Local Adaptation and Sexual Dimorphism in the Waved Whelk (*Buccinum undatum*) in Atlantic Nova Scotia with Applications to Fisheries Management

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ABSTRACT

Kenchington, E. and A. Glass. 1998. Local adaptation and sexual dimorphism in the waved whelk (*Buccinum undatum*) in atlantic Nova Scotia with applications to fisheries management. Can. Tech. Rep. Fish. Aquat. Sci. 2237: iv + 43 p.

The whelk, *Buccinum undatum*, is harvested commercially in the Gulf of St. Lawrence and in the United Kingdom. In 1998, one year exploratory licenses were issued to fishers in eastern Nova Scotia and in Cape Breton. Fishers were assigned discrete fishing areas, identified by lobster fishing areas (LFAs), as previous studies in the Gulf of St. Lawrence had confirmed a high degree of local adaptation in this species.

Scientific advice applicable to other areas can not be reliably applied to whelk populations along the Atlantic coast. This study provides biological information on whelks from 12 inshore areas along the Atlantic coast of Nova Scotia and in the Bay of Fundy, and from whelks collected offshore on the Scotian Shelf. Strong local adaptation in morphology and sexual dimorphism are described, and presented in terms of management considerations.

RÉSUMÉ

Kenchington, E. and A. Glass. 1998. Local adaptation and sexual dimorphism in the waved whelk (*Buccinum undatum*) in atlantic Nova Scotia with applications to fisheries management. Can. Tech. Rep. Fish. Aquat. Sci. 2237: iv + 43 p.

La pêche commerciale du buccin, *Buccinum undatum*, est pratiquée dans le golfe du Saint-Laurent et au Royaume-Uni. Des études antérieures réalisées dans le golfe du Saint-Laurent ayant démontré que l'espèce s'était très bien adaptée localement, on a octroyé, en 1998, des permis de pêche exploratoire d'un an à des pêcheurs de l'est de la Nouvelle-Écosse et du Cap-Breton, auxquels on a attribué des zones de pêche séparées, correspondant aux zones de pêche du homard (ZPH).

Les conseils scientifiques valables pour d'autres zones ne peuvent être appliqués de façon fiable aux populations de buccins de la côte atlantique. L'étude présentée ici fournit des renseignements biologiques sur les buccins de 12 zones côtières du littoral atlantique de la Nouvelle-Écosse et de la baie de Fundy et sur des buccins récoltés en haute mer, dans les eaux du plateau néo-écossais. On y décrit une forte adaptation morphologique et un important dimorphisme sexuel, cette information étant présentée à des fins de gestion de l'espèce.

INTRODUCTION

Interest in the harvest of the waved whelk, *Buccinum undatum* has resulted in the issuance of exploratory licences in the Cape Breton/Eastern Shore area of Nova Scotia. Nine exploratory licences were issued according to lobster district, with three additional licences reserved for various Eastern Nova Scotia Bands (Anonymous, DFO Maritimes Region 1998). In anticipation of this fishery, research on the whelks in that area was undertaken to provide guidelines to the fishers on management areas, yield expectations and size and gear restrictions. Some of this information has been incorporated into the 1998 Management Plan (Anonymous, DFO Maritimes Region 1998). This data also provides baseline information on the size and growth rates of the whelks in various populations prior to exploitation.

GENERAL

Buckie, Waved Whelk, Rough Whelk and Common Whelk are all local names given to the most common local species of *Buccinum*, *B. undatum*. The shell can be up to 15 cm long (Flight 1988) and the flesh of the foot is a mottled black and white which distinguishes it from other whelk species. *B. undatum* is often caught in lobster traps in Atlantic Canada. This species is distributed throughout the North Atlantic, the North Sea, English Channel and west Baltic Sea. On the east coast of North America it is found from New Jersey to Labrador to depths of 180 m. The lower lethal salinity limit is in the range of 18 $^{0}/oo$ (Staaland 1972). Whelks spend much of their time partially buried in the sediment or quiescent on the surface when not feeding or mating (Himmelman 1988).

Buccinum is a carnivore. The whelk will grip a bivalve (mussel, clam, oyster) with the foot, pulling the two valves apart or wedging them with the edge of the shell or siphonal canal (thicker part of shell near the base) as the animal becomes weak. To accomplish the wedging the gastropod may first partially pull open the valves or break the edge of the bivalve shell with its own shell, which is quite thick. The gape in the prey shell permits the whelk to insert its proboscis, and feed (Himmelman 1988). It does not drill a hole in the shell as is commonly believed (*e.g.*, Anonymous). *Buccinum* is known also to be a scavenger and will feed readily on dead fish, hence its attraction to bait in lobster traps.

Whelks feeding on bivalve molluscs are susceptible to the accumulation of phycotoxins (PSP, DSP, etc.) which occur in their prey (Caddy and Chandler 1968, Medcof 1972). PSP has been found in the meats and digestive glands from whelks captured in the Bay of Fundy (Cadegan 1974). Medcof (1972) reports on deaths in Quebec attributed to the consumption of PSP in whelks. Whelks are known to eliminate toxins readily if fed non-toxic food, and so depuration maybe a solution to fishing in contaminated areas (Caddy and Chandler 1968).

The reproductive cycle of *Buccinum* is well documented (*e.g.,* Martel *et al.* 1986a, Martel *et al.* 1986b, Gendron 1992). In mid-May the whelks aggregate for copulation, often migrating shoreward. A female may mate with more than one male, and is able to store sperm for up to eight weeks. Egg laying begins soon after copulation and may extend to the end of August. On average, a female will lay 340,000 eggs per egg mass and the number of egg masses laid per female is unknown (Martel *et al.* 1986a). Martel *et al.* (1986b) observed only 60% to 80% of the females reproducing each year. Feeding by females may be reduced during the egg laying period (Lanteigne and Davidson 1992). Preferred egg laying areas are the irregular surfaces and faces of boulders and the stipes of kelp. Egg masses are vulnerable to predation by sea urchins and to loss through detachment due to storm activity (Martel *et al.* 1986a). Embryos develop in the egg cases and hatch after 5 to 8 months, in the late autumn to late winter (Martel *et al.* 1986a). Only 1% of the eggs hatch, with approximately 3700 hatchlings emerging from a single egg mass (Martel *et al.* 1986a). There is no planktonic larval phase, implying that dispersal is limited (Gendron 1992, Lanteigne and Davidson 1992). The female begins gonad development immediately after egg laying. Large whelks commonly show no sign of sexual maturity (*i.e.*, absence of large oocytes; Gendron 1992), however reproductive senility may be the result of parasitic castration.

Whelks can be aged by counting annuli on the operculum (Santarelli and Gros 1985). On the northern coast of Quebec, males reach sexual maturity at 5-6 yr and sizes of 49 to 76 mm. Females mature later and at a larger size (above 7 years and 60 to 81 mm shell height) (Gendron 1992). Size at sexual maturity appears to be quite variable across populations (Gendron 1992).

Whelks are preyed upon by cod, dogfish, crabs, starfish and lobsters (Thomas and Himmelman 1988, Jalbert *et al.* 1989). The escape response of whelks to starfish is well documented (*e.g.*, Thomas and Himmelman 1988) and involves a rapid twisting action of the foot followed by escape. As with other species (*e.g.*, scallop) this response is triggered by saponins released by the starfish, and can be induced in the lab with starfish extract.

BUCCINUM FISHERIES IN QUEBEC AND ATLANTIC CANADA

Buccinum undatum supports small local fisheries in the Gulf of St. Lawrence and off Newfoundland. The oldest fishery is in Quebec, where landings have ranged from 5 to 1300 mt fresh weight per year since 1949. In recent years, landings have been stable at 700 mt (1991-1993) (Gendron 1992, Lambert and Gendron 1994). In Quebec, this fishery is considered a "complementary fishery" and open only to inshore fishermen (Anonymous 1990). The majority of the landings are in Zones 5 and 6 along the north coast (Lambert and Gendron 1994). Commercial catches of whelk on the east coast of New Brunswick are comparatively poor (Lanteigne and Davidson 1992) as were those in Newfoundland (Flight 1988). In both these areas, the fishery was viewed as a complementary fishery, as in the Quebec Region. Whelks also supply a domestic bait market for groundfish in Atlantic Canada (Anonymous). *Buccinum undatum* supports a commercial fishery in England, Ireland and northern Europe where it is a valued food item (Anonymous).

A survey of whelks on the Nova Scotia side of the Bay of Fundy was carried out in 1973 by the Nova Scotia Department of Fisheries. In general, the results were not promising, with the exception of the Annapolis Basin catches (Cadegan 1974). A variety of traps, pots and nets, as well as bait have been tested and descriptions of these are available (*e.g.*, Cadegan 1974; unpublished DFO Scotia-Fundy Region Central Registry document 2901, John MacInnes, P.O. Box 113, Mabou, N.S.). Preliminary data collected in October 1995 on whelks from the Lobster Bay area (Tusket Island) of south-west Nova Scotia indicate that the size distribution and meat yield are markedly different in this area from that reported for the Gulf of St. Lawrence (Kenchington and Lundy 1996). The maximum shell height (71 mm) in the Tusket Island sample was 20 mm smaller than that reported in the literature for the New Brunswick north coast. The shell weight is considerably greater than those reported for a 60 mm sized whelk from the Gulf or the New Brunswick side of the Bay of Fundy, and may result from selection pressure imposed by the large resident lobster population (*cf.*, Kenchington and Lundy 1996). This evidence for local adaptation in whelks means that each new fishing area will have to be evaluated for the various population and biological parameters necessary for sustainable management.

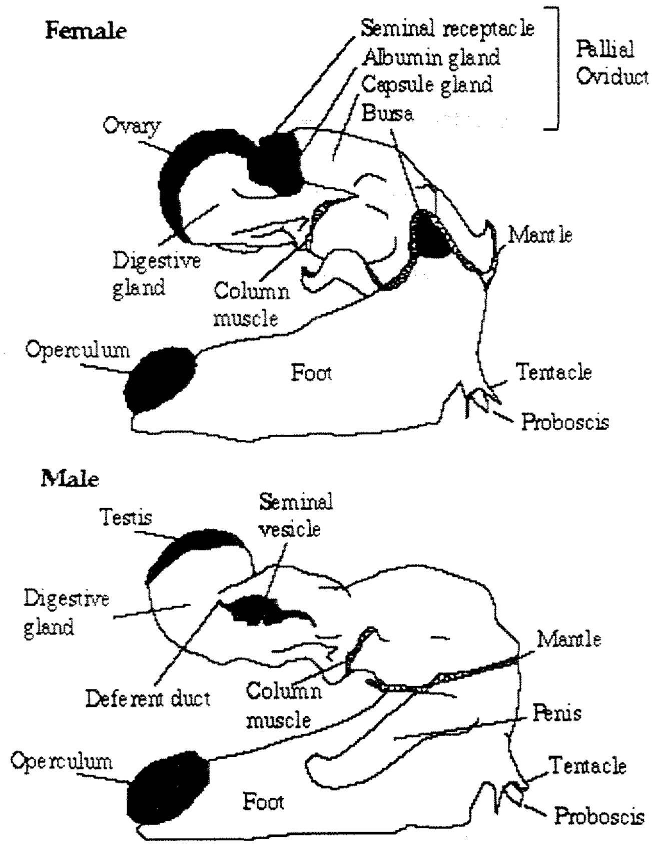
MORPHOMETRIC STUDIES

Whelks were collected from various inshore locations along the Atlantic coast of Nova Scotia and in the Bay of Fundy (Fig. 1). Most of the inshore whelks were obtained as a by-catch by lobster fishermen with the exception of those sites in the Bay of Fundy (Digby, Annapolis Basin and Saint John) which were sampled during the Department of Fisheries and Oceans (DFO) scallop stock assessment surveys. The sampling dates were as follows:

Location:	Collection Date:
Point Aconi, Cape Breton	18 May 1996
Main à Dieu, Cape Breton	01 June 1996
Louisbourg, Cape Breton	23 May 1996
Fourchu, Cape Breton	20 May 1996
Petit de Grat, Cape Breton	13 May 1996
Owls Head, Eastern Shore, N.S	01 June 1996
Osborne Harbour, Southwest N.S.	20 May 1996
Argyle, Southwest N.S.	23 May 1996
Port Maitland, Southwest N.S.	28 May 1996
Annapolis Basin, Bay of Fundy, N.S.	01 June 1997
Digby, Bay of Fundy, N.S.	01 June 1997
Saint John, Bay of Fundy, N.B.	12 May 1996

During the 1996 DFO spring groundfish cruise (March 1, 1996; Cruise No. N255), Waved Whelks (*Buccinum undatum*) were randomly selected from the catch at stations where they were present. The gear used was a Western IIA groundfish Otter trawl fitted with a 1.5" stretched mesh codend liner (P. Fanning, Marine Fish Division, DFO, pers. comm.). A total of 512 whelks were collected and processed. The locations where whelks were found area shown in Figure 2; their distribution was widespread. The large number of whelks per tow at some stations precluded the collection of density information as the primary purpose of the survey was to collect data on groundfish. It should be noted that the whelks caught in the groundfish cruise may not reflect a random sample of those on the bottom (due to selectivity of the gear), and the size may not reflect that caught with other gear types. Nevertheless this data does provide estimates of the yield and size/age relationships of the offshore *Buccinum* stocks. A sample of animals, generally the first "bag full" from a tow, were brought to the lab for further analyses.

The whelks were stored frozen at -5° C for approximately 2 months before being thawed and processed. The total shell height, aperture length and animal wet weight (g) were recorded, and the shell was cracked with a vice. The tissue was removed from the shell and the total tissue weight recorded. The foot was then removed and weighed and in some cases the operculum was removed and stained for aging (see below).



External anatomy of Waved Whelks (after Lanteigne and Davidson 1992)

The male sex was determined by the presence or absence of a penis. If a penis was evident the penis length was measured. Males were considered sexually mature if their penis length/shell height ratios were larger than 0.5 (Martel *et al.* 1986a, Lanteigne and Davidson 1992).

Gonosomatic indices were not determined as the gonad was generally in a poor condition and did not remain intact during dissection and weighing. As a result, this report cannot provide information on size at sexual maturity of females.

Summary statistics for these measurements are presented in Table 1 by location. The shell height range of 19 to 93 mm (Table 1) is similar to that observed from 4190 whelks collected in the southern Gulf of St. Lawrence (34 to 99 mm, Lanteigne and Davidson 1992). The shell height frequency distribution and the cumulative frequency distribution are illustrated for each location in Figures 3 to 13 (with the exception of Annapolis Basin where the sample size was only 7). The size distributions of the samples in this study generally are unimodal with few small animals present. This may be in part due to selection by the gear and movement behaviour of the animals. The trapped and otter trawl samples generally caught larger whelks whereas the samples collected in the Bay of Fundy with scallop drags captured more small animals. As the trapped whelks were caught as lobster by-catch, selection by or presence of the lobsters may have reduced capture of smaller whelks which are more vulnerable to predation. Conversely, the unexploited population state may favour older and larger animals.

The allometric relationship between shell height (X) and the wet foot weight (Y) were determined for each location (Table 2). Functions of the form $Y=aX^b$ were fit using the Levenberg-Marquardt method for computing parameter estimates, using program NLR of the SPSS Release 4.0 software package (SPSS Inc. 1990). At each iteration, the estimates were evaluated against a set of control criteria (approximations to a and b). In these analyses, all iterations were stopped because the relative reduction between successive residual sums of squares was less than 1.000E-8. r^2 values were calculated as: one minus the residual sum of squares/corrected sum of squares. The foot weight for a standard 70 mm shell height varies considerably across locations with Owls Head on the Eastern Shore of Nova Scotia having a 7 g foot weight while offshore samples were 46% heavier with a foot weight of 13.1 g (Table 2).

The ratio of the numbers of male to the numbers of female whelks varied from population to population (Table 3) with a range of 0.11 (Osborne Harbour) to 2.34 (Saint John Harbour). Females generally dominated the samples but in some populations males were clearly more dominant (Table 3).

IMPOSEX

Imposex (the imposition of male sex organs onto the female gonad system) has been defined as the development of male primary sexual characteristics in female gastropods, and is believed to be caused by exposure to tributyltin (TBT). TBT has been used in anti-fouling paints on ship hulls since the early 1970s, but has recently been banned for use on boats and small ships. Varying dose levels show varying responses. In extreme cases, the male organs block the oviduct and prevent release of eggs.

Imposex can be detected when animals possess both ovaries and penis. The penis homologue is often reduced in size. This phenomenon is not to be confused with the gonad reabsorption and penis atrophy associated with trematode parasitic infection (*cf.* Gendron 1992). Under these circumstances only one sex is apparent.

Imposex in *Buccinum undatum* was reported for the first time in 1993 from samples collected from the French coast (Oehlmann *et al.* 1993) and subsequently from the arctic near Spitzbergen, Norway (Brick and Bolte 1994) and the North Sea (Ten Hallers-Tjabbes *et al.* 1994). In the North Sea study, the longest penis measured with the imposex condition was 18 mm. Whelks from their northern-most stations had either no imposex or only an infrequent and minor growth of penis homologues, 2 to 4 mm long. Kenchington and Lundy (1996) reported the first instance of imposex in *Buccinum undatum* in Atlantic Canada in their study of whelks from Tusket Shoal, Southwest Nova Scotia. In our data set, 10% of the animals from Saint John Harbour, N.B. had both a penis and female gonad. This equates to 34.5% of the females in that sample (10 of 29 females had penis homologues). Penis length ranged from 2 to 32 mm with most of the penis homologues being 2 to 6 mm long.

SEXUAL DIMORPHISM AND LOCAL ADAPTATION

The pooled data were analyzed for sexual dimorphism in shell height, aperture length, shell weight, total weight, tissue weight, foot weight and yield using Student's t calculated with independent samples. Pooled- or separate-variance estimates were calculated as indicated by results of F-tests of homogeneity of variance (Levene Test).

Strong sexual dimorphism in shell height, aperture length, shell weight, total weight, tissue weight and percent meat yield was observed (Table 4). The females were significantly larger in shell height and aperture length with significantly heavier total weight, tissue weight and shell weight (Table 4). However, there was no significant difference in foot weight between the sexes, and yield was significantly greater in the males. Kenchington and Lundy (1996) reported similar results in their study of whelks from Tusket Shoal, Southwest Nova Scotia. The shell height distributions by sex and location are illustrated in Figures 3 to 13. Although sexual dimorphism is marked in some characters, the differences in mean values between the sexes are small and it is unlikely that these characters can be used to separate the sexes in the field.

The relationships between the ln-transformed morphological variables were examined using the Pearson product-moment correlation coefficient. As the characters were expected to be positively correlated with one another, a one-tailed significance level was calculated. All relationships were highly significant and positive except for the correlation between yield and shell weight which was negative. The correlations with shell height are given in Table 5.

The high correlation between the transformed variables suggested that analyses for underlying factors might be appropriate. The analysis was performed on the following variables: foot weight, shell height, shell weight, tissue weight, total weight and yield. Aperture length was excluded from the analysis due to a large number of missing values (Table 1). The number of cases was 1432. The ln-transformed variables were initially analyzed with a factor model without rotation. Examination of the initial solution and of the scree plot (total variance associated with each factor) indicated that 2 factors would adequately represent the data (Table 6). The first factor explained 76% of the total variance. The second factor explained another 22%, together accounting for 98.5% of the variance in the data. In the initial unrotated solution (Table 6), Factor 1 had high positive loadings from all variables suggestive of a size-related factor. As the factors are orthogonal, these also represent correlations. The highest correlation with Factor 1 is shell height with yield being the least correlated. Factor 2 had more variable loadings both in magnitude and sign. This axis is most highly correlative with yield (positive) and shell weight (negative). The final statistics after the 2 factors were extracted are given in Table 6. The variables retain a high communality (proportion of the variance accounted for by the factors) with the two factors. The variance was redistributed to enhance interpretation. The factor matrix was rotated using a varimax rotation. This type of rotation attempts to minimize the number of variables that have high loadings on a factor. The rotation was achieved in three iterations and the transformation applied is given in Table 6. The resulting rotated factor matrix show Factor 1 to have a high positive loading from total weight and a low loading from the yield variable. The second factor retained the high loading of yield but lost definition with an increase in the loadings of some of the variables represented in Factor 1 (Table 6).

The mean and standard error of each factor score for each location is illustrated in Figure 14 as well as the magnitude and direction of each of the variable loadings. It can readily be seen that each population is discrete with respect to whelk morphology. The first factor separates the locations but there is no clear geographic trend. The second factor separates the Offshore samples from the others with yield playing a predominate role in the separation. The greater percent yield from the offshore samples is seen in the mean for this variable listed in Table 1. The Annapolis Basin sample has a much larger error value on Factor 1 due to the small sample size (N=7) and the size range of that sample.

Gendron (1992) performed a factor analysis on whelks from the Gulf of St. Lawrence. Using 5 ratio variables she found a much lower percentage of the variation explained by the two axes. Her first axis accounted for only 48.5% of the variance while her second axis accounted for a further 29.6%. She also found significant differences in morphology between different sampling sites as well as strong sexual dimorphism within sites (Gendron 1992). The mean and standard error of each factor score for each location by sex is illustrated if Figure 15. The Annapolis Basin sample was excluded from the illustration as the sample size for each sex was too small (see above). As in the previous figure, variation around the mean on the first factor is greater than that around the mean of the second factor. In all cases the centroids of each sex within a site are significantly different. The greatest dimorphism is seen in the Owls Head site while the least dimorphism is seen in the Digby and offshore samples. The sexes differentiate to the greatest degree on factor 1 which is influenced most by the total weight variable but also by the other weight and size measures. Females consistently have higher scores on this axis than the males do. In the offshore sample and in the Saint John sample greater sexual differentiation is seen on factor 2 with the males having higher scores on this axis than the females. Factor 2 is most influenced by yield (Fig. 14, Table 6).

The influence of depth in this analysis could not be fully determined due to missing data, and depth may be a significant driving force behind the local adaptation. One site, Digby, Nova Scotia, had a broad depth range represented in the sample of 325 whelks (Table 7). At this location, whelk samples were collected from 35 depths providing a 61 m range between 52 and 113 m (Table 7). The relationships between the ln-transformed morphological variables and depth were examined using the Pearson product-moment correlation coefficient. As the direction of the relationship was unknown, a two-tailed significance level was calculated. The only significant correlation with depth was with the percent yield. This showed a weak but significant negative correlation (-0.26, P=0.000) indicating that yield decreases with depth. Many of the other samples were likely collected from shallower sites than those represented in the Digby sample. However, the position of the Digby centroid in the factor analysis relative to shallower collection sites indicates that depth is probably not a strong driving force in this analysis.

AGING

Whelk samples were aged by counting annuli on the operculum following staining with methylene blue (Gendron 1992). The annual deposition of the rings has previously been validated by Santarelli and Gros (1985) and the annulus is marked during the warmer months of the year between June and October. Details of the staining protocol were kindly provided by Dr. Louise Gendron, Department of Fisheries and Oceans, Maurice-Lamontagne Institute, Mont-Joli, Québec, Canada. The opercula are removed from the sole of the foot. Staining was done with methylene blue diluted approximately to 0.2%. The opercula were left in the stain from 1 to 4 minutes and then wiped gently with an absorbing paper to remove the excess stain. The annuli were readily visible, especially on the smaller animals. One difficulty was in the interpretation of the centre of the operculum to find the first annulus. Following the protocol of Dr. Gendron, when the central node was smaller than 0.6 mm in diameter it was not counted; otherwise it would be counted as the first annulus. In most samples the central node was obvious and well surrounded by a ring, however, in some cases the node was not discernible or else there were two nodes. These samples were not included in the analyses. A test sample was aged independently by Dr. Gendron and each of the authors with 95% consistency. Only animals from the Annapolis Basin, Digby and the offshore cruise were aged.

A single von Bertalanffy function was used to describe the growth of the whelks. The function is expressed as $L_t = L_{inf}(1 - \exp(-k(t - t_0)))$, where, L_t is length at age, L_{inf} is the asymptotic length, k is the growth coefficient, and t_0 is the age at which length is 0. Functions were fit using the Levenberg-Marquardt method for computing parameter estimates using program NLR of the SPSS Release 4.0 software package (SPSS Inc. 1990). At each iteration, the estimates were evaluated against a set of control criteria. In these analyses, all iterations were stopped because the relative reduction between successive residual sums of squares was less than 1.000E-08. The r^2 value was calculated as: 1 minus the residual sum of squares/corrected sum of squares.

The data and growth function are illustrated in Figure 16. The function did not explain a high proportion of the variance in the data; r^2 was 0.46 (Table 8). Santarelli and Gros (1985) produced a von Bertalanffy growth function for whelks from the west coast of France (see below). Their function shows a greater height at infinity (L_{inf}) and a smaller Brody growth coefficient (k) than the one produced in this study:

Buccinum undatum	N	L_{inf} (s.e.)	k (s.e.)	$t_{(0)}$ (s.e.)
This study	559	80.473 (5.497)	0.274 (0.054)	1.201 (0.282)
Santarelli and Gros (1985)	1688	112.49	0.125	-0.597

However, the 95% confidence levels around L and k overlap between the two studies. Gendron (1992) published her growth data but did not fit a function to it. It appears from the graphical presentation in her Figure 5 that the whelks in the Gulf of St. Lawrence, Canada have a faster growth than those reported here from the Atlantic coast.

SEXUAL MATURITY

Sexual maturity in males can be evaluated by the ratio of the size of the penis relative to the total shell height (see above). Males with a value of greater than 0.50 for this index are considered to be sexually mature. The frequency distribution of this penis ratio determined from all males in the population and excluding the females with penis homologues is illustrated in Figure 17. The cumulative frequency indicates that approximately 70% of the males in the total sample were mature. The relationship between the penis ratio and shell height is illustrated in Figure 18. It would appear that males reach sexual maturity at sizes ranging from 30 to 70 mm shell height, although the majority (75%) of male whelks were immature until approximately 40 mm shell height (Fig. 18). At 40+ mm shell height, 76% of the males in this study were mature. This range is similar to that reported by Gendron (1992) for the Gulf of St. Lawrence (49 to 76 mm). The percentage of maturity did not reach 100%, however 100% were immature at sizes below 30 mm shell height. A few large males had low penis ratios which may be associated with senility-induced penis atrophy (Gendron 1992).

Analysis of variance of the penis ratio by location, excluding the Annapolis Basin and Port Maitland, showed significant differences between locations (Table 9). The average penis ratio was greater than 0.5 at all locations (Table 9). Post-hoc multiple range tests using the modified Bonferroni test and Scheffe's test with a significance level of 0.05 were performed. The difference between two means is significant if:

MEAN(J)-MEAN(I) >= .1515 * RANGE * SQRT(1/N(I) + 1/N(J))
with the following values for RANGE: 4.72 (Bonferonni); 6.08 (Scheffe)

where I and J are locations and N equals the sample size. Significant differences were found between the offshore and Saint John, Digby and Louisbourg locations, and between Point Aconi and Saint John and Louisbourg locations with the Bonferonni test, and between the offshore and Saint John and Digby with the Scheffe test. There were no differences in penis ratio between other pairs of locations. Therefore, while there is a significant difference in the percentage of sexually mature male whelks between locations, this difference is attributed to only a few of the site pairs.

MANAGEMENT CONSIDERATIONS

Management Areas

Several aspects of the biology of this species warrant a conservative management approach (Caddy 1989). The lack of a planktonic dispersal phase, and the relatively small range of adults (Himmelman 1988, McQuinn *et al.* 1988), suggest that the effective population size is small and local.

Thomas and Himmelman (1988), followed by Gendron (1992), have further suggested that these local populations may be locally adapted to predators and parasites with substantial differences in size-at-maturity and yield among populations. Evidence for strong local adaptation and sexual dimorphism in whelk populations along the Atlantic coast of Nova Scotia is provided here. Therefore, local management zones will be required for management to be consistent with the nature of the resource. This management strategy is being used for sea urchins at present and appears to be highly effective (Miller 1996).

Measures for Sustainability of the Resource

A *minimum size regulation* will be required to conserve broodstock. However, it is clear that this minimum size would have to be determined separately for each fishing area, matching variations in size-at-sexual-maturity of the females (Gendron 1992). At present we have little information on female size-at-sexual-maturity for ***Buccinum*** along the Atlantic coast of Nova Scotia. All of the females in this study possessed a gonad, but the viability of the eggs produced and the fecundity of the animals are unknown. There is no need for a maximum size limit, as large animals are believed to have low fecundity (Gendron 1992). With respect to the males, sexual maturity as indicated by penis ratios greater than 0.50, was observed in the majority (76%) of animals greater than 40 mm shell height.

Gendron (1992) reports that in 7 out of 8 study sites in the Gulf of St. Lawrence, males were sexually mature at a smaller size than the females. If we assume that the females also assume sexual maturity at a greater size along the Atlantic coast and that the relative size difference between sexes observed in the Gulf is also similar, then Gendron's (1992) data can be used to predict the size-of-maturity of the females along the Atlantic coast. In her study, approximately 50% of the females reached sexual maturity (derived from logistic equations, *cf.* Gendron 1992) at average sizes 1.157 times those of the males from the same population (range 1.027 - 1.352). *If* this scale of dimorphism is applicable to the Atlantic coast, then the female size-at-sexual-maturity can be expected to be between 41 and 54 mm shell height. In the absence of further site specific information, *60 mm* should be implemented as a conservative minimum harvest size to allow females to reach sexual maturity before capture. This size will be highly restrictive to the fishery given the size distribution of the whelks identified in this study and illustrated in Figure 3.

In the Quebec region, *trap limits* (100 per license), trap volume limits (max. external vol. $< 0.3m^3$), *area restrictions* and *license limits* are defined in the licensing policy as effort controls (Anonymous 1990). Similar restrictions may be appropriate for a Scotia-Fundy fishery to prevent over-development of the fishery before sufficient knowledge is gathered to permit effective conservation.

Seasonal closures due to PSP can be anticipated particularly on the South Shore of Nova Scotia, and if coincident with the mating and egg laying period (May to August) may prove beneficial to recruitment. In order to sustain local populations, both broodstock and egg laying habitat (kelp, boulders) must be protected. It may be advantageous to identify such areas within each management unit and set them aside as permanent closed areas or *conservation zones*.

Fishers may attempt to compensate for the relatively low market value of the whelk by fishing for a greater catch. It should be recognized that the resource may not be large enough to support the removal of large numbers of animals on a continual basis. In Quebec the fishery is a *complementary* fishery in that fishers hold other licences and only direct for whelks for a portion of the year. Such an approach would seem appropriate for this resource on the Atlantic coast.

Ecological Concerns

Buccinum undatum is a predator and so is higher up on the food chain than the filter feeding molluscs which support large commercial fisheries. Reduction of predation pressure from an ecosystem can have marked and often unpredictable effects on the prey species. It may be assumed that the removal of whelks will result in increased production of clams and other prey species, however, replacement by more voracious predators could result in a loss of shellfish production over the longer term. Along the Atlantic coast, two other whelk species are common and appear to co-exist with *Buccinum*. *Neptunea decemcostata*, the ten-ridged whelk, is found at shallower depths (subtidal to about 70 m) and is also sometimes caught in lobster traps. In some areas, *Neptunea* is more common than *Buccinum*. *Colus stimpsoni* is also found with *Buccinum* and is reported to be the more dominant species offshore on Banquereau Bank (D. Roddick, BIO-DFO, pers. comm.).

Neptunea produces toxins that cause severe illness in man if eaten. The toxins are found in the salivary (or "buccal") glands. The main toxic substance in the glands of *Neptunea decemcostata* is tetramine, but histamine, choline and choline esters have also been identified (G. Burns, Inspection Branch, DFO-Halifax, pers. comm.). The harvest of *Neptunea* and *Colus* are prohibited under the inshore exploratory fishery licence. *Colus* is a permissible by-catch of the Stimpson's Surfclam fishery (offshore). Therefore, removal of *Buccinum* from the ecosystem will most likely result in a replacement by *Neptunea* and or *Colus*.

By-catch

Other species caught in whelk traps include the sea urchin, hermit crab, lobster, sculpin, snow crab, ocean pout, sea cucumber and monkfish, with ocean pout being particularly troublesome (Appendix 1; unpublished DFO Scotia-Fundy Region Central Registry document 2901, John Mac Innes, PO Box 113, Mabou, N.S.).

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Table 1. Whelk Descriptive Statistics

Combined Data by Location

Shell Height (mm)

Location	Mean	Std. Dev.	Minimum	Maximum	N
Point Aconi	46.2	7.9	34	75	41
Main-à-Dieu	52.2	6.5	39	68	46
Louisbourg	48.8	6.4	34	67	113
Fourchu	51.5	6.5	40	64	50
Petit de Grat	45.3	7.9	28	62	66
Offshore	65.8	9.7	33	93	512
Owls Head	56.2	8.3	36	74	40
Osborne Harbour	59.0	6.3	48	77	50
Argyle	57.1	6.3	40	73	81
Tusket Shoal*	59.8	4.5	45	71	191
Port Maitland	55.5	8.2	39	72	29
Annapolis Basin	48.7	15.8	29	71	7
Digby	47.2	11.8	19	69	330
Saint John	49.4	11.9	26	66	101

Total Weight (g)

Location	Mean	Std. Dev.	Minimum	Maximum	N
Point Aconi	19.8	10.2	6.4	59.7	41
Main-à-Dieu	23.5	8.3	9.6	51.4	46
Louisbourg	20.8	7.9	6.6	41.2	113
Fourchu	26.4	8.6	11.5	42.2	50
Petit de Grat	17.5	8.5	3.3	37.9	66
Offshore	32.3	12.2	3.9	71.3	512
Owls Head	27.8	10.5	7.4	50.7	40
Osborne Harbour	32.1	9.3	13.9	54.1	50
Argyle	31.2	9.5	10.6	61.8	81
Tusket Shoal*	39.0	7.7	20.0	58.8	191
Port Maitland	29.6	13.0	9.3	58.6	29
Annapolis Basin	21.2	19.2	3.3	50.4	7
Digby	14.4	8.7	0.8	38.3	330
Saint John	16.6	8.4	2.2	35.1	101

Table 1 cont'd. Whelk Descriptive Statistics

Combined Data by Location

Tissue Weight (g)

Location	Mean	Std. Dev.	Minimum	Maximum	N
Point Aconi	5.9	3.9	1.0	19.6	41
Main-à-Dieu	7.4	3.1	2.4	16.2	46
Louisbourg	6.4	2.6	1.9	13.0	113
Fourchu	8.3	3.1	3.0	15.1	50
Petit de Grat	5.9	3.0	1.1	14.3	66
Offshore	21.1	8.3	2.0	47.4	512
Owls Head	7.4	3.6	2.0	18.0	40
Osborne Harbour	11.5	3.8	4.8	21.4	50
Argyle	8.9	3.4	1.9	19.5	81
Tusket Shoal*	12.1	3.5	5.2	21.3	191
Port Maitland	-	-	-	-	-
Annapolis Basin	8.4	8.4	1.2	22.2	7
Digby	7.1	4.5	0.3	18.4	325
Saint John	7.9	4.7	0.6	18.3	101

Foot Weight (g)

Location	Mean	Std. Dev.	Minimum	Maximum	N
Point Aconi	3.3	2.0	0.6	10.6	41
Main-à-Dieu	4.0	1.7	1.3	9.7	46
Louisbourg	3.5	1.4	1.1	7.2	113
Fourchu	4.9	1.8	2.0	9.5	50
Petit de Grat	3.3	1.6	0.6	7.4	66
Offshore	11.1	4.9	0.6	28.4	512
Owls Head	4.3	2.0	1.3	10.4	40
Osborne Harbour	6.2	1.8	2.6	10.7	50
Argyle	5.7	2.0	1.2	11.7	81
Tusket Shoal*	7.0	2.3	2.4	13.8	191
Port Maitland	-	-	-	-	-
Annapolis Basin	4.3	4.2	0.6	11.3	7
Digby	4.1	2.7	0.2	10.5	330
Saint John	4.9	3.1	0.4	11.4	101

Table 1 cont'd. Whelk Descriptive Statistics

Combined Data by Location

Penis Length (mm)

Location	Mean	Std. Dev.	Minimum	Maximum	N
Point Aconi	27.3	8.6	8	40	20
Main-à-Dieu	27.8	9.1	6	37	21
Louisbourg	24.3	6.1	9	37	36
Fourchu	26.0	4.3	20	36	12
Petit de Grat	25.9	10.0	5	39	26
Offshore	45.5	13.3	6	69	215
Owls Head	23.3	9.7	2	32	6
Osborne Harbour	31.6	9.5	16	39	5
Argyle	30.5	12.4	11	48	18
Tusket Shoal*	28.3	9.8	3	46	60
Port Maitland	-	-	-	-	-
Annapolis Basin	6.0	4.4	3	11	3
Digby	23.9	16.4	4	60	162
Saint John	21.5	15.0	2	46	75

Aperture Length (mm)

Location	Mean	Std. Dev.	Minimum	Maximum	N
Point Aconi	-	-	-	-	-
Main-à-Dieu	-	-	-	-	-
Louisbourg	-	-	-	-	-
Fourchu	-	-	-	-	-
Petit de Grat	-	-	-	-	-
Offshore	33.8	5.6	5	48	189
Owls Head	-	-	-	-	-
Osborne Harbour	-	-	-	-	-
Argyle	-	-	-	-	-
Tusket Shoal	-	-	-	-	-
Port Maitland	-	-	-	-	-
Annapolis Basin	28.4	9.5	16	43	7
Digby	27.0	6.4	11	38	330
Saint John	-	-	-	-	-

Table 1 cont'd. Whelk Descriptive Statistics

Combined Data by Location

Age (yrs)

Location	Mean	Std. Dev.	Minimum	Maximum	N
Point Aconi	-	-	-	-	-
Main-à-Dieu	-	-	-	-	-
Louisbourg	-	-	-	-	-
Fourchu	-	-	-	-	-
Petit de Grat	-	-	-	-	-
Offshore	5.9	1.2	2	9	229
Owls Head	-	-	-	-	-
Osborne Harbour	-	-	-	-	-
Argyle	-	-	-	-	-
Tusket Shoal	-	-	-	-	-
Port Maitland	-	-	-	-	-
Annapolis Basin	4.7	1.6	3	7	7
Digby	5.4	1.3	2	10	323
Saint John	-	-	-	-	-

Yield (%) = (Foot Weight/Total Weight)*100

Location	Mean	Std. Dev.	Minimum	Maximum	N
Point Aconi	16.1	3.5	8.6	23.4	41
Main-à-Dieu	16.7	2.4	11.3	21.2	46
Louisbourg	17.1	2.7	10.7	23.8	113
Fourchu	18.7	2.7	13.9	26.4	50
Petit de Grat	19.0	2.4	13.7	25.9	66
Offshore	36.9	6.8	14.9	57.9	512
Owls Head	19.0	2.4	13.7	25.9	66
Osborne Harbour	19.3	2.3	12.1	25.0	50
Argyle	18.0	2.6	10.7	23.5	81
Tusket Shoal	-	-	-	-	-
Port Maitland	-	-	-	-	-
Annapolis Basin	19.2	1.9	17.2	22.4	7
Digby	27.0	6.4	12.1	42.6	330
Saint John	27.2	8.1	7.1	41.2	101

Table 1 cont'd. Whelk Descriptive Statistics

Combined Data by Location

Shell Weight (g)

Location	Mean	Std. Dev.	Minimum	Maximum	N
Point Aconi	13.9	6.6	5.4	41.5	41
Main-à-Dieu	16.1	5.5	6.8	35.8	46
Louisbourg	14.4	5.4	4.3	29.1	113
Fourchu	18.1	5.8	7.5	27.5	50
Petit de Grat	11.6	5.7	1.9	23.8	66
Offshore	11.3	5.1	1.5	40.8	512
Owls Head	20.4	7.2	5.4	33.2	40
Osborne Harbour	20.6	6.0	9.0	37.3	50
Argyle	22.4	6.5	7.7	42.5	81
Tusket Shoal*	26.9	5.0	14.6	41.7	191
Port Maitland	-	-	-	-	-
Annapolis Basin	12.8	10.9	2.1	28.2	7
Digby	7.5	4.5	0.5	22	330
Saint John	8.7	3.9	1.4	18.0	101

*Data from Kenchington and Lundy (1996)

Table 2. Regression Statistics of Whelk Foot Weight (Y) against Shell Height (X) by Locality

Locality	Regression Equation	Adjusted R^2	Foot Weight 70 mm Shell
Point Aconi	$Y = 0.000007 * X^{3.380}$	0.852	11.9g
Main-à-Dieu	$Y = 0.000094 * X^{2.677}$	0.668	8.2g
Louisbourg	$Y = 0.000061 * X^{2.807}$	0.815	9.2g
Fourchu	$Y = 0.000125 * X^{2.673}$	0.795	10.7g
Petit de Grat	$Y = 0.000047 * X^{2.906}$	0.937	10.8g
Offshore	$Y = 0.000098 * X^{2.779}$	0.739	13.1g
Owls Head	$Y = 0.000109 * X^{2.673}$	0.642	7.0g
Osborne Hbr.	$Y = 0.000200 * X^{2.525}$	0.750	9.1g
Argyle	$Y = 0.000016 * X^{3.143}$	0.835	10.1g
Tusket Shoal	-	-	-
Port Maitland	-	-	-
Annapolis	$Y = 0.000010 * X^{3.265}$	0.986	10.6g
Digby	$Y = 0.000021 * X^{3.109}$	0.933	11.4g
Saint John	$Y = 0.000004 * X^{3.559}$	0.960	14.7g

Table 3. Sex Ratio of Whelks from Different Geographic Areas

Location	Number of Males: Number of Females	
Digby	1.37	
Offshore	0.84	
Annapolis Basin	1.33	
Louisbourg	0.46	
Main-à-Dieu	1.09	
Owls Head	0.25	
Petit de Grat	0.89	
Point Aconi	0.95	
Saint John	2.48*	
Port Maitland	-	
Osborne Harbour	0.11	
Argyle	0.40	
Tusket Shoal	0.46	(Kenchington and Lundy 1996)
Fourchu	0.43	
Gulf of St. Lawrence	0.29	(Lanteigne and Davidson 1992)

*10% of animals with imposex

Table 4. Analyses of Sexual Dimorphism

Variable	Sex	N	Mean	Std. Error	t-value	2-tailed P
Shell Height	Male	654	53.16	0.496	-7.53	0.000*
	Female	771	58.06	0.421		
Aperture Length	Male	259	28.74	0.404	-3.76	0.000
	Female	245	30.93	0.418		
Shell Weight	Male	654	9.85	0.201	-13.39	0.000*
	Female	771	14.28	0.261		
Total Weight	Male	654	21.17	0.475	-9.87	0.000
	Female	771	27.57	0.442		
Tissue Weight	Male	654	11.31	0.348	-4.25	0.000
	Female	771	13.29	0.313		
Foot Weight	Male	654	7.03	0.222	-0.31	0.755*
	Female	770	7.11	0.158		
%Yield	Male	654	30.02	0.418	9.27	0.000*
	Female	770	25.24	0.303		

*separate variance estimates used

Table 5. Pearson Product-Moment Correlations Between Natural Log (Ln)-Transformed Shell Height and Other Variables using a One-tailed Significance Level

Variable 1	Variable 2	N	Pearson Correlation	P
Shell Height	Shell Weight	1433	0.72	0.000
	Tissue Weight	1433	0.96	0.000
	Total Weight	1466	0.94	0.000
	Foot Weight	1432	0.95	0.000
	Aperture Length	526	0.92	0.000
	%Yield	1432	0.42	0.000

Table 6. Factor Analysis Statistics Based on Transformed Whelk Morphometric Characters

Initial Statistics (Unrotated Solution):

Variable	Communality	*	Factor	Eigenvalue	Pct of Var	Cum Pct
LN FOOT WT	1.00000	*	1	4.56315	76.1	76.1
LN SHELL HT	1.00000	*	2	1.34655	22.4	98.5
LN SHELL WT	1.00000	*	3	.05569	.9	99.4
LN TISS WT	1.00000	*	4	.03094	.5	99.9
LN TOTAL WT	1.00000	*	5	.00368	.1	100.0
LN YIELD	1.00000	*	6	.00000	.0	100.0

Factor Matrix:

	Factor 1	Factor 2
LN FOOT WT	.97999	.18816
LN SHELL HT	.98218	-.00611
LN SHELL WT	.74352	-.65370
LN TISS WT	.97932	.16092
LN TOTAL WT	.96598	-.25031
LN YIELD	.43941	.89176

Final Statistics (2 Factors):

Variable	Communality	*	Factor	Eigenvalue	Pct of Var	Cum Pct
LN FOOT WT	.99579	*	1	4.56315	76.1	76.1
LN SHELL HT	.96472	*	2	1.34655	22.4	98.5
LN SHELL WT	.98014	*				
LN TISS WT	.98496	*				
LN TOTAL WT	.99577	*				
LN YIELD	.98831	*				

Factor Transformation Matrix:

	Factor 1	Factor 2
Factor 1	.92896	.37018
Factor 2	-.37018	.92896

Rotated Factor Matrix (Varimax Rotation):

	Factor 1	Factor 2
LN FOOT WT	.84073	.53756
LN SHELL HT	.91467	.35791
LN SHELL WT	.93268	-.33203
LN TISS WT	.85018	.51201
LN TOTAL WT	.99001	.12505
LN YIELD	.07809	.99107

Table 7. Depth Distribution of Whelk Samples from Digby, Nova Scotia

Depth (m)	Frequency	Percent	Cumulative Percent
52	3	.9	.9
69	1	.3	1.2
70	7	2.1	3.3
71	1	.3	3.6
72	8	2.4	6.1
73	1	.3	6.4
74	28	8.5	14.8
75	13	3.9	18.8
76	11	3.3	22.1
77	9	2.7	24.8
78	13	3.9	28.8
79	3	.9	29.7
80	2	.6	30.3
82	18	5.5	35.8
83	2	.6	36.4
86	2	.6	37.0
87	7	2.1	39.1
88	24	7.3	46.4
89	46	13.9	60.3
90	7	2.1	62.4
91	5	1.5	63.9
93	15	4.5	68.5
94	23	7.0	75.5
96	6	1.8	77.3
98	25	7.6	84.8
99	10	3.0	87.9
100	2	.6	88.5
101	13	3.9	92.4
102	3	.9	93.3
103	2	.6	93.9
107	8	2.4	96.4
108	2	.6	97.0
111	1	.3	97.3
112	7	2.1	99.4
113	2	.6	100.0
Total	330	100.0	100.0

Statistics:

Variable	Mean	Std. Dev.	Range	Minimum	Maximum
DEPTH	87.66	11.06	61	52	113

Table 8. Calculation of the Von Bertalanffy Growth Function for the Aged Whelk Sample

Nonlinear Regression Summary Statistics

Source	DF	Sum of Squares	Mean Square
Regression	3	1717876.47467	572625.49156
Residual	556	58600.52533	105.39663
Uncorrected Total	559	1776477.00000	
(Corrected Total)	558	108086.08587	

R squared = 1 - Residual SS / Corrected SS = .45783

Parameter	Estimate	Asymptotic Std. Error	Asymptotic 95 % Confidence Interval Lower	Upper
L_{inf}	80.4731	5.4968	69.6761	91.2701
k	.2744	.0540	.1684	.3804
$t_{(0)}$	1.2010	.2818	.6475	1.7545

Asymptotic Correlation Matrix of the Parameter Estimates

	L_{inf}	k	$t_{(0)}$
L_{inf}	1.0000	-.9730	-.8047
k	-.9730	1.0000	.9116
$t_{(0)}$	-.8047	.9116	1.0000

Table 9. ANOVA of Penis Ratio by Location with Summary Statistics

Analysis of Variance

Source	D.F.	Sum of Squares	Mean Squares	F Ratio	F Prob.
Between Groups	10	6.2841	.6284	13.6943	.0000
Within Groups	574	26.3399	.0459		
Total	584	32.6240			

Group	Count	Mean	Standard Deviation	Standard Error	95 Pct Conf Int for Mean		
Argyle	18	.5526	.2132	.0502	.4466	TO	.6586
Digby	162	.4607	.2679	.0211	.4191	TO	.5022
Fourchu	12	.5411	.0910	.0263	.4833	TO	.5989
Louisbourg	36	.5366	.1272	.0212	.4935	TO	.5796
Main à Dieu	21	.5654	.1809	.0395	.4831	TO	.6478
Osborne Hbr	5	.6096	.1778	.0795	.3888	TO	.8303
Owls Head	6	.5143	.2174	.0888	.2861	TO	.7425
Petit de Grat	26	.5977	.2259	.0443	.5064	TO	.6889
Saint John	65	.4388	.2364	.0293	.3803	TO	.4974
Offshore	214	.6892	.1788	.0122	.6651	TO	.7133
Point Aconi	20	.6359	.1883	.0421	.5478	TO	.7240
Total	585	.5687	.2364	.0098	.5495	TO	.5878

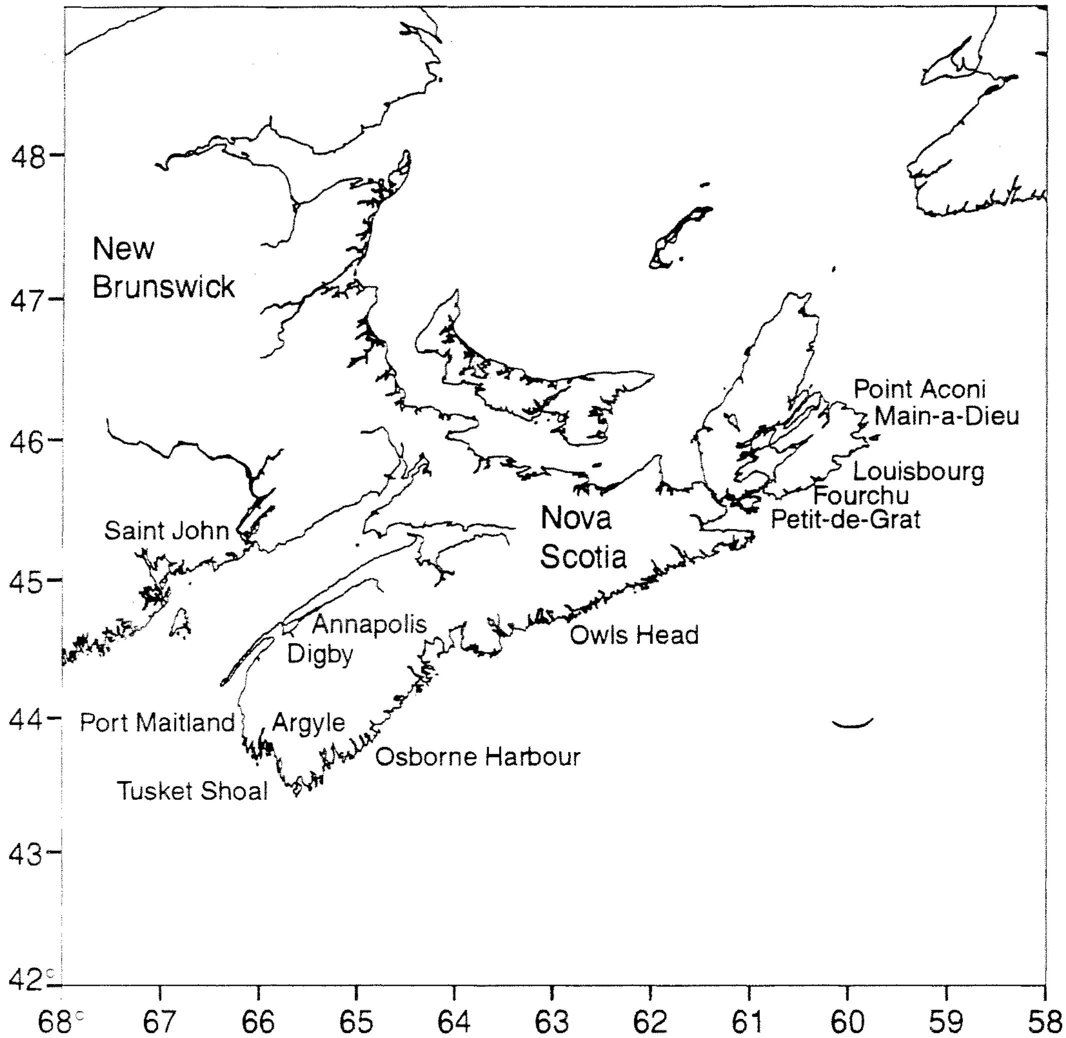


Figure 1. *Buccinum undatum.* General location of inshore whelk sampling sites in New Brunswick and Nova Scotia.

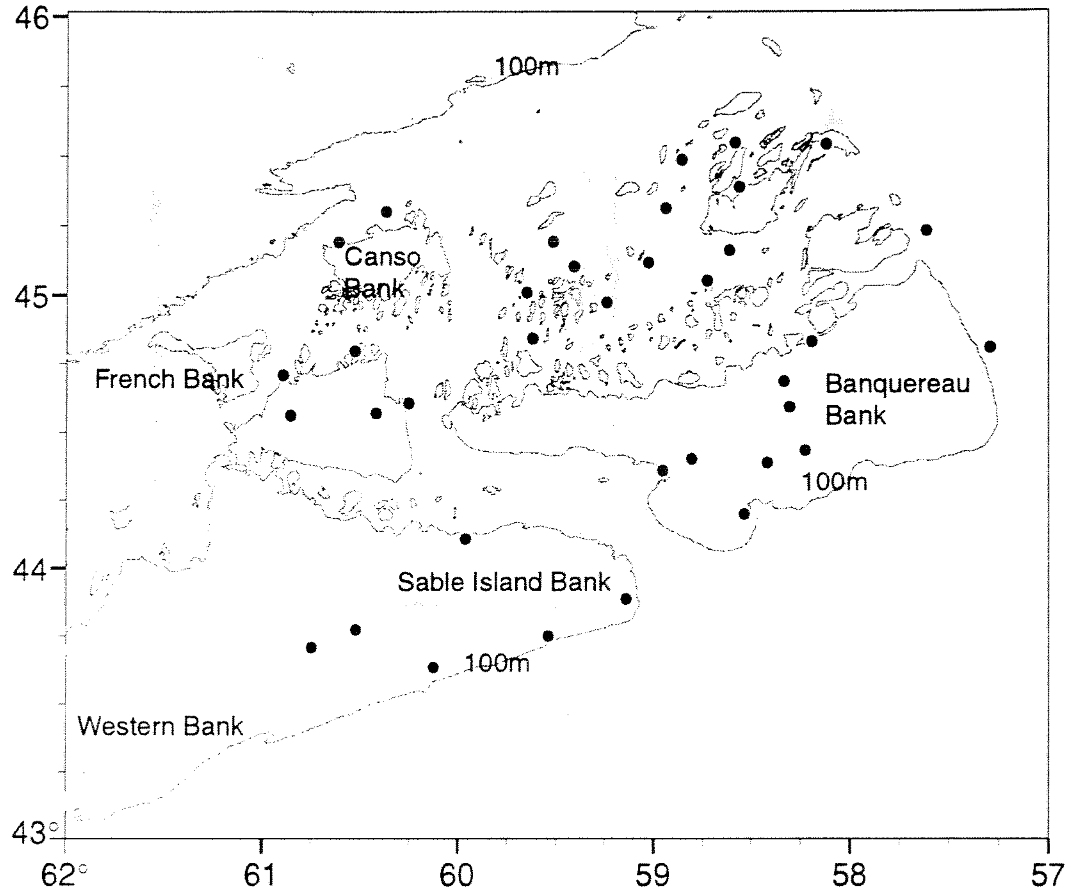
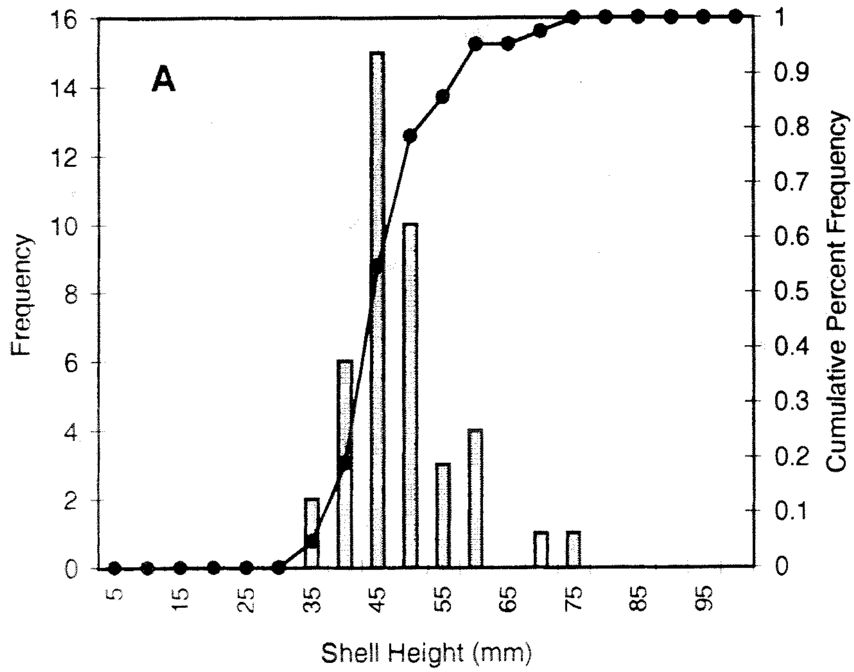


Figure 2. *Buccinum undatum*. Location of offshore whelk samples collected during the 1996 DFO spring groundfish cruise (N255).

POINT ACONI, CAPE BRETON



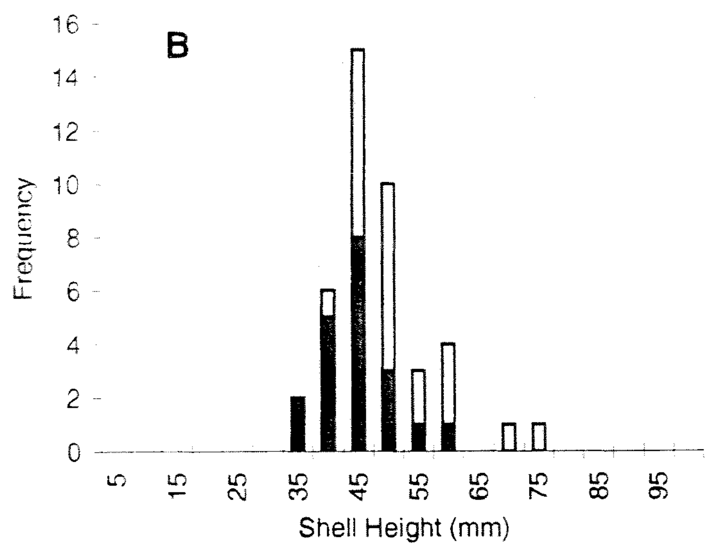


Figure 3. A) Cumulative percent frequency and frequency of whelks collected at Point Aconi, Cape Breton. B) Percent frequency of whelks by sex; male shaded, female open.

MAIN A DIEU, CAPE BRETON

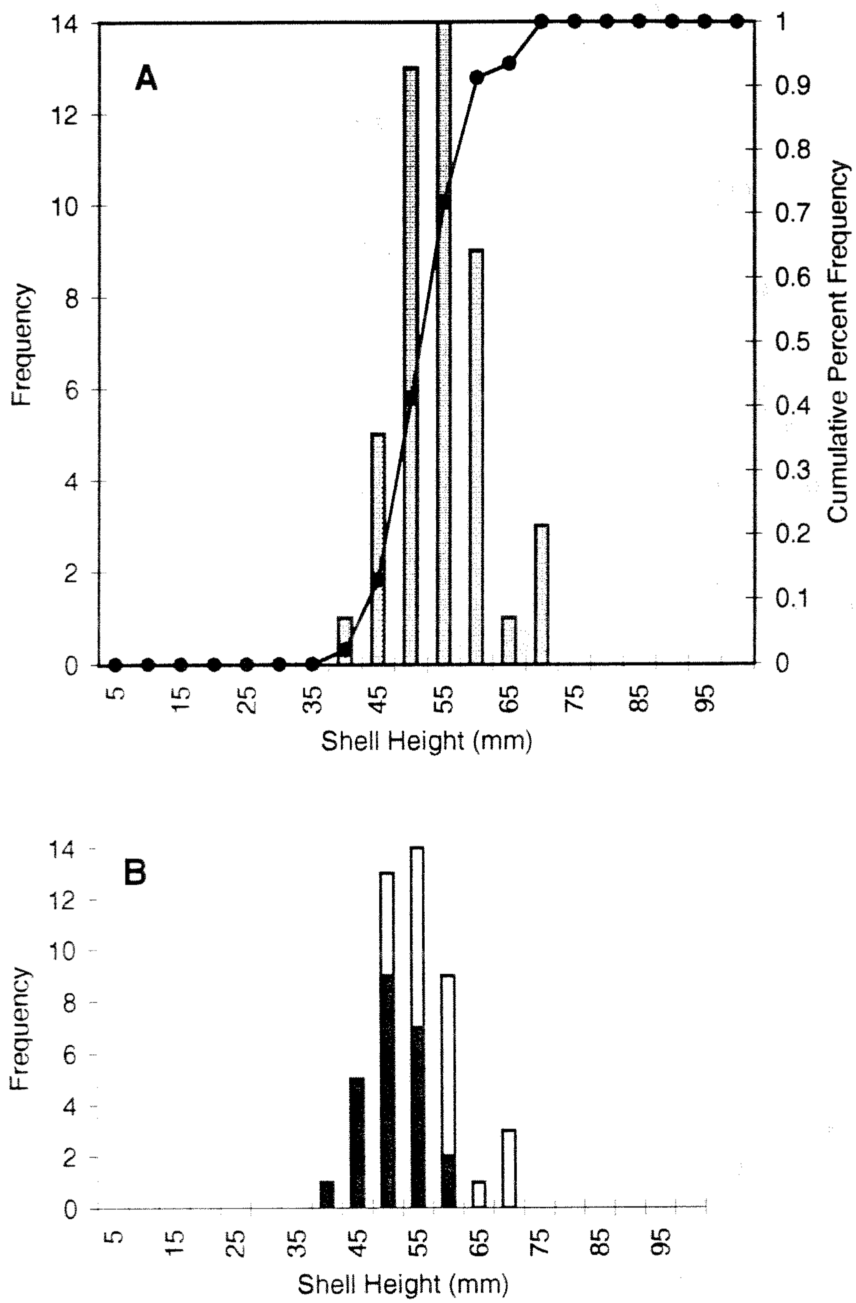
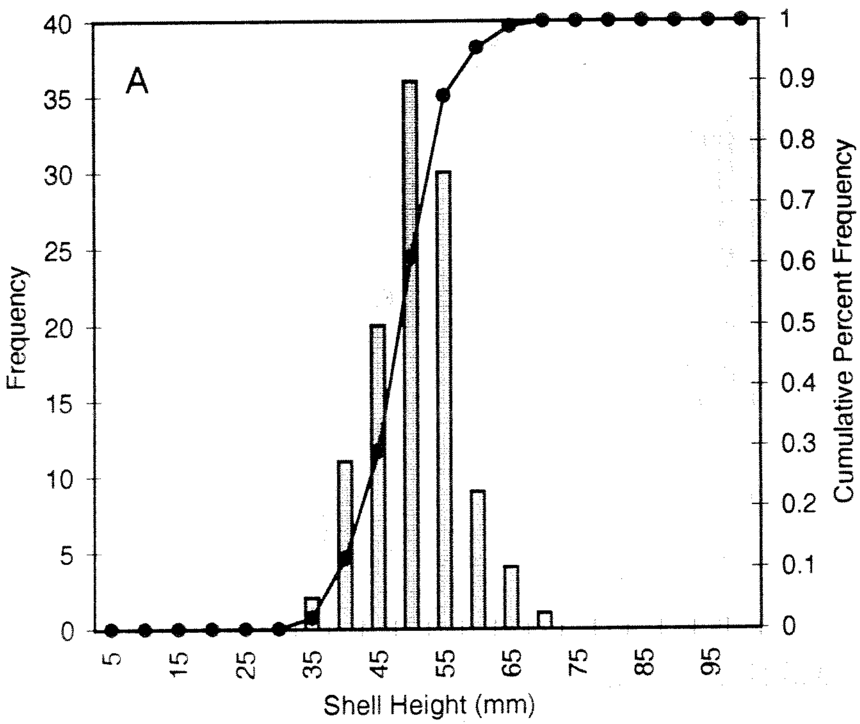


Figure 4. A) Cumulative percent frequency and frequency of whelks collected at Main a Dieu Cape Breton. B) Percent frequency of whelks by sex; male shaded, female open.

LOUISBOURG, CAPE BRETON



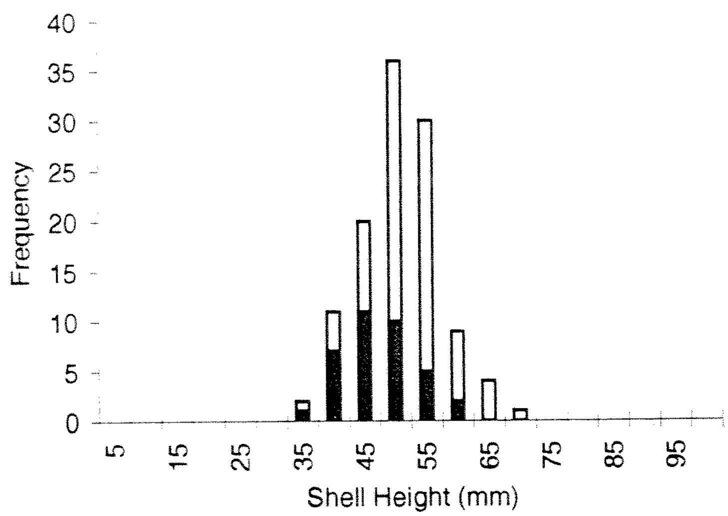


Figure 5. A) Cumulative percent frequency and frequency of whelks collected at Louisbourg, Cape Breton. B) Percent frequency of whelks by sex; male shaded, female open.

FOURCHU, CAPE BRETON

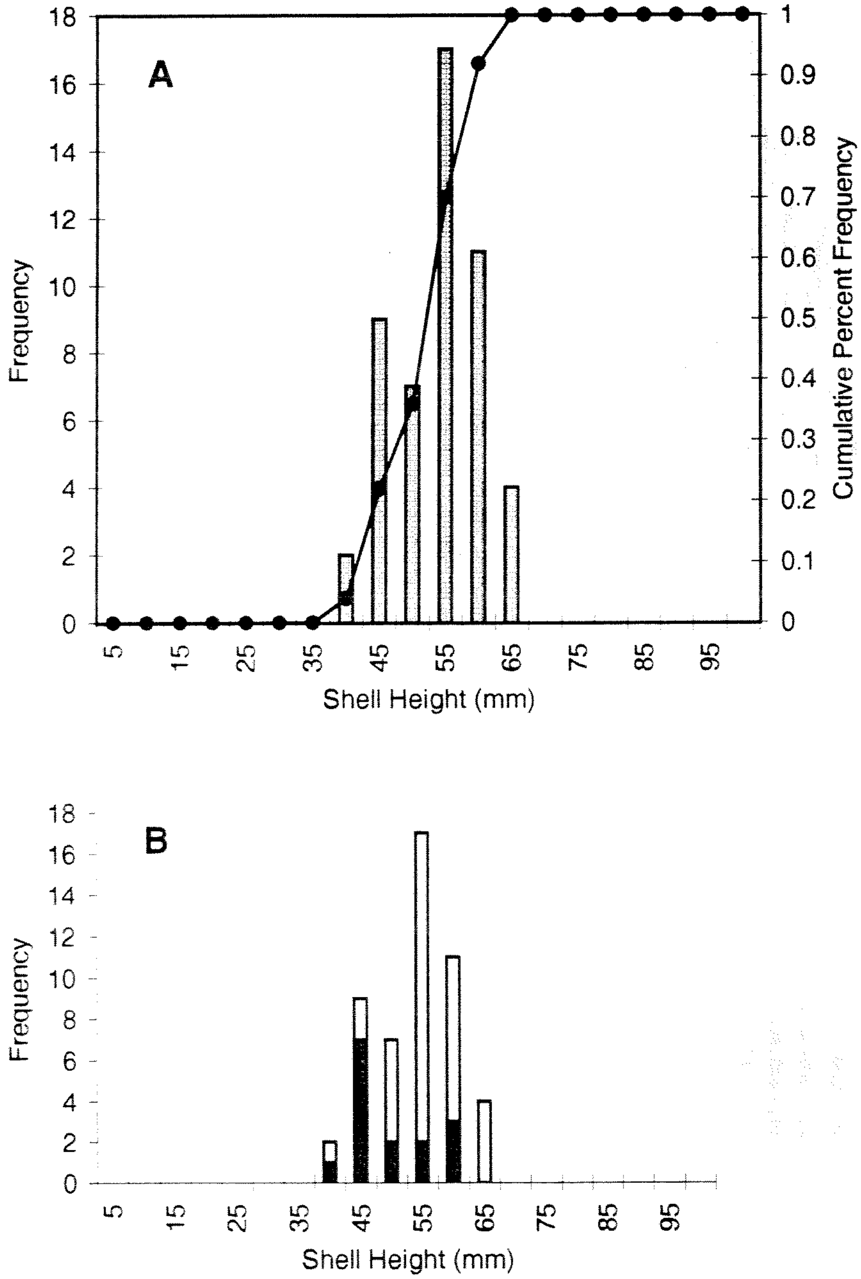


Figure 6. A) Cumulative percent frequency and frequency of whelks collected at Fourchu, Cape Breton. B) Percent frequency of whelks by sex; male shaded, female open.

PETIT DE GRAT, CAPE BRETON

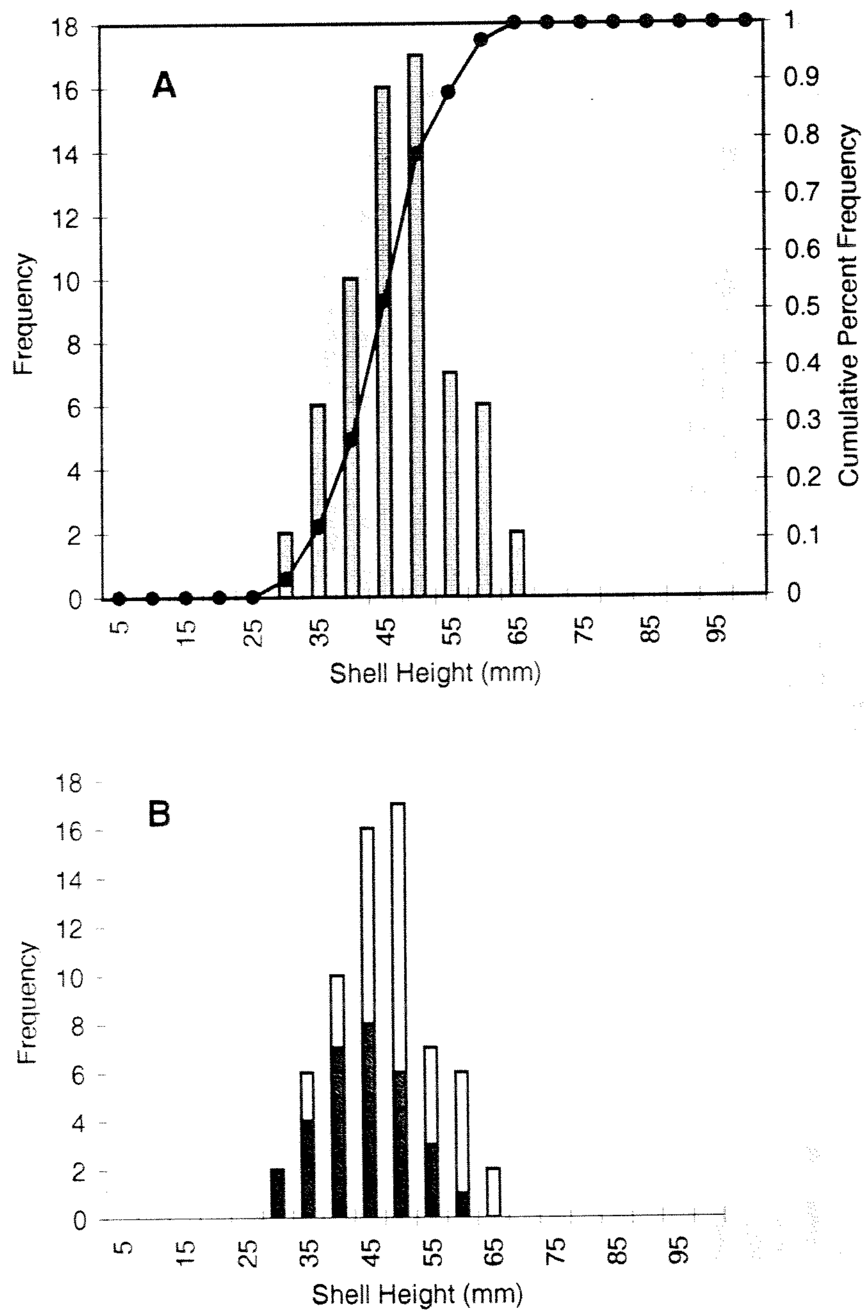


Figure 7. A) Cumulative percent frequency and frequency of whelks collected at Petit de Grat Cape Breton. B) Percent frequency of whelks by sex; male shaded, female open.

OFFSHORE SHELF

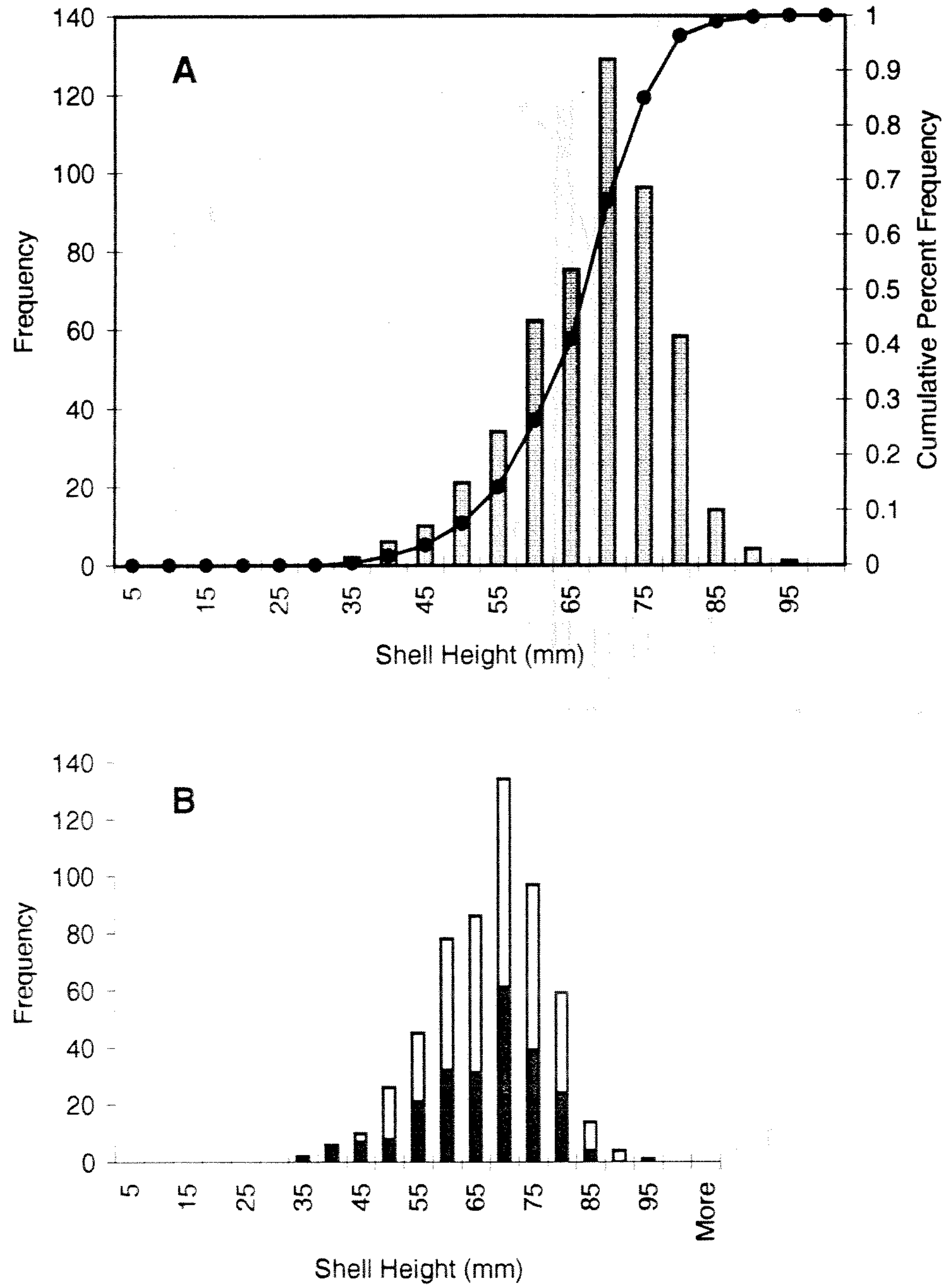
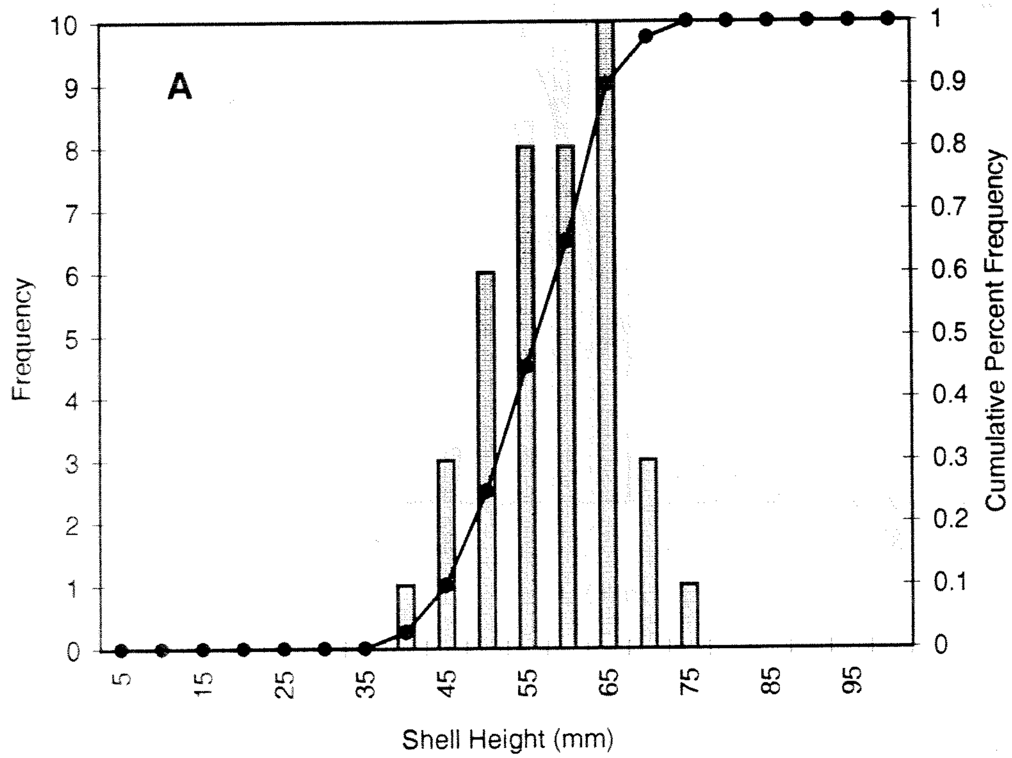


Figure 8. A) Cumulative percent frequency and frequency of whelks collected offshore N.S. (see Fig. 2 for location). B) Percent frequency of whelks by sex; male shaded, female open.

OWLS HEAD, EASTERN SHORE, NOVA SCOTIA



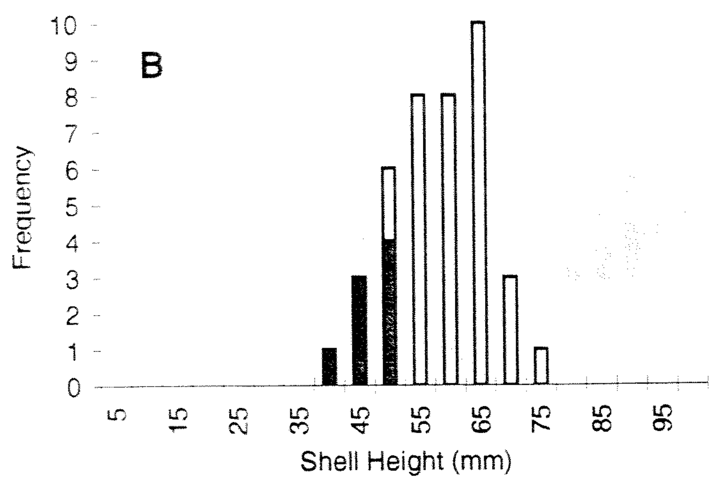


Figure 9. A) Cumulative percent frequency and frequency of whelks collected at Owls Head, Eastern Shore, N.S. B) Percent frequency of whelks by sex; male shaded, female open.

OSBORNE HARBOUR, SOUTHWEST NOVA SCOTIA

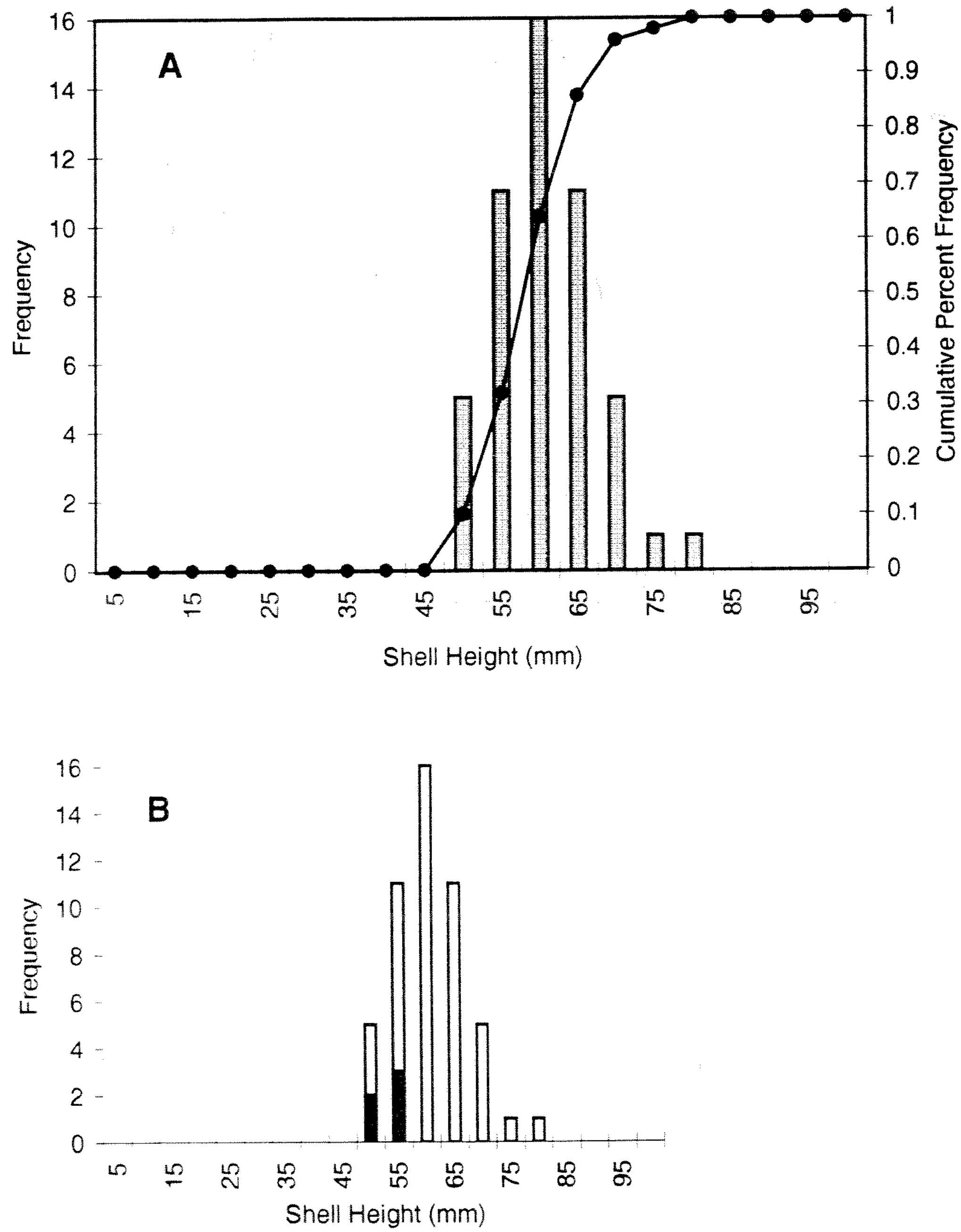


Figure 10. A) Cumulative percent frequency and frequency of whelks collected at Osborne Hbr., southwest N.S. B) Percent frequency of whelks by sex; male shaded, female open.

ARGYLE, SOUTHWEST NOVA SCOTIA

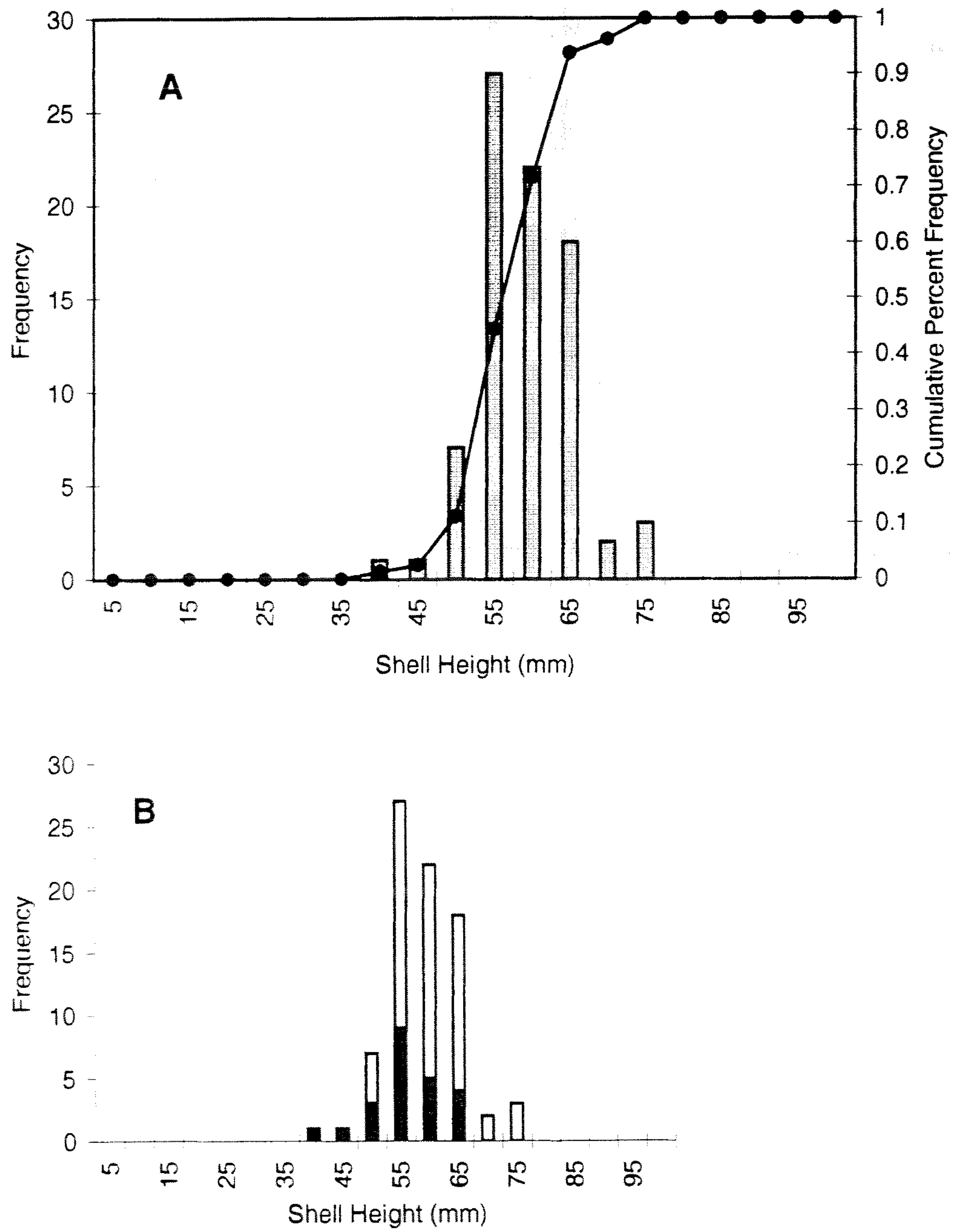


Figure 11. A) Cumulative percent frequency and frequency of whelks collected at Argyle, southwest N.S. B) Percent frequency of whelks by sex; male shaded, female open.

DIGBY, BAY OF FUNDY, NOVA SCOTIA

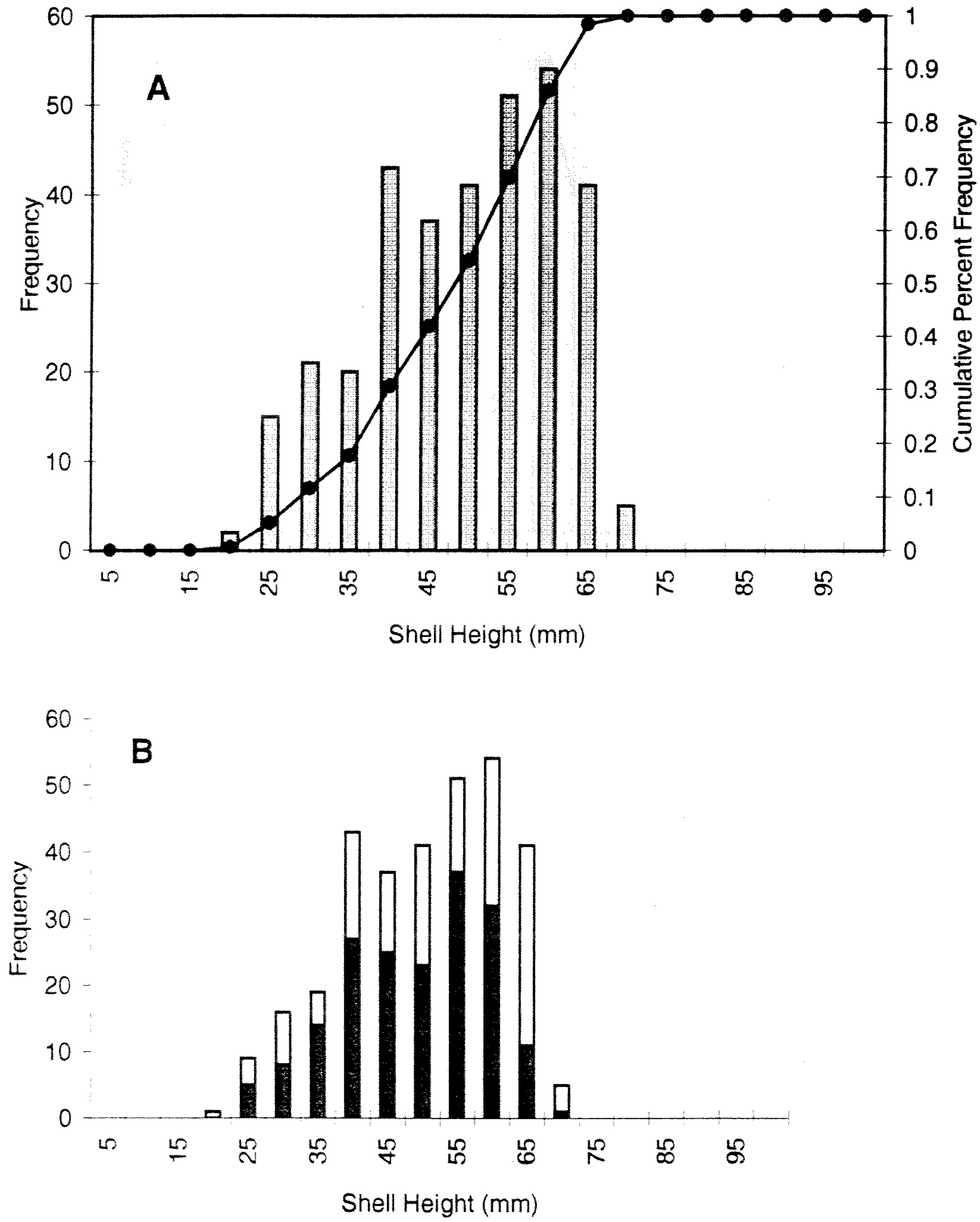


Figure 12. A) Cumulative percent frequency and frequency of whelks collected at Digby, N.S. B) Percent frequency of whelks by sex; male shaded, female open.

SAINT JOHN, NEW BRUNSWICK

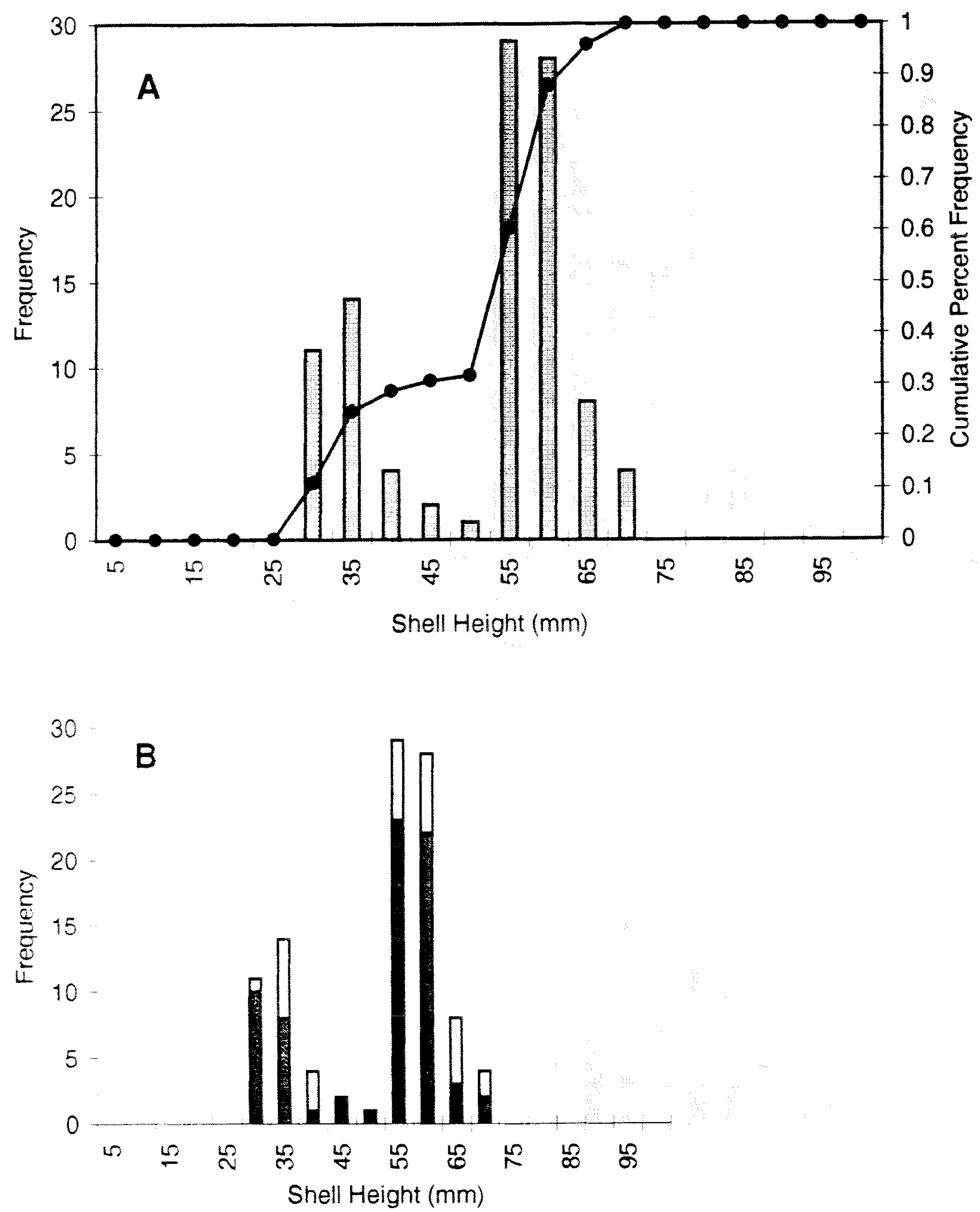


Figure 13. A) Cumulative percent frequency and frequency of whelks collected at Saint John, N.B. B) Percent frequency of whelks by sex; male shaded, female open.

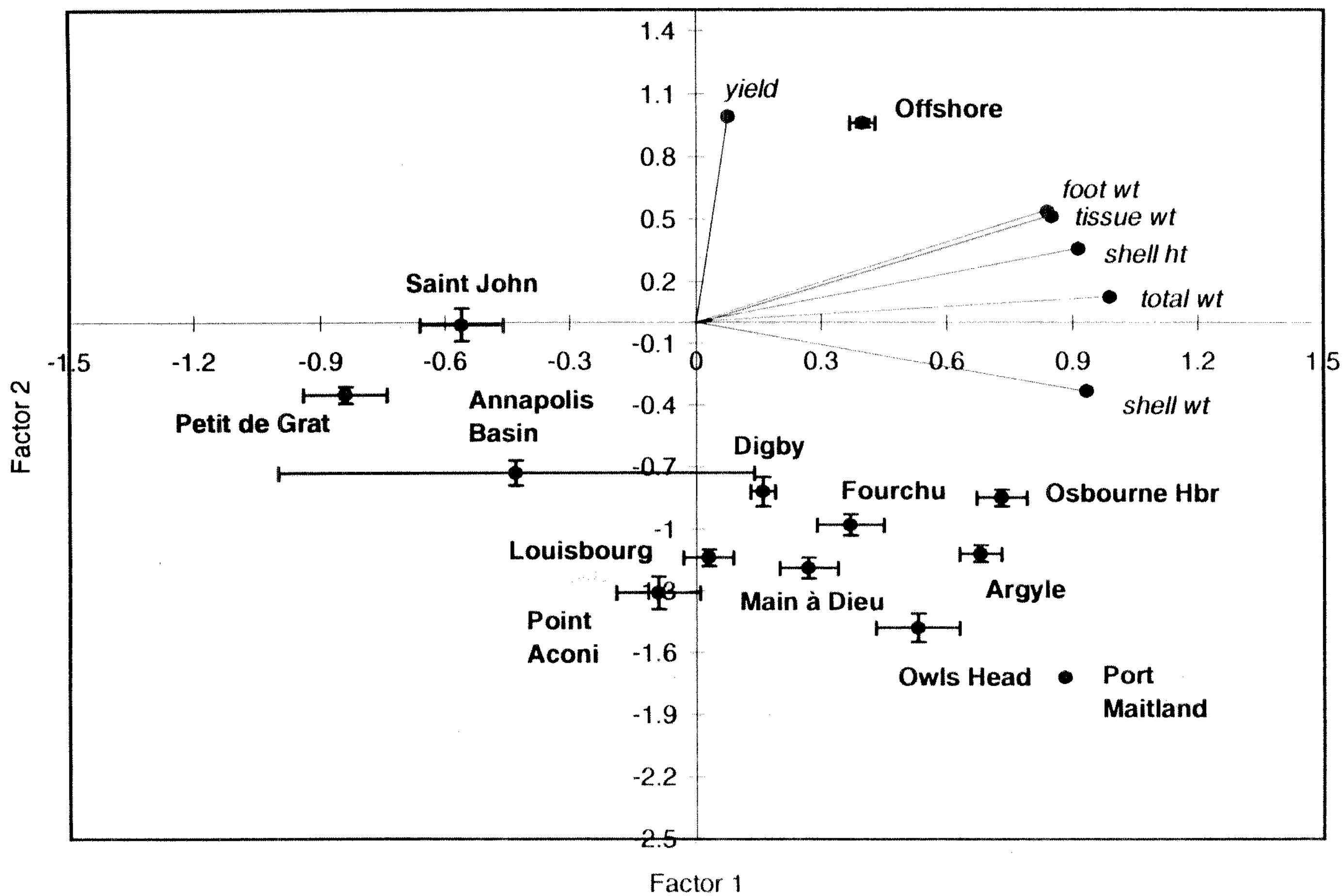


Figure 14. *Buccinum undatum*. Factor Analysis. Position of population (solid circle) means with standard error. Population names are indicated near the mean symbol. The weighting of each morphometric character is illustrated as a vector (see Table 6).

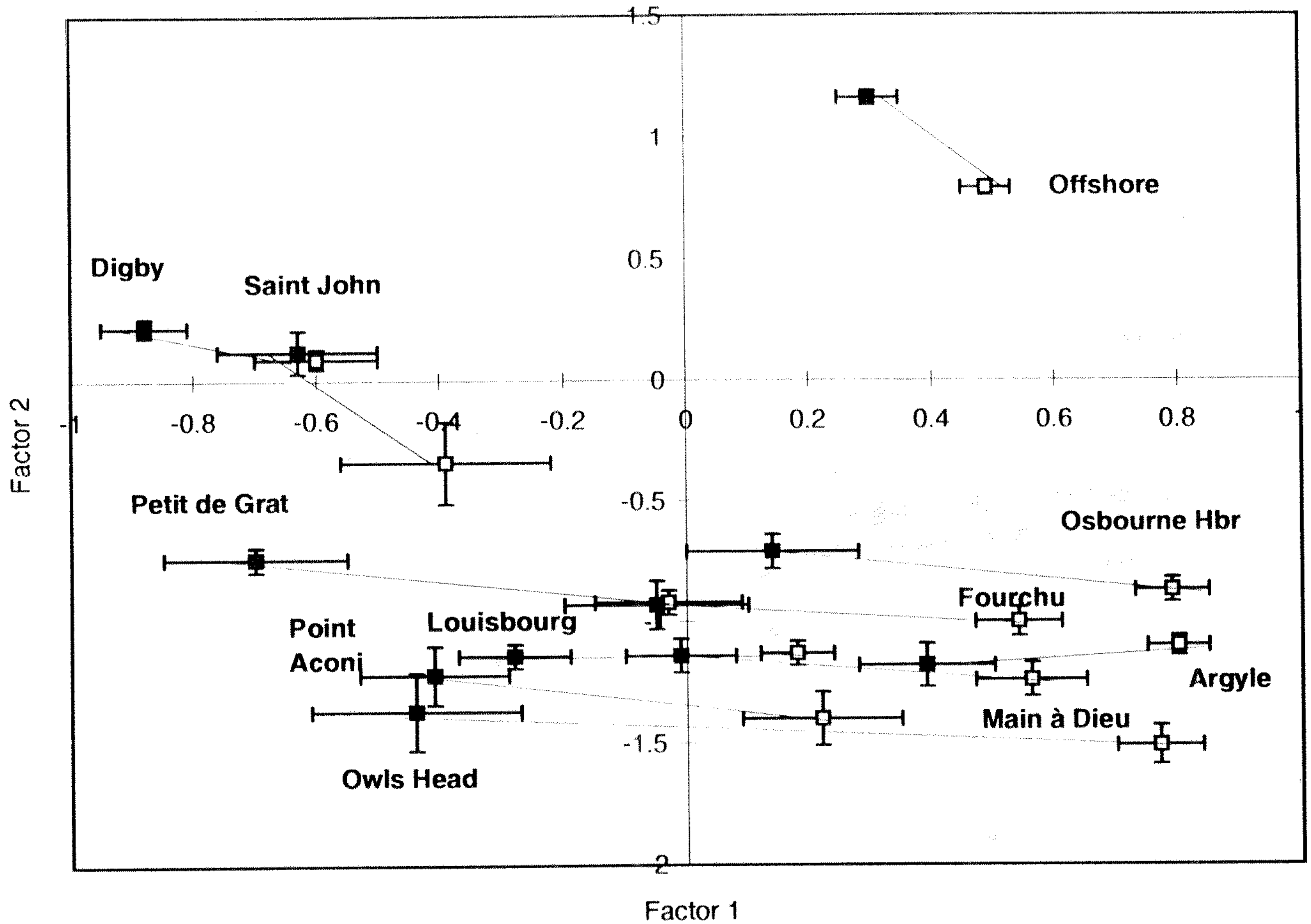


Figure 15. *Buccinum undatum* . Factor Analysis. Position of male (solid square) and female (open square) population means with standard error. Population names are indicated near the mean of one of the sexes.

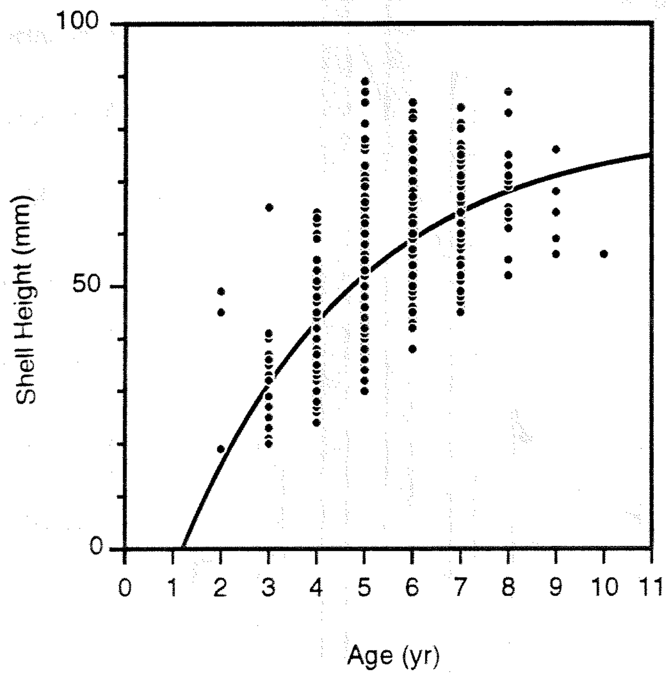


Figure 16. Relationship between shell height and age in *Buccinum undatum*. Von Bertlanffy growth function is displayed (Lage=80.47(1-exp(-0.27(age-1.20))). The function fits the data with an r2 value of 0.46.

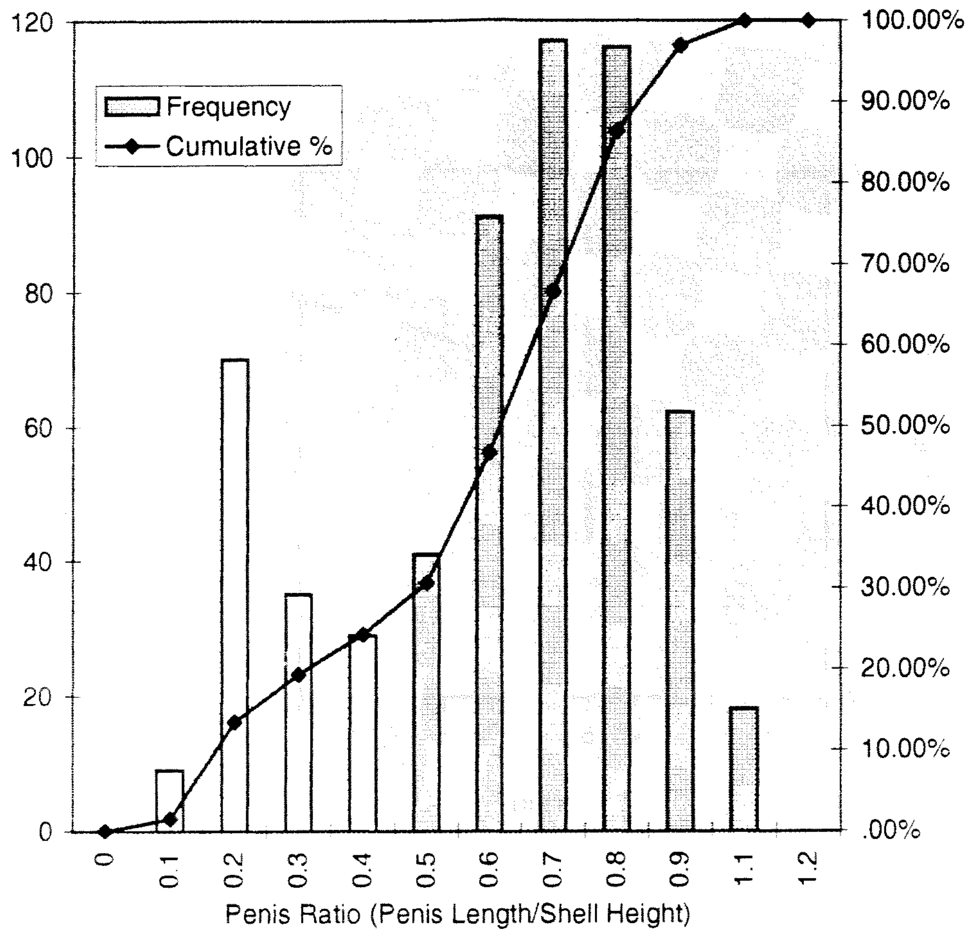


Figure 17. Frequency distribution of the ratio of the penis length to the total shell height in male whelks. Penis ratios > 0.5 indicate sexually mature males and are indicated in shaded bars. The cumulative percentage of males is also indicated. Approximately 24% of the males in this study were immature.

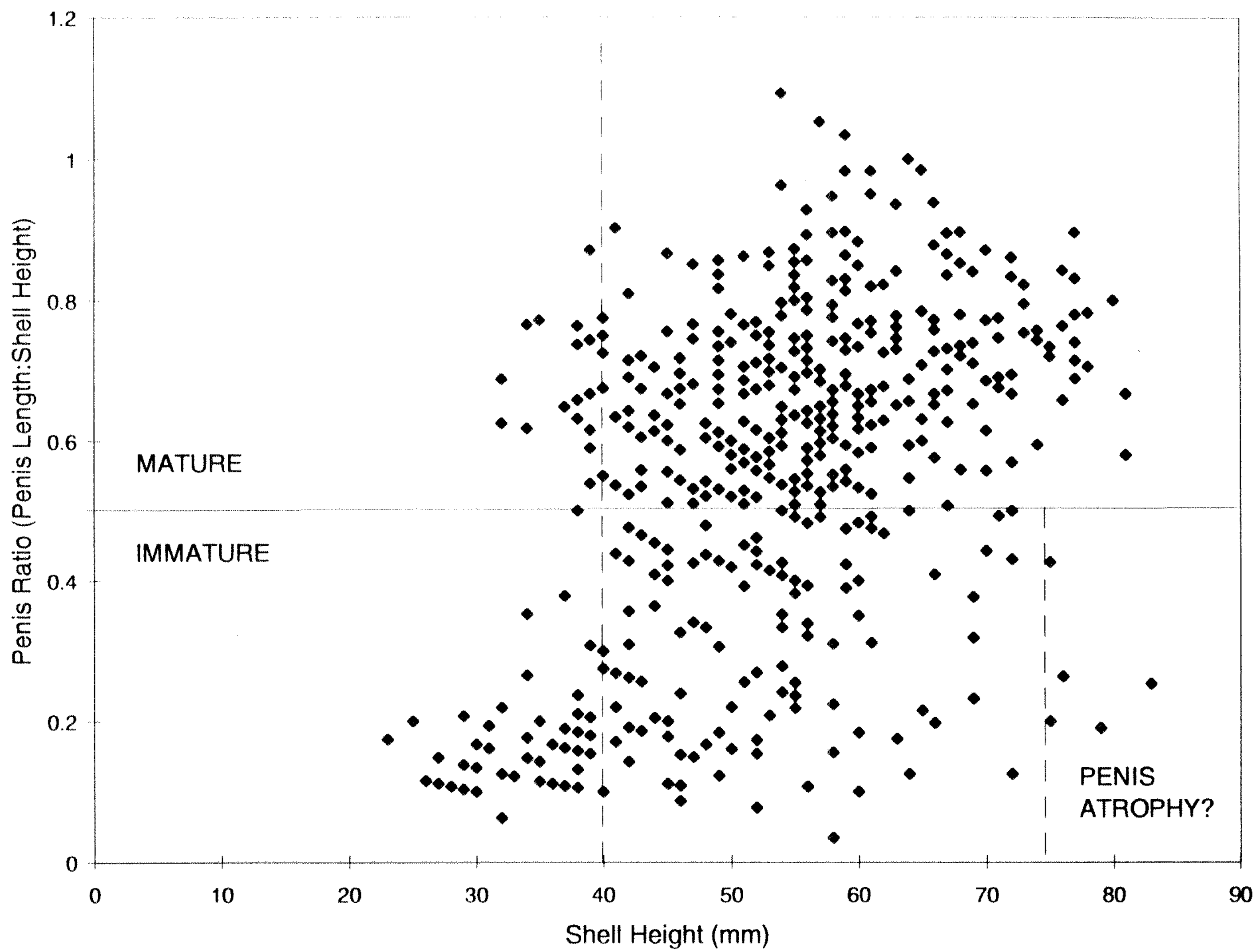


Figure 18. Relationship between penis ratio and shell height in male *Buccinum undatum*. Penis ratios greater than 0.50 are considered to be mature.