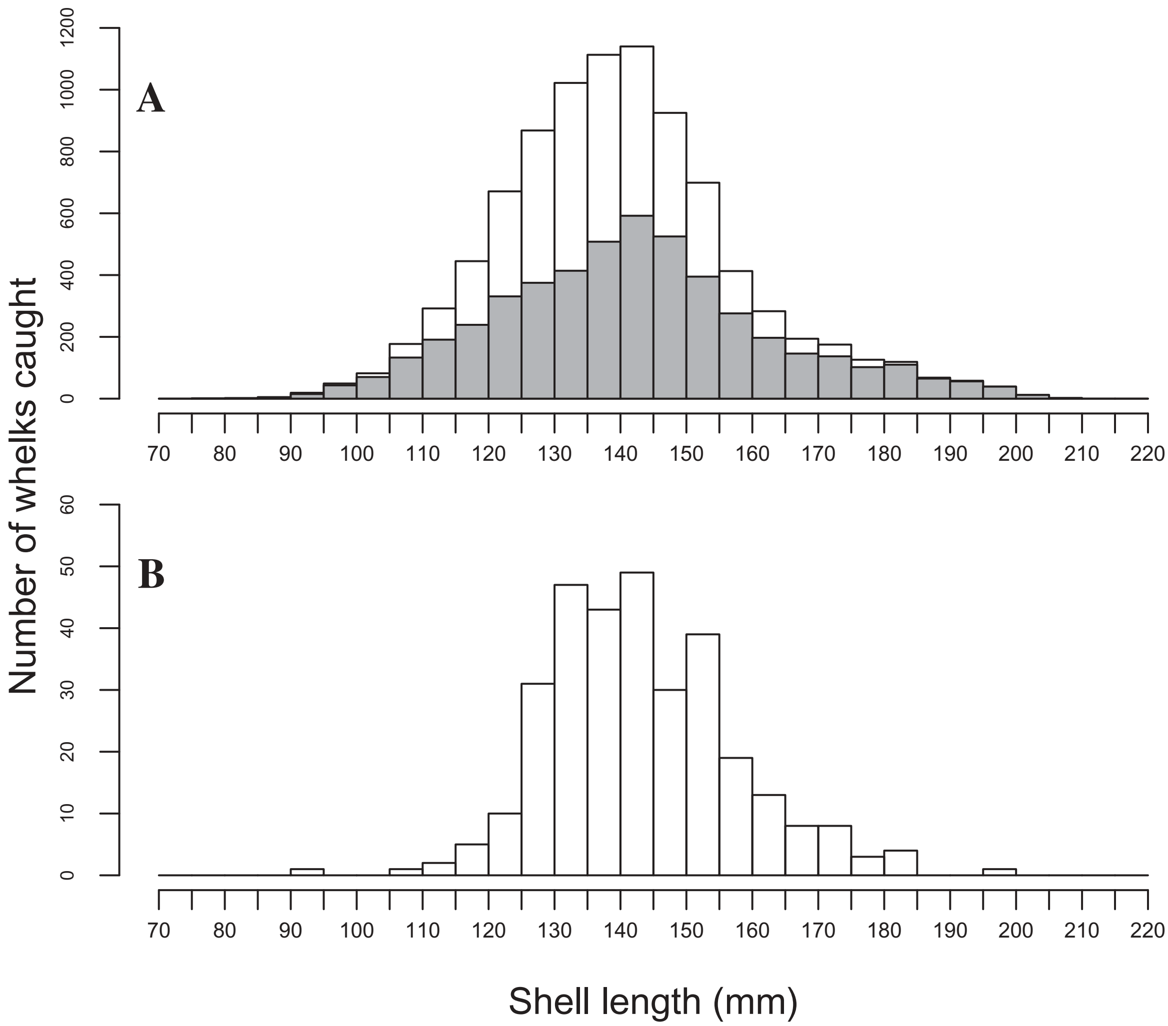

FIGURE 2. Shell length frequencies (in 5-mm intervals) for channeled whelks captured from Buzzards Bay, Massachusetts, in 2010–2012: **(A)** all whelks captured in 2010 (unshaded bars) or 2011 (gray-shaded bars); and **(B)** marked whelks that were recaptured in 2011 and 2012.

and the LW–MSW and SL–MSW regressions were significant for the subset of 176 whelks from which MSW measurements were obtained (Figure 3; Table 2).

Overall, 314 usable (i.e., not visibly damaged) whelks (3.6% of marked individuals) were recaptured 1–2 years after their initial release (Table 1). Shell length frequencies of recaptured whelks were similar to those of captured whelks but were truncated below 125 mm (Figure 2). Whelks were at liberty from 0.94 to 2.26 years; the mean TaL was 1.18 ± 0.02 years for group 10-1a and 2.28 ± 0.03 years for group 10-2 (Table 1). Length increments were less than or equal to 0 mm for 26 recaptured whelks (Figure 4A), and 37 whelks had W_{inc} values that were less than or equal to 0 mm; those whelks were considered to have been damaged, so they were excluded from initial growth analyses. Groups 10-1a and 10-1b (recaptured in October 2011 and November 2011, respectively) were not significantly different in L_{inc} (t = –1.452, df = 162, P = 0.1485) or W_{inc} (t = –0.400, df = 160, P = 0.6895), indicating that little shell growth occurred at that time of year. When analyzed separately by sex, there was no difference in L_{inc} between those two dates for females ($F_{3,\ 20}$ = 0.613, P = 0.608) or males ($F_{3,\ 20}$ = 0.340, P = 0.566). Therefore, all whelks that were released in 2010 and recaptured in 2011 (groups 10-1a and 10-1b) were combined for further analysis as “group 10-1.”

Initial SLs of known-sex whelks that were recovered after 1 year at liberty were 143.3 ± 6.5 mm (mean ± SE) for females and 130.3 ± 1.7 mm for males. The L_{inc} values were 19.0 ± 3.2 mm for female whelks and 8.9 ± 0.7 mm for males (Table 3). However, mean growth cannot be compared directly between sexes because it was highly dependent on the size at release.

Regression of positive L_{inc} values (L_{inc} > 0 mm) versus SL at release showed that growth was much greater for female whelks than for males (Figure 4B). Additionally, all regressions of L_{inc} or W_{inc} versus SL or LW at release were

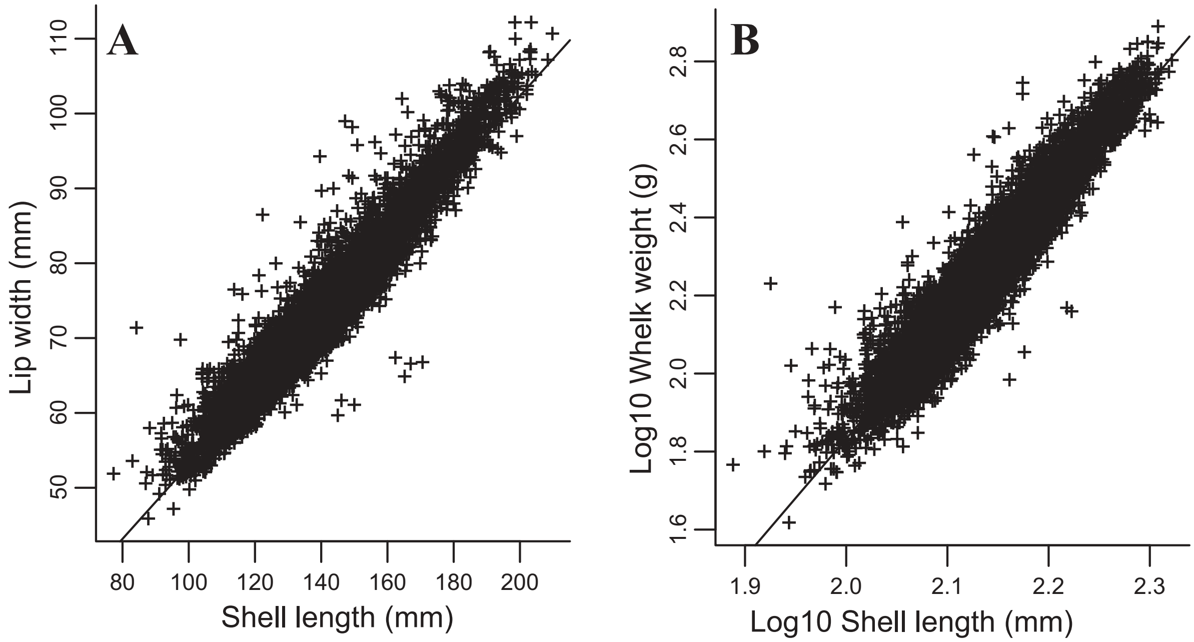

FIGURE 3. Regressions of size measurements for channeled whelks captured from Buzzards Bay during 2010–2011: **(A)** lip width versus shell length; and **(B)** $\log_{10}$(whole wet weight) versus $\log_{10}$(shell length). Regression equations are given in Table 2.

significantly negative (Table 2). Covariance analysis demonstrated that the intercepts and slopes for the L_{inc}–SL regression and the W_{inc}–LW regression were significantly different from zero for females, but the incremental differences between slopes for males and females were not significant (Figure 4; Table 4). Predicted maximum SL (the size at which 1 year growth should equal 0 mm) was calculated as –intercept/slope (from Table 2) and was 170.4 mm for male whelks and 196.7 mm for females; predicted maximum LW was calculated as 81.9 mm for males and 103.7 mm for females. The largest marked male whelk recovered was 172.6 mm SL, and the largest marked female whelk recovered was 196.4 mm SL.

From the LDA, the best separation of male and female whelks was produced with training set 3 (131 whelks with either L_{inc} or $W_{inc} > 0$ mm) using the variables LW, L_{inc}, and W_{inc} (Table 5). The proportion of correct classifications produced was 98.2% for males (108 of 110), 81.0% for females (17 of 21), and 95.4% overall ($F = 198.7$; Table 5). Only two groups were analyzed, so all of the separation was attributed to a single discriminant function. Use of all four variables produced a slight increase in the F-value (199.4) but did not result in better classification; all other combinations produced lower classification accuracy and F-values. After all whelks of unknown sex were classified as either male or female, the combined data set of whelks with known and predicted sex (56 females and 258 males) was reanalyzed. Differences in SL, LW, L_{inc}, and W_{inc} between the original (known sex) data set and the combined data set were not significant (Table 3). However, precision was improved by the increased sample sizes, such that SE values were less than 10% of the SEs for the original (known sex) data. Note that the prediction rates for the training set of 131 whelks were probably better than those observed for the complete data set of 174 unsexed whelks. Although 98.2% of the unsexed whelks had positive growth in at least one dimension (like the training set), prediction rates could not be determined for the remainder.

New regression equations were produced for growth (L_{inc} and W_{inc}; Figure 4C, D; Table 2), and covariance analysis was conducted for whelks that were at liberty for approximately 1 year. There was a significant difference between known-male and predicted-male whelks in terms of both the intercept and slope for L_{inc} (L_{inc} versus SL, $P < 0.05$; Table 2). This difference was primarily due to a small group of (predicted-sex) males with SLs greater than 160 mm and L_{inc} values less than 5 mm and was not due to differences between release years (2010 versus 2011; ANOVA: $P > 0.295$). There was no difference in L_{inc} between known-female and predicted-female whelks and no difference in W_{inc} (W_{inc} versus LW) between known and predicted whelks of either sex. Analysis of the linear regression residuals showed little departure from normality, thereby supporting the use of the linear model and implying that growth rates were more or less constant across the size range of recaptured whelks.

Within sexes, all L_{inc}–SL or W_{inc}–LW regressions for whelks that were at liberty for 2 years declined faster than those for whelks with a TaL of only 1 year, such that the lines intersected (Figure 5). Covariance analysis demonstrated that both the intercept and slope of the L_{inc}–SL regression differed

TABLE 2. Regression relationships for shell length (SL), lip width (LW), maximum shell width (MSW), whole wet weight (Wt), growth increment in length (L_{inc}), and growth increment in width (W_{inc}) relative to initial measurements for channeled whelks that were captured from Buzzards Bay during 2011–2012 (all = all measured whelks; subset = 176 whelks that were measured for MSW; 1 year or 2 years = nominal time at liberty [TaL] for recaptured whelks only). Covariance analysis was conducted to determine whether the intercept or slope significantly differed (*$P < 0.05$) between whelks of known sex and those for which sex was predicted (whelks with a TaL of 1 year only).

			Known-sex whelks					Whelks of known and predicted sex					
Group	Sex	Regressed variables	Intercept	Slope	df	r^2	*P*	Intercept	Slope	df	Adjusted r^2	*P*	Known sex versus predicted sex: *P* (intercept, slope)
All	M+F	LW vs. SL	3.72	0.49	8,997	0.92	<0.001						
	M+F	$\log_{10}$(Wt) vs. $\log_{10}$(SL)	–4.25	3.04	8,976	0.90	<0.001						
	M+F	$\log_{10}$(Wt) vs. $\log_{10}$(LW)	–3.68	3.20	8,975	0.93	<0.001						
Subset	M+F	LW vs. MSW	10.64	0.78	174	0.94	<0.001						
	M+F	MSW vs. LW	–8.05	1.21	174	0.94	<0.001						
	M+F	SL vs. MSW	22.77	1.46	174	0.94	<0.001						
	M+F	MSW vs. SL	–9.97	0.65	174	0.94	<0.001						
1 year	M	L_{inc} vs. SL	41.84	–0.25	81	0.39	<0.001	50.1	–0.31	214	0.38	<0.001	0.038,* 0.038*
	F	L_{inc} vs. SL	74.8	–0.38	11	0.75	0.001	69.9	–0.36	45	0.69	<0.001	0.355, 0.441
	M	W_{inc} vs. LW	25.96	–0.32	86	0.61	<0.001	25.7	–0.32	205	0.41	<0.001	0.965, 0.886
	F	W_{inc} vs. LW	35.73	–0.34	11	0.55	0.004	33.6	–0.32	45	0.57	<0.001	0.530, 0.563
2 years	M	L_{inc} vs. SL	87.45	–0.59	17	0.62	<0.001						
	F	L_{inc} vs. SL	99.21	–0.56	4	0.84	0.011						
	M	W_{inc} vs. LW	35.25	–0.46	15	0.46	0.003						
	F	W_{inc} vs. LW	47.42	–0.52	4	0.81	0.014						

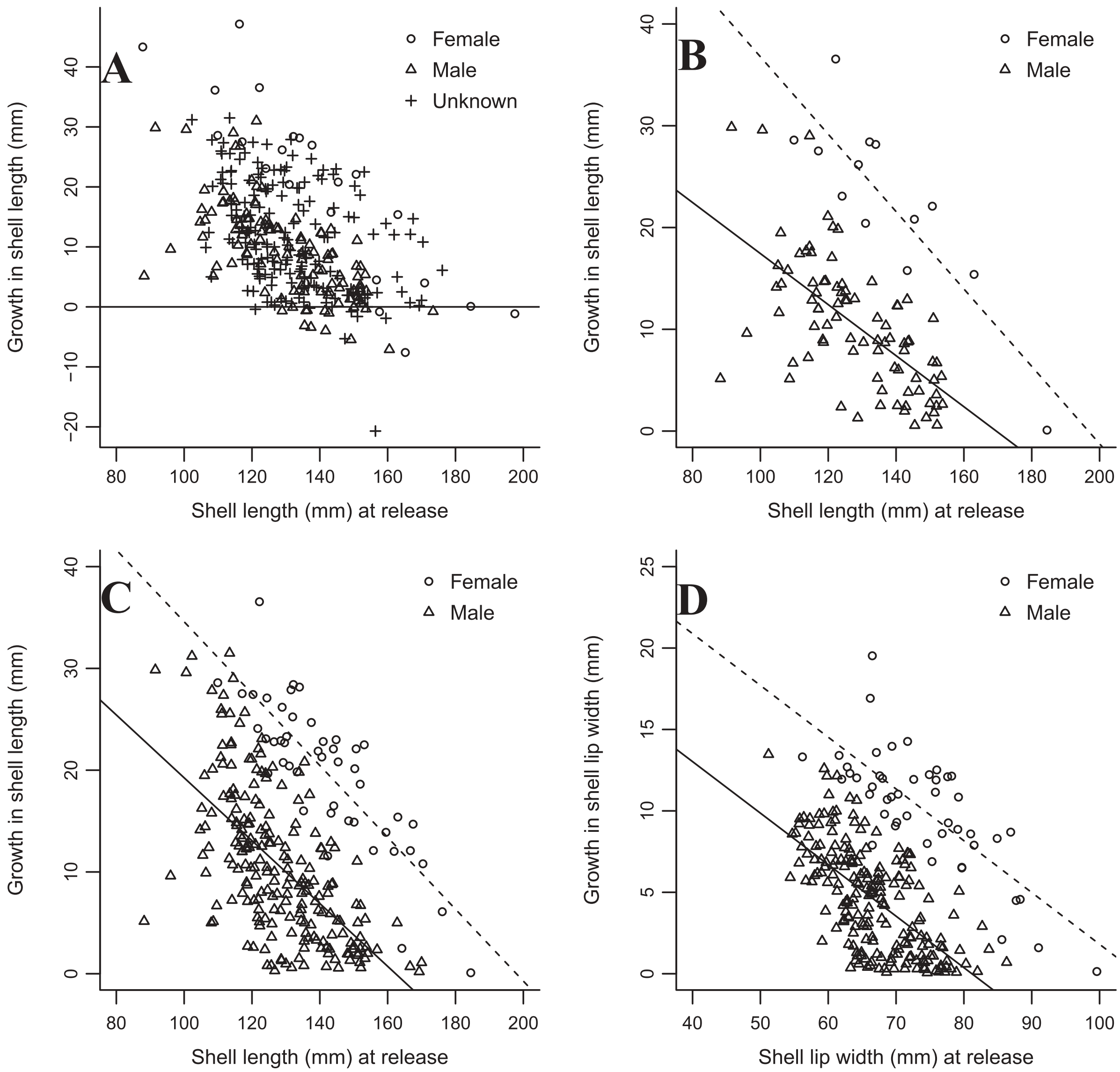

FIGURE 4. Growth of marked and recaptured channeled whelks in Buzzards Bay: **(A)** growth in shell length (SL) for all whelks regardless of sex or time at liberty; **(B)** SL growth in whelks of known sex that were at liberty less than 2 years and with length increments greater than 0 mm; **(C)** SL growth in known-sex whelks plus the whelks whose sex was predicted by linear discriminant analysis (LDA); and **(D)** lip width growth in known-sex whelks plus the whelks whose sex was predicted by LDA. In panels B, C, and D, regressions for males and females are signified by solid and dashed lines, respectively. Regression equations are given in Table 2.

between years at liberty for both males and females, whereas neither the intercept nor the slope of the W_{inc}–LW regression differed between years for either sex (Figure 5; Table 4). Thus, the relationship between initial size and growth varied with TaL for L_{inc} but not for W_{inc}.

Three male whelks that were marked and released in 2010 (initial SLs = 111.6, 115.2, and 151.2 mm, respectively) were recaptured twice: once in 2011, after which they were released, and again in 2012. The L_{inc} values for those individuals were 17.4, 12.9, and 1.8 mm, respectively, in the first year and were 1.8, 11.9, and –0.8 mm in the second year, resulting in total growth values of 19.2, 26.8, and 1.0 mm, respectively. Thus, one whelk added 91% of its 2-year growth during the first year at liberty, another individual grew equal amounts (48% and 52% of its total growth) in each year at liberty, and the third whelk grew only about 1 mm over a

TABLE 3. Mean (±SE) shell length (SL), lip width (LW), growth increment in SL (L_{inc}), and growth increment in LW (W_{inc}) after approximately 1 year at liberty for male and female channeled whelks that were marked and recaptured in Buzzards Bay during 2011–2012 (n = sample size; P-values are from t-tests comparing measurements for known-sex whelks with those for whelks of known and predicted sex combined).

	Known-sex whelks		Whelks of known and predicted sex			
Variable	Females	Males	Females	Males	Females P	Males P
n	15	96	56	258		
SL	143.3 ± 6.5	130.3 ± 1.7	142.2 ± 0.4	129.6 ± 0.1	0.758	0.741
LW	73.8 ± 3.2	67.8 ± 0.8	74.1 ± 0.2	67.7 ± 0.0	0.685	0.855
L_{inc}	19.0 ± 3.2	8.9 ± 0.7	19.4 ± 0.2	9.5 ± 0.0	0.801	0.691
W_{inc}	9.6 ± 1.6	4.3 ± 0.3	9.8 ± 0.1	3.8 ± 0.0	0.904	0.406

period of 2 years. Growth in LW for the three males followed the same pattern, with total growth of 3.8, 13.2, and 0.1 mm, respectively, over 2 years.

DISCUSSION

Our data clearly support three primary conclusions regarding the growth of channeled whelks. First, annual growth is a function of initial size and declines with increasing size. Second, there is a strong sex differential in size-specific growth, with females growing almost twice as fast as males of the same size. Third, despite initial expectations, growth increments for whelks that were at liberty for 2 years declined at a faster size-specific rate than the growth of whelks that were at liberty for only 1 year.

Within the size range of channeled whelks that we recaptured (100–200 mm SL), annual growth increments (and consequently proportional growth) declined linearly with initial size, regardless of the measurement used (SL or LW). There was little growth from October to November 2011, suggesting that growth is not a continuous process and may be episodic, so we did not try to calculate growth per TaL. The trend of declining growth should not be extrapolated to much smaller whelks, as annual growth increments for juvenile whelks at very small sizes (i.e., during their first few years) are lower than those predicted by the regression equations we presented (see below).

Sisson (1972) marked and released 2,688 channeled whelks in Narragansett Bay, Rhode Island, and recovered 183 individuals 1–20 months later, along with useful information from the commercial fishery. Whelk growth ranged from 0 to 20 mm, but average growth was only 1.8 mm over all periods at liberty (i.e., 1.4 mm/month; Sisson 1972). However, the sex of whelks was not determined in that study and the dimension measured to determine growth was not stated, but we assumed that it was maximum width. If so and if we extrapolate to an annual growth of 16.8 mm (1.4 mm/month × 12 months), this can be converted to an equivalent W_{inc} of 13.1 mm (using the equations in Table 2), which is greater than the mean growth we observed for female channeled whelks (9.6 mm; Table 3) and greater than anything we observed for males. Such growth would also indicate a pregrowth size of 41 mm LW (75 mm SL) for males (smaller than any we measured) or 66 mm LW (126 mm SL) for females (within our observed range). Thus, the information provided by Sisson (1972) was limited because whelks were not sexed and because growth was not related to TaL.

TABLE 4. Covariance analysis of the growth increment in shell length (L_{inc}) versus initial shell length (SL) and the growth increment in lip width (W_{inc}) versus initial lip width (LW) for channeled whelks of different sexes and different times at liberty (TaL; ~1 or 2 years). Whelks were marked and released in Buzzards Bay during 2010–2011 and were recaptured in 2011–2012. Values are P-values from t-tests for the intercepts and slopes (*P < 0.05; **P < 0.01; ***P < 0.001). Within each row, the second value for the intercept or slope (i.e., for males or for TaL = 2 years) represents the significance of the increment due to that variable. For example, a lack of significance for the male slope indicates no difference from the female slope.

Group	Regressed variables	Intercept 1	Intercept 2	Slope 1	Slope 2	Adjusted r^2
		Females (slope or intercept value 1) versus males (value 2)				
TaL = 1 year	L_{inc} vs. SL	<0.001***	0.003**	<0.001***	0.090	0.605
TaL = 2 year	W_{inc} vs. LW	<0.001***	0.037*	<0.001***	0.676	0.713
		1 Year at liberty (value 1) versus 2 years at liberty (value 2)				
Males	L_{inc} vs. SL	<0.001***	0.001**	<0.001***	0.002**	0.447
Females	L_{inc} vs. SL	<0.001***	0.046*	0.001***	0.037*	0.768
Males	W_{inc} vs. LW	<0.001***	0.152	<0.001***	0.148	0.565
Females	W_{inc} vs. LW	0.001***	0.276	0.004**	0.255	0.644

TABLE 5. Results of linear discriminant analysis for a training set of known-sex channeled whelks that were marked and released in Buzzards Bay during 2010–2011 and recaptured during 2012. The best model included three variables: lip width (LW) at recapture, growth increment in shell length (L_{inc}), and growth increment in lip width (W_{inc}). Whelks of known sex were reclassified into predicted sexes, and the proportions of correct and incorrect classifications within each sex were calculated. The proportions of whelks that were correctly classified (e.g., females classified as females) or incorrectly classified (e.g., males classified as females) are also presented. The total proportion of whelks that were correctly classified is the sum of the diagonal cells in the last two columns (0.130 + 0.824 = 0.954).

		Predicted sex		Proportion of total	
Known sex	Number	Females	Males	Females	Males
Females	21	17 (0.81)	4 (0.19)	0.130	0.031
Males	110	2 (0.02)	108 (0.98)	0.015	0.824
Total	131	19	112		

Growth of knobbed whelks (66–130 mm SL) that were at liberty for 380–400 d near Beaufort, North Carolina, ranged from 4 to 30 mm SL, including five whelks that grew an average of 5.6 mm SL and two individuals that grew an average of 25 mm SL (Magalhaes 1948); these values are similar to the range we observed for male and female channeled whelks. Magalhaes (1948) reported that growth increased with TaL, although she did not distinguish between the sexes. Magalhaes (1948) did not provide pregrowth measurements but classified the whelks as small (<66 mm SL), medium (66–130 mm SL), large (131–180 mm SL), or very large (>180 mm SL). Reanalysis of her data indicates that small and very large knobbed whelks grew the least (4.5 and 4.0 mm, respectively), whereas medium whelks grew 15.3 mm on average and large whelks grew 12.6 mm on average. Kraeuter et al. (1989) marked and released knobbed whelks on a tidal flat near Wachapreague, Virginia, and recovered them up to 7 years later. After converting all negative growth to 0 mm, Kraeuter et al. (1989) found that the growth rate of female knobbed whelks declined from 18 mm/year for 130–139-mm SL whelks to less than 1 mm/year for whelks larger than 230 mm SL; few males were tagged or recovered during that study. Kraeuter et al. (1989) concluded that most of the growth occurred between May and October, and they calculated growth rates based on an annual period of 183 growing days. Furthermore, Kraeuter et al. (1989) hatched and raised knobbed whelks in the laboratory; the highest growth rate was exhibited during the first year, when the whelks grew from 4 mm SL initially to 36.5 mm SL. Over a period of 9 years, the knobbed whelks that were held in the laboratory grew 13.2 mm/year on average.

Sex-specific differences in the growth rate of channeled whelks in our study were so large and significant that it was possible to employ LDA to predict the sex of whelks after measurement. Therefore, any study on the growth of channeled whelks should be conducted on a sex-specific basis. Sex-based differentiation in growth may not occur among the smallest whelks; within the subsample we (Peemoeller and Stevens 2013) studied for maturity analysis, differential growth was not apparent until the whelks reached a size of about 80 mm SL (i.e., at 4 years of age). This statement is supported by the finding that the sex ratio (M:F) for whelks smaller than 110 mm SL was 1.26, compared with 4.3 for 110–160-mm SL whelks and 0.1 for whelks exceeding 170 mm SL (Peemoeller and Stevens 2013). These data suggest that after whelks attain 100 mm SL, their growth rates diverge dramatically due to either an increase in the female growth rate or a decrease in the male growth rate. If the cause was differential mortality, we would have observed a gradual decline in sex ratio rather than a sudden increase as males reached maturity. Regardless of the cause, the result is that very few females occur in the 120–150-mm size range, and virtually all whelks larger than 160 mm are females.

The finding that growth was less after 2 years at liberty than after 1 year was unexpected. Negative growth is apparently normal for knobbed whelks, as it was observed by both Magalhaes (1948) and Kraeuter et al. (1989), who reported negative growth in 38–43% of marked knobbed whelks that were recovered after 209–279 d at liberty. However, we expected that after excluding channeled whelks with negative growth, we would observe greater growth among whelks at liberty for 2 years than among those at liberty for only 1 year. Although that expectation was true for smaller whelks of each sex, the opposite was true for the largest whelks, which grew less in 2 years than in 1 year. In addition, this effect was significant for SL but not for LW. Repeated analyses of various subsets of the data all supported the conclusion that this is a real phenomenon rather than an artifact of location or sample size, and we offer a potential explanation. Although SL is easier to measure than LW, it is also more variable, especially when compared with weight (see Figure 4C, D; and r^2 values in Table 2). Such variability is the result of damage to the siphonal canal and a subsequent loss of length, as evidenced by a number of whelks that were anomalously short. It is unknown whether this is due to (1) handling and discard of sublegal whelks, (2) natural breakage while the whelks are foraging (Kraeuter et al. 1989), or (3) predation (e.g., Magalhaes 1948). Nonetheless, it is obvious that whelks can repair breakage, and repair rates probably mirror the growth rates (i.e., declining with size). Thus, SL is the result of several processes, including growth, breakage, and repair. As long as repair rates exceed breakage rates, whelks will continue to grow. However, if breakage rates are constant rather than size dependent or if breakage is a function of other factors (e.g., foraging or environmental conditions), then growth and repair rates will eventually become too low to

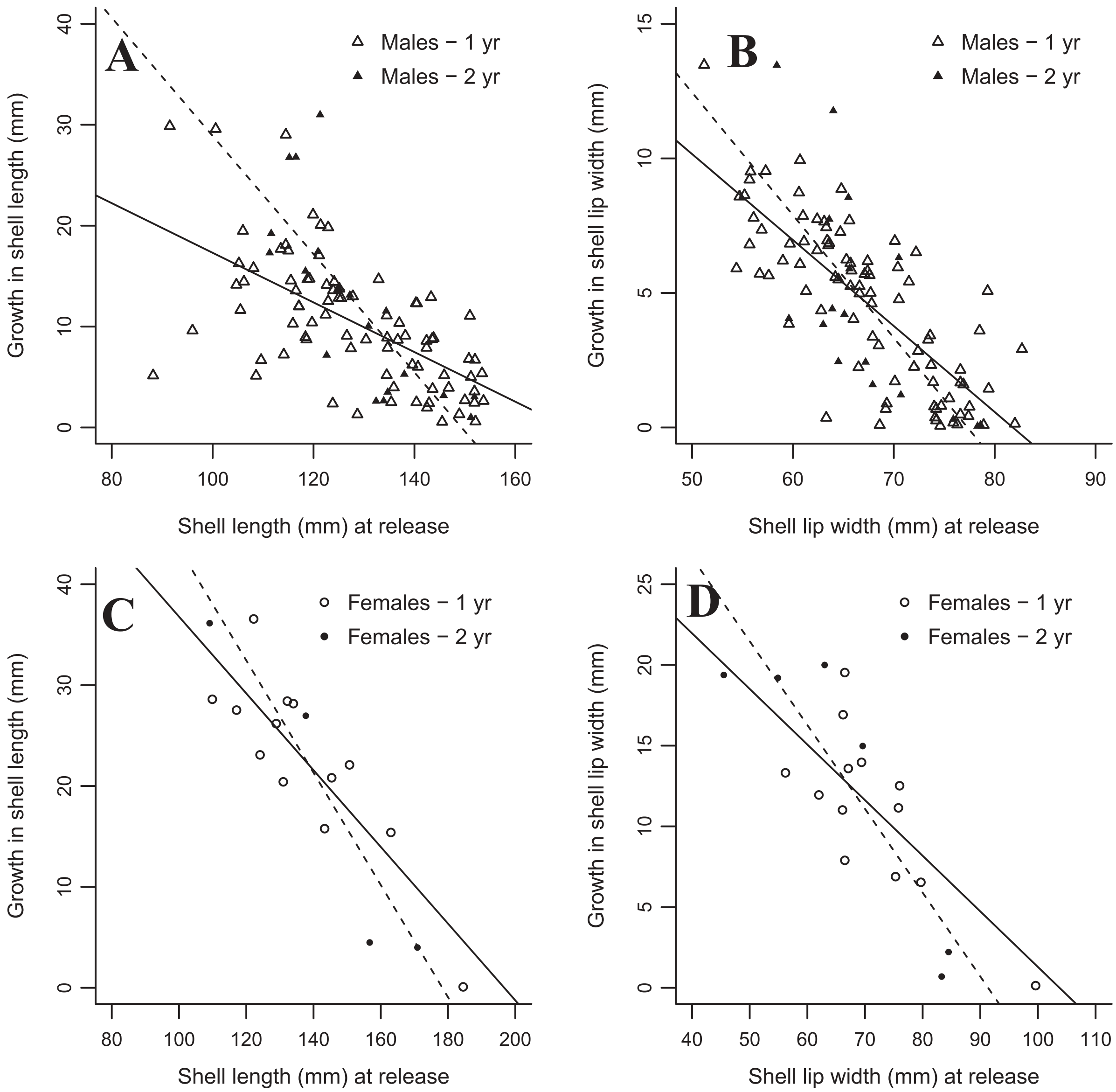

FIGURE 5. Growth versus size at release for channeled whelks that were recaptured after 1 or 2 years at liberty in Buzzards Bay: **(A)** male length increment (L_{inc}) versus shell length (SL), **(B)** male lip width increment (W_{inc}) versus lip width (LW), **(C)** female L_{inc} versus SL, and **(D)** female W_{inc} versus LW (solid line = growth after 1 year; dashed line = growth after 2 years). Regression equations are given in Table 2.

keep up with breakage rates, at which point growth becomes negative. The fact that W_{inc} did not show such negative growth indicates that breakage of the upper whorl is much less likely and proportionally less than reductions in SL. After 1 year of growth, most of our marked whelks were near their maximum size, so any breakage during their second year would have had a much greater effect on SL than during the first year. Our results demonstrate that SL is not the best measurement for use in assessing the size of channeled whelks due to the probability of shell damage and subsequent reduction in length. We believe that LW is less prone to damage-induced reduction and may be a more precise measurement than SW because it is measured by using specific landmarks on the shell. However, additional study would be needed before LW or another measurement can be recommended as the preferred method.

Assuming that shell breakage is a normal part of the growth process, one could argue that even whelks with positive growth could have suffered some breakage and that those with negative growth should have been included in the data sets used for regression analysis. Although both arguments may be valid, negative growth is a sure sign that breakage has occurred, so we took the conservative path and removed those whelks from the data set. Other authors have chosen to either ignore it or recode negative growth as 0 mm (e.g., Kraeuter et al. 1989) in order to determine average growth.

Growth of channeled whelks is probably discontinuous. Although we did not sample throughout the year, growth of whelks recaptured in October (TaL = 1.18 years) and November (TaL = 1.28 years) was not significantly different, indicating that little growth occurs at that time of year. Magalhaes (1948) and Kraeuter et al. (1989) indicated that growth of knobbed whelks was highly episodic, with some individuals showing no growth for up to 810 d (Magalhaes 1948). Data from the three channeled whelks that we recaptured twice demonstrated that growth could occur in one, both, or neither of two consecutive years. The largest of the three whelks was close to the maximum size for males, so little growth was expected. At that size, mature whelks probably put more energy into reproduction than into growth.

Use of the LDA results to reclassify the sex of known-sex whelks was relatively accurate (95.4%), although accuracy was better for males (which constituted a larger proportion of the recaptured whelks) than for females. After reclassification, there were only minor changes in the growth regressions, supporting the accuracy of that process. One exception was the regression for male growth in SL, which differed due to the presence of several large putative males that exhibited little growth; these individuals were most likely classified accurately since females of that size grow more than 15 mm/year. We (Peemoeller and Stevens 2013) previously found slight sex-specific differentiation in the LW–SL relationship but no difference in the Wt–SL relationship for 292 whelks of known sex. Maximum sizes predicted from the regression equations for each sex matched the largest animals found, except for a single 214.2-mm-SL female that was kept for dissection (Stevens and Peemoeller 2013). Thus, in our opinion, regression equations generated from the combined data sets are more precise and should be considered definitive, despite any minor inaccuracies caused by LDA classification.

The Massachusetts Division of Marine Fisheries (MADMF) has recognized the need for change in channeled whelk management; since 2014, the MADMF has begun to increase the minimum size by a marginal amount annually, with the goal of approaching the size at female maturity (R. Glenn, MADMF, personal communication). Increased size limits would have an initial impact on the fishery by reducing overall catch, perhaps substantially, but could lead to increases in the mean size of whelks over the long term. However, in recent years, the use of minimum size limits as a management tool has come under increasing scrutiny due to the consequent effects on size at reproduction, sex ratio, and mating opportunities (Zhou et al. 2010). The combination of a rapidly growing fishery, slow growth, and late maturity make channeled whelks highly vulnerable to overfishing. Increasing the minimum size limit will result in a fishery that almost exclusively targets mature females. Consequently, it may be prudent to consider alternative management strategies, such as slot limits, limits on landings, or individual quotas. An inherent but rarely stated assumption of whelk management is that all small whelks (i.e., those below the minimum size limit) will eventually grow to become large whelks if they are not captured. If growth rates differ between sexes, however, then only a fraction of small whelks (i.e., females) will eventually grow past a certain size, and targeting of larger whelks by the fishery will lead to depletion of females relative to males. This phenomenon would require different approaches for managing male and female channeled whelks.

Management of busyconid whelks has typically been conducted by enforcing selective fishing methods that are borrowed from other fisheries: such “6-S” strategies include restrictions on the species, size, stocks, sex, season, and/or space (as well as effort) allowed for any particular fishery. Whelks, however, show minimal migratory movements and are essentially sedentary; furthermore, their fisheries are small in scale and spatially structured, qualifying as “S-type” fisheries (Orensanz et al. 2005). Such fisheries are extremely difficult to manage due to the high impacts of localized fishing and multiple landing sites and the ineffectiveness of effort controls—all factors that pose a hindrance to centralized management schemes. Effective management of S-type fisheries can best be achieved by using appropriate incentives (rights-based management), participation of fishers in management (including monitoring and decision making), and social group enforcement (Orensanz et al. 2005). States are understandably reluctant to impose new management regimes, but with the cooperation of fishers, it should be possible to establish experimental management within a restricted portion of the whelk fishery so as to determine whether alternative management practices provide an improvement over traditional methods.

ACKNOWLEDGMENTS

This project was supported by the Saltonstall–Kennedy Grant Program (Grant Number NA10NMF4270007) and the Living Marine Resources Cooperative Science Center (for the salary of B.G.S.). We thank R. Bemis, S. Lawrentz, and K. Amagada for their help in capturing and measuring the whelks. We are especially grateful to Captain J. Drake of the F/V *Cynthia Lee* for his assistance and experience in capturing channeled whelks and to the University of Massachusetts Dartmouth for allowing us to use their seawater laboratory. The manuscript benefited greatly from reviews provided by D. Murie and two anonymous reviewers.

REFERENCES

ASMFC (Atlantic States Marine Fisheries Commission). 2013. Addendum XXII to Amendment 3 to the American lobster fishery management plan. ASMFC, Washington, D.C.

Avise, J. C., A. J. Power, and D. Walker. 2010. Genetic sex determination, gender identification and pseudohermaphroditism in the knobbed whelk, *Busycon carica* (Mollusca: Melongenidae). Proceedings of the Royal Society of London B 271:641–646.

Bruce, D. G. 2005. An assessment of the Delaware Bay knobbed whelk dredge fishery. Journal of Shellfish Research 24:641.

Castagna, M., and J. N. Kraeuter. 1994. Age, growth rate, sexual dimorphism and fecundity of knobbed whelk *Busycon carica* (Gmelin, 1791) in a western mid-Atlantic lagoon system, Virginia. Journal of Shellfish Research 13:581–585.

Davis, J. P., and R. T. Sisson. 1988. Aspects of the biology relating to the fisheries management of New England populations of the whelks, *Busycotypus canaliculatus* and *Busycon carica*. Journal of Shellfish Research 7:453–460.

Edwards, A. L. 1988. Latitudinal clines in shell morphologies of *Busycon carica* (Gmelin 1791). Journal of Shellfish Research 7:461–466.

Edwards, A. L., and M. G. Harasewych. 1988. Biology of the recent species of the subfamily Busyconinae. Journal of Shellfish Research 7:467–472.

Glenn, R., and S. Wilcox. 2012. Profile of the channeled whelk pot fishery. Report to the Massachusetts Marine Advisory Commission by the Massachusetts Division of Marine Fisheries, Invertebrate Fisheries Program, New Bedford.

Kent, B. W. 1983. Natural history observations on the busyconine whelks *Busycon contrarium* (Conrad) and *Busycotypus spiratum* (Lamarck). Journal of Molluscan Studies 49:37–42.

Kraeuter, J. N., M. Castagna, and R. Bisker. 1989. Growth rate estimates for *Busycon carica* (Gmelin, 1791) in Virginia. Journal of Shellfish Research 8:219–225.

Magalhaes, H. 1948. An ecological study of snails of the genus *Busycon* at Beaufort, North Carolina. Ecological Monographs 18:379–409.

Orensanz, J. M., A. M. Parma, G. Jerez, N. Barahona, M. Montecinos, and I. Elias. 2005. What are the key elements for the sustainability of "S-fisheries"? Insights from South America. Bulletin of Marine Science 76:527–556.

Peemoeller, B.-J., and B. G. Stevens. 2013. Age, size, and sexual maturity of channeled whelk (*Busycotypus canaliculatus*) in Buzzards Bay, MA. U.S. National Marine Fisheries Service Fishery Bulletin 111:265–278.

Peterson, C. H. 1982. Clam predation by whelks (*Busycon* spp.): experimental tests of the importance of prey size, prey density, and seagrass cover. Marine Biology 66:159–170.

Power, A. J., E. Covington, T. Recicar, R. L. Walker, and N. Eller. 2002. 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., C. J. Sellers, and R. L. Walker. 2009. Growth and sexual maturity of the knobbed whelk, *Busycon carica* (Gmelin, 1791), from a commercially harvested population in coastal Georgia. Occasional Papers of the University of Georgia Marine Extension Service 4:1–24.

R Development Core Team. 2011. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna.

Sisson, R. T. 1972. Biological and commercial fisheries related research on the channeled whelk *Busycon canaliculatum* (Linne) in Narragansett Bay, Rhode Island. Master's thesis. University of Rhode Island, Kingston.

Stevens, B. G. 1976. A study of seasonal changes in component indices and lipid content of the digestive gland, ovary, and foot of *Busycon carica*. Master's thesis. College of Charleston, Charleston, South Carolina.

Turgeon, D. D., J. F. Quinn Jr., A. E. Bogan, E. V. Coan, F. G. Hochberg, W. G. Lyons, P. M. Mikkelsen, R. J. Neves, C. F. E. Roper, G. Rosenberg, B. Roth, A. Scheltema, F. G. Thompson, M. Vecchione, and J. D. Williams. 1998. Common and scientific names of aquatic invertebrates from the United States and Canada: mollusks, 2nd edition. American Fisheries Society, Special Publication 26, Bethesda, Maryland.

Turner, J. T., D. G. Borkman, J. A. Lincoln, D. A. Gauthier, and C. M. Petitpas. 2009. Plankton studies in Buzzards Bay, Massachusetts, USA. VI. Phytoplankton and water quality, 1987 to 1998. Marine Ecology Progress Series 376:103–122.

Walker, D., A. J. Power, M. Sweeney-Reeves, and J. C. Avise. 2007. Multiple paternity and female sperm usage along egg-case strings of the knobbed whelk, *Busycon carica* (Mollusca; Melongenidae). Marine Biology 151:53–61.

Walker, R. L. 1988. Observations on intertidal whelk (*Busycon* and *Busycotypus*) populations in Wassaw Sound, Georgia. Journal of Shellfish Research 7:473–478.

Zhou, S., A. D. M. Smith, A. E. Punt, A. J. Richardson, M. Gibbs, E. A. Fulton, S. Pascoe, C. Bulman, P. Bayliss, and K. Sainsbury. 2010. Ecosystem-based fisheries management requires a change to the selective fishing philosophy. Proceedings of the National Academy of Science of the USA 107:9485–9489.