A POPULATION SURVEY OF THE WEST INDIAN TOPSHELL OR WHELK (*CITTARIUM PICA*) IN THE U.S. VIRGIN ISLANDS

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Abstract

Populations of the West Indian topshell, *Cittarium pica* (Gastropoda: Trochidae), were surveyed at 41 areas in the U.S. Virgin Islands between June 2003 and May 2004. The size and density of *C. pica*, known locally as whelk, varied substantially among sites, but was not significantly different between northern islands (St. Thomas, St. John, associated cays) and the southern island (St. Croix). Average size was significantly different between island groups and showed a non-significant negative relation to density. Observed spatial variability was partly explained by habitat exposure: whelk at windward sites (offshore cays, exposed points) had larger average size and occurred at lower density, whelk at leeward sites (bays, semi-protected coasts) had smaller average size but occurred at higher density. Larger adult *C. pica* were rare or absent at most sites although their densities were comparatively high within two marine protected areas, a restricted-entry area, and at a number of sites characterized by exposure to high wave energy. Comparison to limited historic USVI data for *C. pica* suggests a decline in the relative abundance of large individuals. Together, these observations suggest that harvesting is a major influence upon, if not the primary determinant of, *C. pica* population structure in the USVI. Data from paired-sampling (leeward and windward sides) indicate that whelk young-of-the-year (YOY) are more abundant on leeward coasts, which suggests that local patterns of whelk recruitment may be influenced by nearshore oceanographic processes. A peak in YOY density was observed in spring and the significance of this observation is discussed in relation to periods of annual spawning. Recommendations for additional studies are presented.

Introduction

The West Indian topshell, *Cittarium pica*, is a trochid gastropod that inhabits rocky shorelines which are exposed to wave action (Randall 1964). It is commonly found in the intertidal and shallow subtidal areas - the yellow and pink zones (Lewis 1960, Kaplan 1988) - where it grazes on a variety of predominantly filamentous forms of algae (Randall 1964). *C. pica* is distributed throughout the Caribbean and Bahamas, with comparatively recent extinctions reported from Bermuda and Florida (Abbott 1976). It attains a relatively large size of about 10 to 12 cm and Fisher (1978) reports a maximum length of 13.6 cm. Owing to its edible qualities (Clench and Abbott 1943), *C. pica* is commonly harvested for food throughout much of its range (Fisher 1978). Near human population centers, larger individuals are rare (Clench and Abbott 1943) and overexploitation has become a concern throughout much of its range (Carter 2002).

In the United States Virgin Islands (USVI), West Indian topshells are also a popular food item, known locally as whelks (Randall 1964), and humans have harvested whelks from local shorelines since pre-Columbian times (R. Boulon pers. comm.). Presently, whelks are also harvested commercially in the USVI and whole animals (in the shell) are sold for about US$10 per pound (Holt and Uwate 2004, R. Gomez pers. comm.). Although commercial, recreational, and subsistence harvesting occurs in the USVI (Clavijo *et al.* 1984), little is known of the fishery and less still is known about the impact of harvesting upon *C. pica* populations. In the late 1980's, concerns over declining whelk stocks (deGraaf and Moore 1987) prompted Territorial regulations on whelk harvest, including a minimum harvest size and a 6-month closed season. However, the efficacy of these policies to protect and restore *C. pica* stocks was never evaluated.

This study was undertaken to collect baseline information on *C. pica* populations in the USVI. Our objectives were to quantify the abundance and size structure of *C. pica* across a large spatial scale, to compare populations between island groups, to evaluate results in light of existing information, and to identify significant data needs. The expansive spatial scale of sampling necessarily led us to quite different locales within the USVI. It became apparent during our surveys that some of the variability in *C. pica* population structure was related to differences in physical attributes among habitats. Therefore, an attempt was made to incorporate observations on habitat into the findings of this study.

Materials and Methods

Study Location

This study was conducted in the U.S. Virgin Islands (USVI). The northern USVI are composed of two large islands - St. Thomas and St. John - and numerous smaller associated islands or cays (Dammann and Nellis 1992) which arise from the Puerto Rico-Virgin Islands Platform (Nagle and Hubbard 1989). St. Croix lies on a separate platform situated about 40 miles to the south. St. Croix is separated from the northern USVI by a deep oceanic trench and it has four associated cays. Collectively the USVI has about 380 km of shoreline distributed roughly as follows: St. Croix with 113 km, St. Thomas with 85 km, St. John with 80 km, and the outlying cays and islands with another 98 km (Dammann and Nellis 1992). Only about 80 km of shoreline is sand beach located in bays and between headlands. The linear amount of shoreline which is potentially available as whelk habitat (*i.e.* intertidal hard substrate) is unknown. Tidal exchange is generally small (< 20 cm) in the USVI and of mixed semi-diurnal nature (Hubbard 1989).

Fisher Interviews and Site Selection

In an attempt to focus our sampling efforts to suitable whelk habitat, and to minimize sampling from inappropriate habitats, DFW staff sought advisement from USVI commercial fishers. Between March and July of 2003, a query was made of those fishers who harvest whelk, as identified through a review of reported commercial landings from 1998 to 2003 (commercial catch report database maintained by DFW). An announcement describing the study was also prepared and distributed. Each fisher was asked to identify substantial whelk populations by marking areas on a map. There were 10, 18 and 3 respondents on St. Croix, St. Thomas, and St. John, respectively. Typically, fishers identified large stretches of rocky coastline, headlands, or offshore cays (Table 1). These responses guided the selection of specific survey sites. Additional sites were included for comparison to historic data (see below) and/or to increase the geographic coverage of the study.

Body Size Measurement

Whelk body size has been reported in terms of shell length (Randall 1964), shell height (Debrot 1990a), and shell width (Schmidt *et al*. 2002). To standardize our data collection in a manner most useful for management, we used a measure of shell width: the maximum diameter obtained as measured with calipers across the base of the shell (Debrot 1987). Because minimum harvest size for whelk in the USVI is 2-7/16^{ths} inches (61.92 mm) or 62 mm shell size (I. Mateo cited in Schmidt *et al.* 2002), we used a value of $\geq$ 62 mm shell width to delineate harvest-size whelks in our samples. However a more accurate interpretation is noted here. USVI regulations specify minimum whelk harvest-size as the inability of a shell to pass through a measuring loop of nominal diameter 2-7/16^{ths} inches (see USVI Code 1994). This differs substantively from a linear measure of maximum shell width. For example, a whelk of 62.5 mm shell width will not pass through such a loop when oriented with the shell base parallel to the plane of the loop but, due to its 3-dimensional nature (conical, irregular), the same shell will easily pass through the loop if oriented at an angle (J. Aubain pers. comm.). Strict adherence to the latter definition would specify whelk of a substantially larger minimum size (perhaps as large as 65-70 mm shell width). Exactly *how* to measure the legal harvest-size of whelks should be clarified for the public and resource managers alike.

Evaluation of Field Sampling Protocols

Previous researchers have used a number of different survey methods to study *C. pica* populations (*e.g*. Randall 1964, Clavijo *et al*. 1984, Boulon 1987, Debrot 1987, 1990a, 1990b, Bell 1992). We sought a quantitative survey method that was applicable across a wide variety of habitats. Two protocols were evaluated here: a quadrat method (Debrot 1990b modified from Hughes 1971) and a cross-shore “strip transect” method (Boulon 1987). The quadrat method is described below. Boulon’s (1987) cross-shore transects are linear swaths (1.0 m wide) oriented perpendicular to the shoreline. Their length is not pre-defined. Instead, cross-shore transects begin at the highest intertidal zone and extend to a specified depth (1 m) in the shallow subtidal zone. Cross-shore transects are advantageous because in each replicate whelk are sampled from all intertidal zones. Their primary disadvantage is that the length of each cross-shore transect will be determined by shoreline topography (*i.e*. by the width of the rocky intertidal zone itself). Width of the intertidal zone may vary considerably within and among sites in the USVI depending upon slope and substrate composition (Toller pers. obs.).

In May-June of 2003, preliminary surveys were conducted at Sprat Hall (SPH), St. Croix, using both methods. SPH site lies on the western shore (leeward shore) where wave action is usually moderate during summer months, making it amenable to studies. At SPH, whelks inhabit a short (~150 m in length) contiguous stretch of rocky coastline. Results from the cross-shore transect method and the quadrat method are shown in Table 2. The two methods yielded indistinguishable size frequency distributions for *C. pica* (not shown). Estimates of abundance from cross-shore transects were approximately twice those estimates derived from quadrats but quadrat estimates had lower variance. When scaled to total habitat area, the two estimates showed good agreement (Table 2). Given an overall similarity of results obtained from these methods, the quadrat method was selected because: 1) density was considered a preferable unit of measure for comparisons among sites, and 2) the quadrat method was more practical for sampling from a diversity of habitats, often under challenging sea conditions.

Field Sampling Methods

The quadrat method was as follows. A 100 m transect tape or a 100-m rope (marked at 1 m intervals) served as a reference line running parallel to shore. It was affixed in the littoral zone and was stretched haphazardly through suitable *C. pica* habitat - the yellow-to-pink zones of intertidal substrate (Lewis 1960, Kaplan 1988). The reference line was secured to intermediate tie-down points to resist wave action, usually resulting in a zigzag pattern that traversed emergent and submerged littoral zones multiple times within each site. At pre-selected random distances, a 1.0 m^2 PVC quadrat was placed over appropriate *C. pica* habitat. All whelks found within the quadrat frame were collected and shell width was measured to the nearest mm using calipers. The area within each quadrat was searched visually (with the aid of a mask for subtidal portions) and by probing crevices and running hands through macroalgae until no more whelks were encountered. Between 8 and 17 replicate quadrats were done per survey site depending upon *C. pica* abundance and prevailing sea conditions.

From initial observations (at SPH and elsewhere) and previous reports (*e.g*. Boulon 1987), it was anticipated that harvest-size *C. pica* ($\geq$ 62 mm shell width) would occur in very low densities at some USVI sites. To adequately sample this rare, but economically important, part of the population, a belt transect method was employed. Duplicate belt transects (50 m^2) were conducted parallel to the shoreline. Two divers surveyed 0.5 m on either side of a reference line (a 1.0 m-wide swath) for 50 m, collecting all individuals estimated at $\geq$ 62 mm shell width. Shells were measured (as above) and whelks were returned to their site of capture. The belt transect method was included to sample from a larger area than would be possible using 1.0 m^2 quadrats its use serves a different purpose than the cross-shore transect method of Boulon (1987) that was discussed previously (see above).

Placement of the reference line was the same for quadrats and belt transects. In principle, this could result in double sampling. In practice, however, the actual overlap of sampling areas was relatively limited (see Results). This was due to: substantial 3-dimensional habitat complexity at most sites, habitat width > 1 m (typically over 2 m), and ever-present wave action that caused inshore-offshore sway of the reference line. Nonetheless, at each survey site belt transects were conducted prior to quadrat sampling to eliminate confounding effects of the latter on the former.

Field observations suggested that whelk population structure was influenced by the physical energy of their habitat (*sensu* Debrot 1990b). This was examined further in two ways. First, we did a *post-hoc* analysis of our dataset in which each site was placed into one of three categories (Bays, Points and Cays) based upon predominant coastal morphology and a subjective assessment of exposure to prevailing seas. Second, we utilized a deliberate sampling strategy at a limited number of sites to test the hypotheses that whelk populations would have greater average size and lower population density in habitats exposed to high wave energy, and that whelk would have smaller average size and greater population density in comparatively sheltered habitats. Our paired-sample design consisted of 1) a sample from a relatively exposed coastline (*e.g*. rocky headland) and 2) a matched sample from an adjacent but relatively protected coastline (*e.g*. bay). For each pair, the two samples were taken less than 600 m apart. Six replicate sites (four on St. Croix and two on St. John) were surveyed by paired-sampling: Hughes Point (HP-1 and HP-2), Europa Bay (EU-1 and EU-2), Buck Island (BI-1 and BI-2), Whistling Cay (WST-1 and WST-2), Pull Point (PP-1 and PP-2), and Long Point West (LPW-1 and LPW-2). Replicate sites (independent pairs) were separated by > 5 km, and each represents a unique combination of exposure to wind, seas, and swell. The difference in physical energy within and among pairs was not measured.

Data Analysis

Raw survey data were entered into Microsoft Excel for manipulation and graphical analyses. Statistical analyses were performed with Statistica (Statsoft, Inc., Tulsa, OK). For inter-island comparisons, data were pooled by island group (northern vs. southern islands) and tested with a Students t-test (two-tailed, assuming unequal variance). For inter-habitat comparisons of size and abundance, data were pooled by group and tested with a one-way ANOVA. Data for paired-site comparisons were pooled by group and tested with a two-tailed Students t-test, assuming unequal variance.

To estimate the number, density and percentage of reproductively mature individuals in samples, an estimate of *C. pica* size at first reproduction was required. Review of the literature showed great inconsistency. For the USVI, Randall reported that the smallest male and female *C. pica* she observed were, respectively, 32.4 mm and 33.7 mm shell length (as measured from tip of spire to distal lip). In Costa Rica, Schmidt *et al*. (2002) calculated *C. pica* mean size at first maturity to be 29.2 $\pm$ 1.1 mm shell length (as measured across widest diameter at base of shell). Debrot (1990b) presented gonadal index data for *C. pica* from the Bahamas that compounds the discrepancies among reported measures. In the absence of a clear consensus, an intermediate value of 30.5 mm shell width was selected and applied to the data for this analysis (*i.e*., all *C. pica* $\geq$ 31 mm shell width were considered reproductively mature).

In order to make comparisons to historic data from Henley Cay and Cockroach Island (Clavijo *et al*. 1984), our datasets for HEN and CRI were modified as follows. For each, quadrat data was scaled proportionally to belt transect survey area (100 m) and the two types of data were pooled to generate a combined frequency distribution. Because historic data for Henley Cay and Cockroach Island did not contain information on whelks < 20 mm shell width (Clavijo *et al*. 1984), these size classes were excluded from contemporary data sets to generate comparable size frequency distributions. We note that the historic collections done at Henley Cay and Cockroach Island were not quantitative (a CPUE method was used, but amount of effort was not reported). This precludes comparisons of absolute abundance or density.

Results

Between June of 2003 and May of 2004, whelk populations were surveyed at 41 areas in the USVI (Figures 1 and 2, Table 3). In the northern islands (St. Thomas and St. John), 26 surveys were conducted at 24 areas. In St. Croix, 21 surveys were conducted at 17 areas. Six of the survey areas were paired-site comparisons conducted at St. Croix (4 pairs) and St. John (2 pairs).

In quadrat surveys, a total of 4,722 *C. pica* were observed (1,880 on St. Croix and 2,842 on St. Thomas and St. John). In belt transects, a total of 593 individuals were observed (249 on St. Croix and 344 on St. Thomas and St. John). Undersized individuals (<62 mm shell width) were also incidentally collected in belt transects on St. Croix (n = 6) and on St. Thomas and St. John (n = 103). These data were excluded from subsequent analyses but are presented in Appendices.

Whelks were common in most quadrat samples. Average density by island group was 7.5 and 8.9 individuals per m^2, for southern and northern islands, respectively. These densities were not significantly different between island groups (Table 4). Density estimates varied considerably among sites, both within and between island groups, as indicated by a high variance-to-mean ratio (9.9 to 20.4, Table 4).

Harvest-size whelks ($\geq$ 62 mm shell width) were comparatively uncommon in belt transect surveys. Average density of harvest-size individuals by island group was 7.3 and 6.6 individuals per 50 m^2 for southern and northern groups, respectively (Table 4), or about $1/50^{th}$ of the total population density (as estimated from quadrats). Differences in density of harvest-size *C. pica* between island groups were not significant (Table 4) and the data were also characterized by a high variance-to-mean ratios (>15, Table 4).

Whelk body size also varied considerably among sites. Based upon quadrat data, this difference was significant between island groups ($P < 0.001$, Table 4). Size frequency distributions (Figure 3A,B) for data pooled by island group show that St. Croix populations are characterized by both a smaller median size (~ 20 mm shell width; Table 4) and a proportionately broader size range of large whelks (> 70 mm shell width) at low frequency. A marked decline in the relative abundance of 35-40 mm size classes was observed for both island groups (Figure 3A,B), suggesting that mortality of whelks increases substantially in this age group. Collectively, reproductively mature individuals ($\geq$ 31 mm) comprised 16.3 % and 24.5 % percent of these samples for southern and northern island groups, respectively. Although pooling data (e.g. Figure 3) largely obliterates the identification of annual cohorts, whelk size distributions from individual sites (see Appendices 3-5) often showed two or more distinct size class peaks.

Results from belt transect surveys showed a significant difference in whelk body size between island groups ($P < 0.001$, Table 4). On average, harvest-size adults were larger on St. Croix (85.3 mm) than in the northern islands (78.6 mm). Size frequency distributions of harvest-size whelk are shown in Figure 4A,B).

Site-to-site variability in *C. pica* size and abundance was pronounced (*e.g.* Appendices 1 and 2) and a negative (though not significant) relation was observed between average body size and average density (Figure 5A,B). A comparison across three broad habitat types (bays, points, cays) revealed significant differences (Table 5) in whelk population structure. In bays, whelks were more abundant and had a smaller average size than at points or cays. Harvest-size whelks were rare in bays (0.65 individuals/50m^2) and were most abundant at cays (11.4 individuals/m^2;

Table 5). This relation was examined further in paired-sampling (Figure 6A,B). Whelk on windward (exposed) sides of points and cays were larger, on average, than whelks on Leeward (protected) sides. Total whelk density was higher on leeward sides than windward sides. At some sites, the leeward side had substantially more whelk young of the year (HP-2, EU-2, WST-2, LPW-2; see Appendix 6). At half the sites, the density of harvest-size whelk was greater on the windward side [HP-1, EU-1, WST-1].

To examine the reproductive status of studied populations, we used belt transect data and quadrat data for each site. The abundance of larger whelk ($\geq$ 62 mm shell width, presumably all mature) was compared to the abundance of small reproductive individuals ($\geq$31 mm shell width) as derived from quadrat data. These measures showed a weak positive relation for northern and southern island groups (St. Croix, $r^2 = 0.784$; St. Thomas and St. John, $r^2 = 0.21$). Site accessibility was plotted onto these data for whelk reproductive status (Figure 7). Sites that were either restricted to casual access or to harvesting had whelk populations with a higher proportion of reproductive individuals (Figure 7) compared to those sites where access was easy.

Sampling was conducted over the course of almost one year, enabling us to examine our data for evidence of seasonal trends in abundance of *C. pica* young of the year (YOY). We did not observe individuals smaller than 2 mm in our sampling. Assuming that *C. pica* recruits reach a size of 4-5 mm at about 6 months of age (calculated from Randall 1964 and Bell 1992) we used a minimum size of $\leq$ 5 mm to identify YOY in our collections. On St. Croix, a single, distinct peak in YOY density was observed during spring sampling (Figure 8A). Otherwise, in St. Croix samples YOY were only observed at relatively low densities (< 0.2 individuals/m^2). On St. Thomas and St. John, a more pronounced abundance peak of YOY was also observed in spring samples, with additional smaller peaks during the winter (Figure 8B). We note that small whelks could be observed sporadically throughout most of the year-long study period (*e.g.* Appendix 1).

We compared historic USVI surveys of *C. pica* populations at Henley Cay [HEN] and Cockroach Island [CRI] to data obtained in this study. Size frequencies of whelk from HEN were comparable to data from c.1981 (Figure 9A). Whelk size frequencies at CRI show pronounced differences (Figure 9B), and suggest that average size has decreased substantially at this site.

Anecdotal Observations

Size-specific zonation of *C. pica* has been observed previously on St. John (Randall 1964, Boulon 1987), Barbados (Lewis 1960), Bahamas (Debrot 1990a), and Costa Rica (Schmidt *et al*. 2002). Although not quantified in this study, we made similar observations. Generally, the youngest size classes (2-8 mm shell width) were observed higher in the intertidal while larger individuals (> 80 mm shell width) were observed below mean low water. Often these larger whelks were deep within crevices or under boulders.

Evidence of predation on *C. pica* was seen rather infrequently at several sites during these surveys. Shoreline feeding activities of American oystercatchers (*Haemotopus ostralegus*) were deliberately interrupted to examine the size of whelk upon which they were feeding. Three species of gastropods were observed preying upon *C. pica* in the intertidal zone: the widemouthed rock drill (*Purpura patula*), the deltoid rock drill (*Thais deltoidea*) and another unidentified species of rock drill (*Thais* sp.). Octopus predation on *C. pica* was implicated by shells found adjacent to octopus caves. Most observations indicated that predation was directed towards young adult whelks (c. 25-35 mm shell width) and no instances of natural predation on harvest-size individuals were observed.

Discussion

Randall (1964) stated that *Cittarium pica* is "probably the most common large gastropod of the exposed rocky littoral region" in the West Indies. Our study confirms that small individuals of *C. pica* may be locally quite common, especially in bays and semi-protected habitats. Our results, however, do not indicate that "large" individuals of *C. pica* are particularly common in the USVI and, similar to reports from elsewhere (*e.g*. Clench and Abbott 1943, Flores 1981, Schmidt *et al*. 2002), we found them to be a rare fraction of the total population at most sites.

The abundance and size of whelk was highly variable among sites. Whelk density was not significantly different between northern and southern island groups in the USVI. Average size was different between north and south, and although this observation might be attributed to differing fisheries, a cautious interpretation is recommended. As discussed below, we feel that habitat is such a powerful modifying factor on the structure of whelk populations that definitive conclusions about inter-island size differences should adequately account for an unequal distribution of habitat types among those islands.

In this study, we considered only one aspect of whelk habitat – the relative degree to which an intertidal shoreline is exposed to physical wave energy – and this is clearly an oversimplification of numerous biotic and abiotic factors influencing whelk populations. Nonetheless, the relation between whelk size and exposure, as suggested previously (Randall 1964, Clavijo *et al*. 1984), was quite evident along gradients of habitat exposure: sheltered bays had high densities of almost exclusively small whelk, while at the other extreme, some exposed cays or points had remarkable stands of large adult whelks. Debrot (1990b) also identified wave action as a significant factor modifying Bahamian whelk populations; however he showed a negative relationship between body size and exposure. We found the opposite: increased exposure was positively related to whelk body size. It is highly likely that site exposure to high seas limits access by fishermen, thereby creating harvest refugia which enable *C. pica* to reach a larger average size.

In comparison to exposed coastlines, juveniles of *C. pica* were relatively abundant on leeward/protected shorelines. This observation suggests greater recruitment of whelk to leeward shores. Caselle and Warner (1996) observed an increase in recruitment of reef fish larvae to leeward sites on St. Croix which they attributed to physical transport processes. Alternatively, whelk may suffer lower mortality rates during their early post-settlement period at such sites. Large adult whelk could conceivably reduce densities of their conspecific recruits by incidental grazing, as has been suggested for some species of abalone (Naylor and McShane 2001). A third possibility still is that adult grazing modifies resident algal communities to which whelk larvae are cued for settlement, but no such cues are presently known (Bell 1992).

The striking spatial variability that we observed may have implications for stock management. Similar to abalone, whelk may exist as metapopulations (Mayfield *et al*. 2001). Whelk share many life-history attributes that create sub-structuring of abalone populations, and not coincidentally also contribute to their vulnerability to overharvesting. Whelk habitat is a narrow intertidal band which is generally accessible to humans. Whelks have extremely low mobility - in tagging studies, adults were observed to move < 100 m over 6 months (Randall 1964, Debrot 1990a). Their larvae have a very short planktonic duration of 2.5 to 5 days (Bell 1992) that potentially greatly limits their dispersal capacity. Whelk may also be susceptible to an Allee effect (Quinn *et al*. 1993) – where fertilization success drops dramatically when adult density is reduced below a threshold value, leading to catastrophic population collapses - but presently too little is known of whelk spawning [see below] to determine if such effects occur. Taken together, these factors would indicate that *C. pica* might best be managed as a mosaic of partially isolated groups.

The reproductive biology of whelk has not received much attention. It is assumed that sexes are separate in *C. pica*. Their fertilization is external, and Bell (1992) gives an account of *C. pica* spawning observed in aquaria in the Bahamas. Apparently, there are no seasonal or interannual observations for whelk spawning in the USVI, although circumstantial evidence can be drawn from recruitment patterns. Randall (1964) observed a pronounced recruitment of very small (~1 mm) *C. pica* in January. Boulon (1987) saw an influx of April “post-recruits” at Windswept Beach, St. John. Bell (1992) observed a *C. pica* recruitment pulse in the Bahamas from January to May, and used larval growth rates to show that recruits originated from a spawning in early October. Bell (1992) also calculated that an October spawning date would explain the timing of whelk recruitment observed by Randall on St. John. In our surveys, whelk young-of-the-year (YOY) were most abundant in spring. Our data are not recruitment patterns *per se*, as spatially-distributed sampling may confound temporal patterns. The data are nonetheless consistent with an annual peak spawning of *C. pica* that occurs in autumn.

In the USVI, the annual 6-month closed season on whelk harvesting reopens on October 1 of each year. The foregoing information indicates that this reopening date should be re-evaluated carefully with data for USVI whelk populations. An October reopening date may be tragically close to the annual peak spawning date for *C. pica*, and thus may be particularly ineffective in protecting spawning stocks. The relation of reproductive output to body size has not been studied in whelks (but see Debrot 1990b for gonadal indices), however it is assumed that large individuals contribute disproportionately to total reproductive output (Boulon 1987). Adequate protection of whelk stocks through their [actual] peak spawning period would add a measure of security against recruitment failure.

Our quantitative whelk surveys are presented here as a baseline for population density in the USVI. Over a timescale of four to five decades, it seems probable that our “baseline” whelk populations have dropped precipitously from historic values – a phenomenon called shifting baseline syndrome (Pauly 1995). In southern California, for example, declines in average body size of intertidal gastropods began almost 40 years ago (Roy *et al*. 2003) and our only available comparisons (from 1980’s, Figure 9B) also suggests a trend towards decreased body size in *C.*

pica. Accounts from the USVI dated earlier (c.1960) suggest that whelk were once vastly more abundant. “Whelks were so plentiful twenty years ago along the rocky edges of the north or northwest shoreline off St. Croix, that it was dangerous to walk on the rocks; you would slip on the whelks as they slid out from under your feet. Ten years ago, they were gone from above the waterline, but you could catch them at night with a light. Today to find whelks, you must dive, and then you are lucky to find any.” (T. Skov quoted in deGraff and Moore 1987). In the 1950’s and 60’s, a person could wade through the intertidal zone at Sprat Hall and easily fill a sack with large whelk (H. Rivera, pers. comm.). Today these abundances seem almost unimaginable - our surveys at these same areas [NTP, MAH, SPH] revealed few large whelk. Unfortunately, quantitative data for this time period do not exist and reconstruction of pre-exploitation abundances (*e.g*. Rogers-Bennett *et al*. 2002) is probably not possible. It is unlikely we will ever know how robust these historic whelk populations actually were.

Marine Protected Areas (MPAs) are an attractive possibility for management of *C. pica* populations. In Costa Rica, *C. pica* populations within an MPA were substantially larger and more abundant than at sites where harvesting is chronic (Schmidt *et al*. 2002). Three of our sites were within MPAs (BI-1, BI-2, ROT) and densities of large *C. pica* were comparatively high (Figure 7). The highest densities of large whelk, however, were observed outside of formal MPAs, but in areas where harvesting is restricted or reduced. At Hovensa Breakwater (HOV), fishers are excluded for shipping security reasons and robust populations of adult whelks were found there. Similarly, Flanagan Island (FLA) had remarkable populations of large adult whelks. FLA is thought to be only lightly harvested because of uncertainty over jurisdictional control, distance from population centers, and exposure to seas (S. Gordon, pers. obs.). The latter two sites (HOV, FLA) may function as *de facto* marine reserves, similar to reserves in British Columbia where abalone populations benefited from inadvertent harvest restriction (Wallace 1999). These observations suggest that MPAs could protect whelk populations, adding a safeguard against possible Allee effects (Quinn *et al*. 1993). However, some authors report that the effective protection of desirable intertidal invertebrates requires that humans are physically excluded from those environments (Castilla and Duran 1985, Keough and Quinn 2000, Roy *et al*. 2003). It is improbable that such strict measures would ever gain acceptance in the USVI.

How effective are existing whelk management policies of minimum harvest size and closed season? Insufficient information exists to make any definitive conclusions. The dates for whelk closed season should be re-evaluated after data are collected on spawning activities of whelk in the USVI. Our data also suggest that the minimum harvest size is not widely observed. At the majority of our sampling sites, size-frequency distributions showed an abrupt truncation in body size at ~ 35-40 mm shell width suggesting that, at many sites, whelk mortality increases sharply in approximately their 3rd year. Natural mortality (due to predation) seems an unlikely explanation as it was only infrequently observed and was apparently directed towards smaller size classes of whelk. Harvest by fishers may be the primary source of mortality for larger size classes of *C. pica* (Boulon 1987) and our data suggest that fishing mortality extends to individuals that are considerably smaller than the legal minimum harvest size.

Worldwide, declines or collapses of fisheries for nearshore marine invertebrates are now commonplace (Jackson *et al*. 2001, Leiva and Castilla 2002). Mannino and Thomas (2002) reviewed a number of factors that influence the susceptibility of intertidal gastropods to stock depletion. Two factors seem applicable to the persistence of whelk populations despite the as yet unquantified level of harvesting. First, *C. pica* appears to attain reproductive maturity at a young age (~ end of its second year) and small size, whereas their meat yield is low until about their third year (see Clavijo *et al*. 1984 for a shell width-meat weight curve). Second, harvest refugia may have maintained pockets of large whelk at high density, ensuring successful spawning and recruitment despite localized depletions of larger whelk from more accessible areas.

Data Needs

- There is a critical need to collect accurate information on seasonal reproductive patterns of *C. pica* in the USVI. In particular, timing of annual spawning activity needs careful study. A relatively straightforward study design (Bell 1992) conducted at a small number of sites among islands would potentially yield vital information for evaluating the closed season on whelk.

- Further studies should be conducted on the reproductive biology of *C. pica* in the USVI, including minimum size and age at reproductive maturity, the relation between reproductive output and age/size, spawning behavior, and fertilization success in relation to population density.

- There is a clear need for more information about the harvest of whelk in the USVI. Fishery-dependent data from commercial and recreational sectors (see Clavijo *et al*. 1984) are needed to estimate their relative contribution to *C. pica* harvest. As with many other rocky intertidal invertebrates (*e.g*. Keough and Quinn 2000), other forms of take such as subsistence harvesting or collecting for fishing bait may also be of considerable impact to *C. pica* populations.

- The degree of compliance with existing regulations should be evaluated. Action should be taken to inform and educate groups that are prone to non-sustainable whelk harvesting practices.

- There is a need to understand the USVI whelk fishery in a wider geographic context. Only one published account of a whelk fishery is available (Schmidt *et al*. 2002). Instances of localized extirpations have been cited (Carter 2002) without detail. Resource managers would benefit from a Caribbean-wide comparison to identify best- and worst-case scenarios for whelk management.

- Whelks present an unusual opportunity for an integrated study of recruitment/dispersal in relation to population genetics (*sensu* Taylor and Hellberg 2003 but with a commercially important organism). These data would be directly applicable to resource management.

- Establishment of a whelk monitoring program is considered a low-priority item. Usefulness of monitoring data will depend critically upon prior quantification of whelk exploitation (known fishing effort, harvest patterns, size preferences, *etc*.) and parallel advances in our knowledge of *C. pica* biology (see above). Such basic biological information should inform study design. For example, whelk generation time should dictate the sampling frequency of a monitoring study. However, the maximum lifespan of *C. pica* is largely unknown [a minimum estimate of > 6.5

years comes from Randall’s (1964) observations on a single individual of 93 mm shell length]. The design of future monitoring studies must recognize the limitations imposed by such unknowns. Study design should also include sites within new or proposed MPAs and should use explicit stratified sampling with survey sites chosen based upon specified monitoring objectives. These objectives should be closely tied to realistic options for management action to conserve whelk stocks.

Acknowledgments

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List of Tables and Figures

Table 1. Areas of abundant whelk (*Cittarium pica*) as identified by USVI commercial fishers.

	Area Name	Fisher Score*	Survey Site
St. Thomas Fishers – 18 respondents			
(13 areas)	Salt and West Cays	10	+
	Outer Brass (Rough Pt. and west side)	8	-
	Dog Island	7	+
	Saba Island (west & south side)	6	+
	Cockroach Island	5	+
	Little Hans Lollick (north-northeast side) [1]	5	+
	Sprat Point on Water Island	5	+
	Savana Island (south-southwest side)	4	-
	Coculus Rocks and Rotto Cay	2	+
	Great Thatch Cay (north side)	2	+
	Hassel Island (south side)	2	+
	Little St. James (north side)	1	-
	Mandal to Magens Bay Point	1	+
St. John Fishers – 3 respondents			
(6 areas)	Flanagan Island	2	+
	Leduck Island	2	-
	Ram Head to Nanny Point [2]	2	+
	Reef Bay	2	+
	Waterlemon Cay	1	+
	Whistling Cay	1	+
St. Croix Fishers – 10 respondents			
(13 areas)	East Point (a.k.a. Point Udall)	7	+
	Hovensa Breakwater	5	+
	Annaly Bay	3	+
	Barons Bluff	2	+
	Hams Bay	2	+
	Hams Bluff to Maroon Hole	2	+
	Hughes Point	2	+
	Lamb Bay	2	-
	Tidepools on NW Shore	2	+
	Buck Island	1	+
	Grassy Point	1	+
	Grapetree Point	1	+
	Sprat Hall to Butler Bay	1	+

* Fisher score refers to the number of fishers who said an area has or had a substantial population of whelk.
1 Little Hans Lollick was surveyed on the south side only
2 Ram Head was surveyed on the western (leeward) side only

Table 2. Comparison of methods for surveying *Cittarium pica*: cross-shore transects and quadrats.

	Method	
	Cross-Shore Transect (Boulon 1987)	Quadrat
General attributes		
Primary Advantage	Samples integrate across intertidal zones	Values are comparable among different sites
Primary Disadvantage	Cumbersome in rough seas Transect length is not pre-defined	Inshore-offshore quadrat placement is subjective
Unit of Observation	1.0 m-wide strip of variable length Oriented perpendicular to shore	1.0 m^2 quadrat Placed in zone of highest *C. pica* abundance
Unit of Abundance	Linear (No. Individuals / m shoreline)	Density (No. Individuals / m^2)
Results from Sprat Hall Surveys		
No. of Observations	20 cross-shore transects	20 quadrats
Total No. of *Cittarium*	149	70
Average Abundance	7.45 / m shoreline	3.50 / m^2
St.Dev.	6.45	5.20
SEM	1.44	1.16
95% Confidence Interval	4.4 to 10.5	1.07 to 5.93
Range	0 to 25	0 to 19
Estimated Population Size*	745 Individuals	889 Individuals
95% Confidence Interval	442 to 1,046	271 to 1,506

* In order to compare cross-shore transect data (a linear measure) to quadrat data (a density measure), the observations had to be scaled to an appropriate value. This was the estimated population size [EPS] of whelk within the 100 m-long study area at SPH. Cross-shore transect data were multiplied by 100 m (i.e. the length of shoreline) to obtain EPS. For quadrat data, EPS was calculated as follows: whelk density x shoreline length x intertidal habitat width. Intertidal habitat width was measured at each of the 20 quadrat sampling positions and yielded an average width of 2.54 m $\pm$ 1.78 (St.Dev.

Table 3. Survey sites.

Site Name	Site Code	Survey Date	Survey Location Lat (N)	Survey Location Long (W)
St. Croix				
Sprat Hall	SPH	20 Jun 03	17° 44.391’	64° 53.533’
Hams Bay	HAM	23 Jun 03	17° 46.049’	64° 52.893’
Barons Bluff	BRB	15 Aug 03	17° 46.990’	64° 46.575’
Long Point, East	LPE	3 Oct 03	17° 40.931’	64° 50.046’
Annaly Bay	ANB	22 Oct 03	17° 45.829’	64° 50.602’
Knights Bay	KNB	24 Oct 03	17° 45.439’	64° 35.425’
Grassy Point	GRP	28 Oct 03	17° 43.987’	64° 36.596’
Grapetree Point	GTP	29 Oct 03	17° 44.710’	64° 35.837’
Watch Ho	WHP	31 Oct 03	17° 41.931’	64° 43.122’
East Point	EPT	21 Nov 03	17° 45.284’	64° 33.883’
Buck Island-1	BI-1	25 Nov 03	17° 47.255’	64° 36.685’
Buck Island-2	BI-2	25 Nov 03	17° 47.191’	64° 36.729’
Hovensa Breakwater	HOV	29 Dec 03	17° 41.275’	64° 44.416’
Hughes Point-1	HP-1	29 Mar 04	17° 44.697’	64° 35.126’
Maroon Hole	MAH	5 Apr 04	17° 46.140’	64° 52.000’
NW Tidepool	NTP	7 Apr 04	17° 45.980’	64° 51.515’
Long Point, West-1	LP-1	15 Apr 04	17° 40.813’	64° 50.263’
Long Point, West-2	LP-2	15 Apr 04	17° 40.799’	64° 50.333’
Hughes Point-2	HP-2	26 Apr 04	17° 44.728’	64° 35.213’
Pull Point-1	PP-1	28 May 04	17° 45.918’	64° 39.298’
Pull Point-2	PP-2	28 May 04	17° 45.856’	64° 39.296’
St. Thomas				
Rotto Cay	ROT	16 Oct 03	18° 18.791’	64° 51.924’
Dog Island	DGI	17 Oct 03	18° 17.698’	64° 48.831’
Secret Harbor	SEC	18 Oct 03	18° 19.117’	64° 51.193’
Thatch Cay	THC	21 Oct 03	18° 21.681’	64° 51.173’
Salt Cay	SLT	23 Oct 03	18° 21.581’	65° 03.024’
Stumpy Bay	STB	23 Oct 03	18° 21.802’	65° 00.543’
Water Island	WAT	30 Oct 03	18° 19.076’	64° 56.605’
Hassel Island	HAS	30 Oct 03	18° 19.539’	64° 56.144’
Little Hans Lollick	LHL	31 Oct 03	18° 24.434’	64° 54.493’
Inner Brass	IBR	31 Oct 03	18° 23.077’	64° 58.526’
Saba Island	SAB	4 Nov 03	18° 18.336’	65° 00.146’
Lovango	LOV	20 Jan 04	18° 21.765’	64° 47.894’
Cockroach Island	CRI	7 May 04	18° 24.192’	65° 03.543’
Mandal	MAN	27 May 04	18° 21.783’	64° 53.951’
St. John				
Turner Bay	TUR	21 Oct 03	18° 19.285’	64° 47.694’
Flanagan Island	FLA	24 Oct 03	18° 19.636’	64° 39.168’
Reef Bay	RFB	13 Jan 04	18° 19.402’	64° 44.830’
Round Bay	RND	14 Jan 04	18° 19.769’	64° 40.611’
Europa Bay-1	EU-1	16 Jan 04	18° 18.947’	64° 43.912’
Henley Cay	HEN	16 Jan 04	18° 21.176’	64° 47.453’
Waterlemon Cay	WLM	22 Jan 04	18° 22.060’	64° 43.404’
Whistling Cay-1	WST-1	9 Mar 04	18° 22.218’	64° 45.550’
Whistling Cay-2	WST-2	30 Mar 04	18° 22.161’	64° 45.409’
America Point	AMP	30 Mar 04	18° 21.479’	64° 45.088’
Ram Head	RAM	2 Apr 04	18° 18.003’	64° 42.220’
Europa Bay-2	EU-2	26 Apr 04	18° 19.095’	64° 43.512’

Table 4. Comparison of *Cittarium pica* density and size between northern and southern islands groups of the USVI.

	Density				Size (shell width, mm)			
Method	Quadrat (No./m^2)		Belt (No./50 m^2)		Quadrat Method		Belt Transect	
Island Group[1]	STX	STT+J	STX	STT+J	STX	STT+J	STX	STT+J
Mean	7.5	8.9	7.3	6.6	20.7	22.2	85.3	78.6
Variance	73.7	180.8	113.7	103.7	197.7	185.7	160.6	87.8
Var/Mean ratio	9.9	20.4	15.5	15.7	9.5	8.4	1.9	1.1
St. Dev.	8.6	13.4	10.7	10.2	14.1	13.6	12.7	9.4
Observations	252	320	34	52	1880	2842	249	344
df	548	-	68	-	3935	-	591	-
t Statistic	-1.535	-	0.306	-	-3.448	-	7.341	-
P(T<=t) two-tail	0.125	-	0.760	-	0.001	-	< 0.001	-
t Critical two-tail	1.964	-	1.995	-	1.961	-	1.964	-
Significance	ns		ns		*		*	

1 Data were pooled by island group: STX = St. Croix, STT+J = St. Thomas, St. John, and associated cays.
An asterisk (*) indicates a significant difference ($P < 0.05$) using Students t-Test (two-Sample, assuming unequal variances, hypothesized mean difference =0, two tailed test).and an "ns" indicates not significantly different at the 0.05 probability level.

Table 5. Results of ANOVA to test differences in *Cittarium pica* population structure among three types of coastline.

Comparison	Groups[1]	Count	Sum	Avg	Var	Source of Variation	SS	df	MS	F	P-value	F crit
Abundance (quadrats)	I. Bay	136	1446	10.63	186.97	Between Groups	2357.2	2	1178.6	12.981	0.000	3.014
	II. Point	178	1183	6.65	43.35	Within Groups	45035.4	496	90.8			
	III. Cay	185	972	5.25	65.88	Total	47392.6	498			*	
Abundance (belt transects)	I. Bay	20	13	0.65	2.13	Between Groups	1380.9	2	690.4	7.016	0.002	3.126
	II. Point	26	221	8.50	128.10	Within Groups	6987.5	71	98.4			
	III. Cay	28	318	11.36	138.68	Total	8368.4	73			*	
Body Size (quadrats)	I. Bay	1446	28453	19.68	64.23	Between Groups	60836.5	2	30418.3	170.003	0.000	2.998
	II. Point	1183	25202	21.30	242.46	Within Groups	643784.0	3598	178.9			
	III. Cay	972	28709	29.54	272.28	Total	704620.5	3600			*	
Body Size (belt transects)	I. Bay	13	996	76.62	80.26	Between Groups	811.6	2	405.8	3.271	0.039	3.012
	II. Point	221	18143	82.10	152.50	Within Groups	68106.9	549	124.1			
	III. Cay	318	25433	79.98	105.97	Total	68918.5	551			*	

An asterisk (*) indicates a significant difference ($P < 0.05$) and “ns” indicates not significantly different at the 0.05 probability level.

1. For this analysis, survey sites were classified by coastline morphology and sea exposure into one of three groups: I. Bay (embayments, leeward or semi-protected coastlines, and tidepools), II. Point (points, headlands and exposed open coastlines) or III. Cay (cays and small islands, offshore islands). Group I sites were: SEC, WAT, RFB, HAS, RND, TUR, STB, KNB, HAM, SPH, and NTP (n =11). Group II sites were: LPE, WHP, MAH, GRP, HP-1, EU-1, HOV, EPT, AMP, GTP, ANB, RAM, BRB, PP-1, and LP-1 (n= 15). Group III sites were: LHL, LOV, WLM, SAB, FLA, IBR, BI-1, WST-1, SLT, ROC, CRI, HEN, THC, and DGI (n = 14). Paired sampling sites (EU-2, PP-2, WST-2, BI-2, LPW-2, HP-2) were excluded. MAN was also excluded because surveys there spanned two habitat categories (tidepools and exposed open coastline).

Figure 1. Location of sites for surveying *Cittarium pica* populations on St. Croix, U.S. Virgin Islands. Sites are indicated with closed circles and numbers (see text for site names). Four paired-sampling sites are shown with open circles. Map redrawn from Kendall et al. (2001).

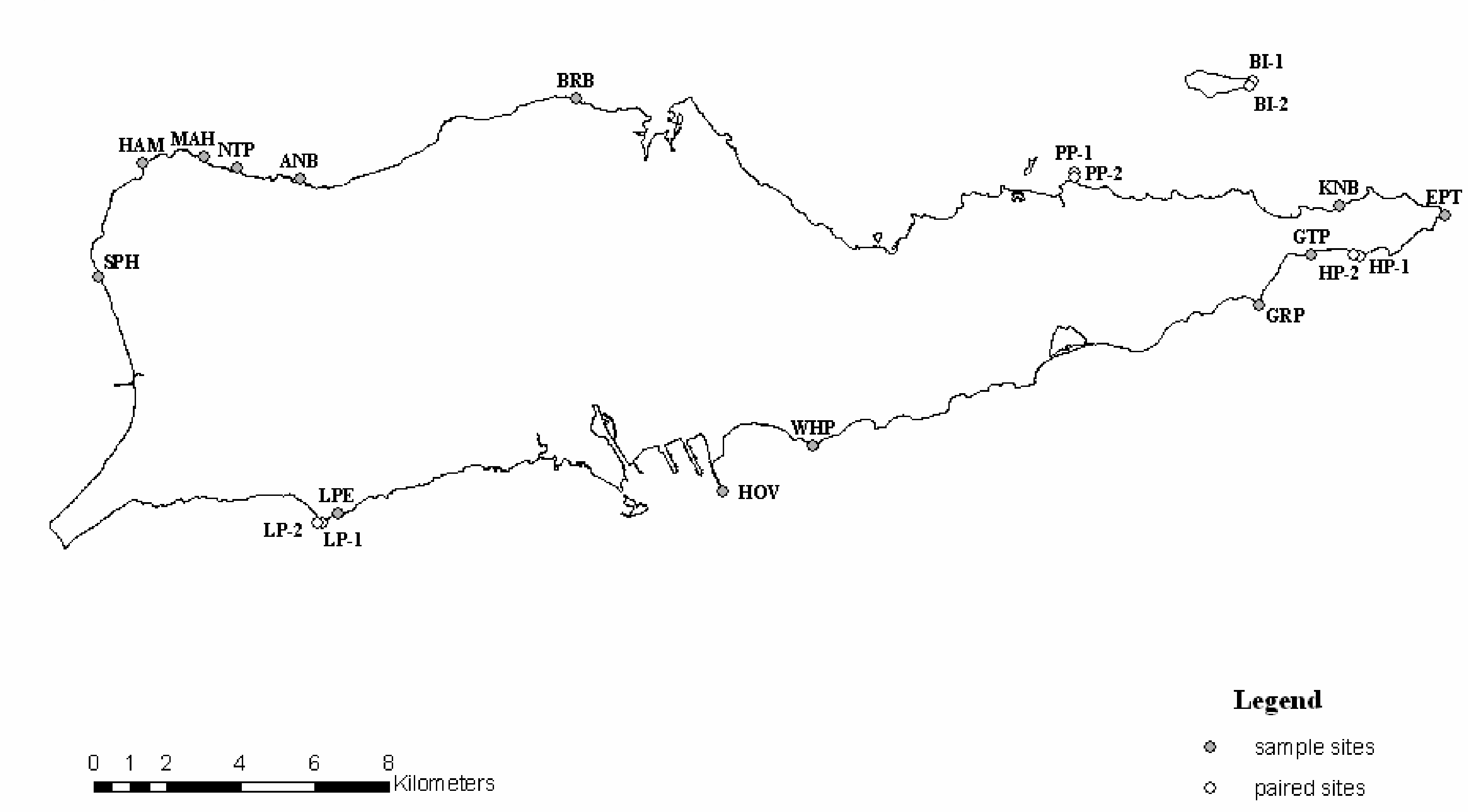


Figure 2. Location of sites for surveying *Cittarium pica* populations on St. Thomas, St.John and associated cays of the northern U.S. Virgin Islands. Sites are indicated with closed circles and numbers (see text for site names). Two paired-sampling sites are shown with open circles. Map redrawn from Kendall *et al*. (2001).

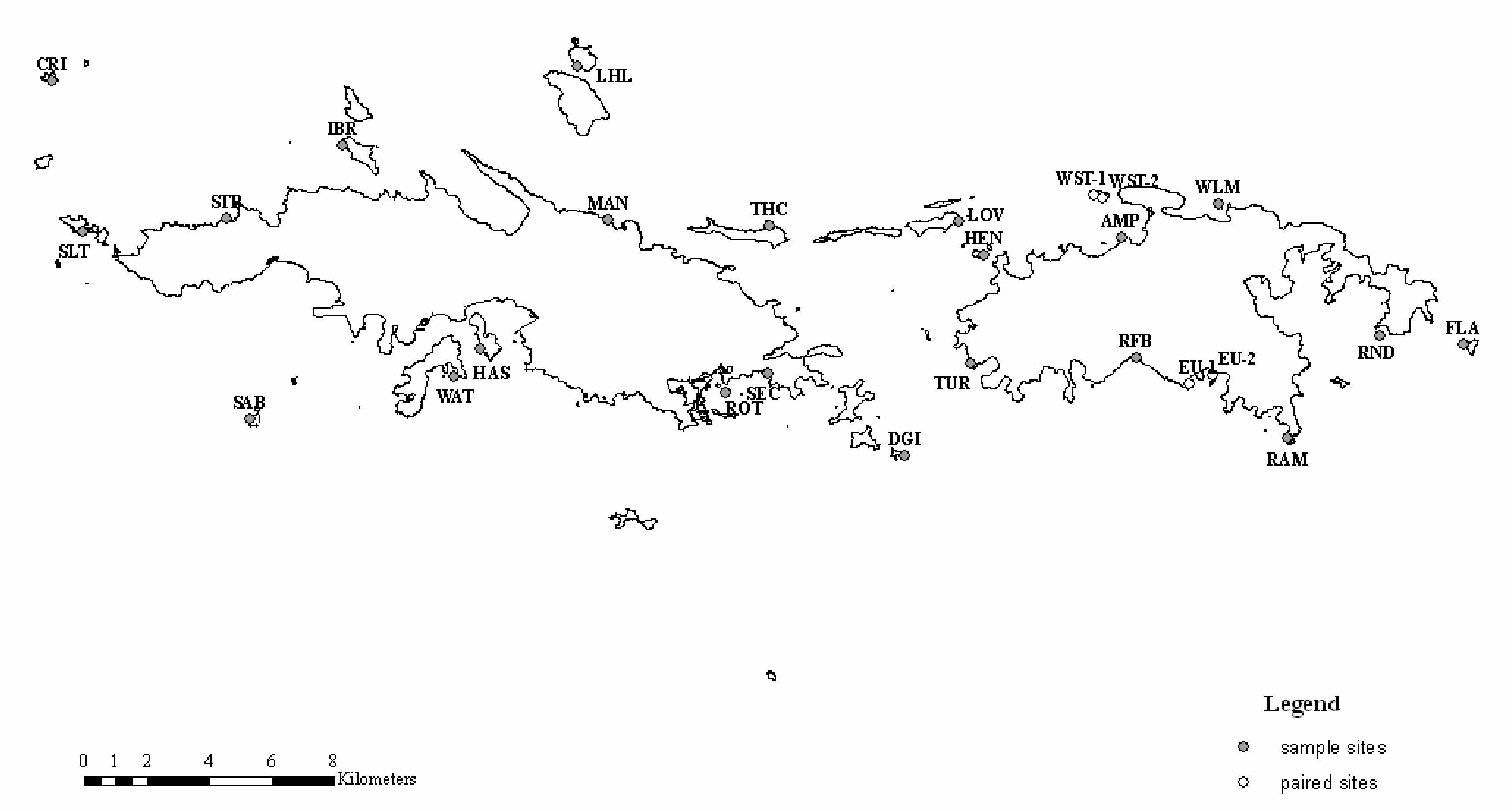
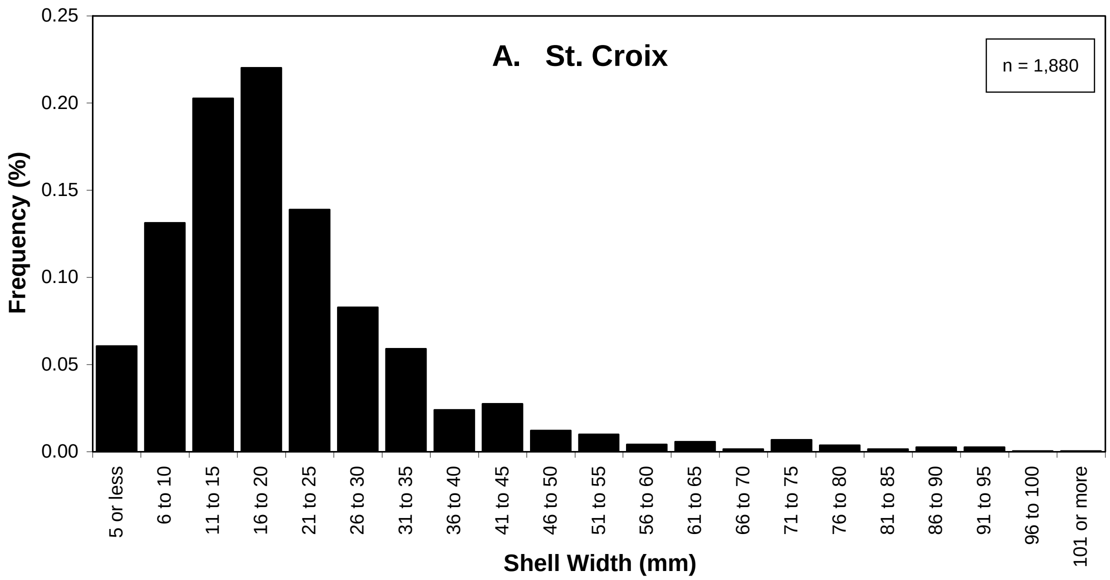


Figure 3. Size distribution of *Cittarium pica* obtained in quadrats. Quadrat data were pooled by island group. **A.** Southern island of St. Croix (21 surveys). **B.** Northern islands of St. Thomas, St. John, and associated cays (26 surveys).



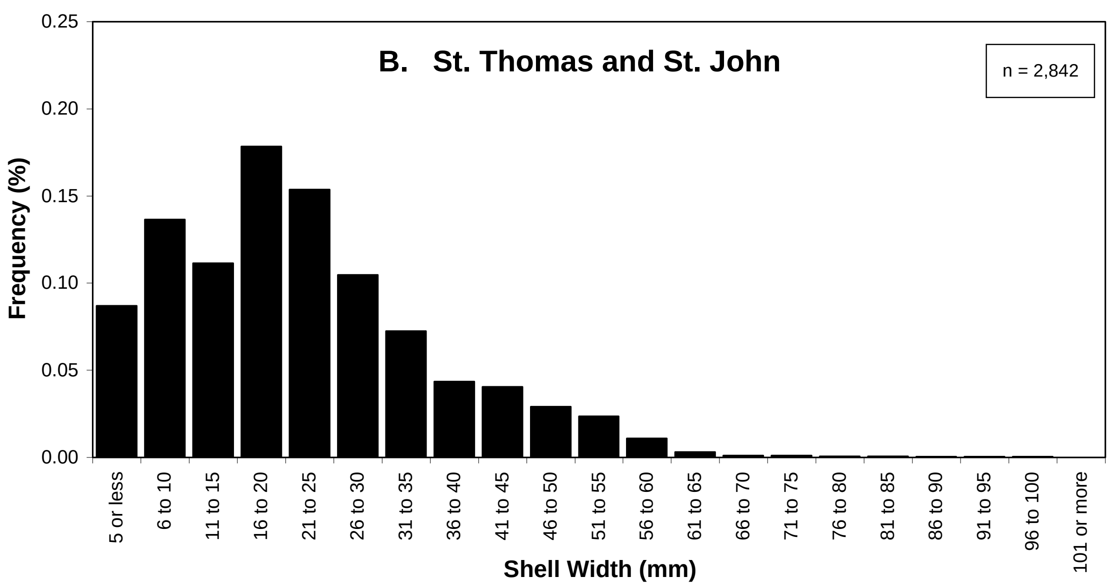


Figure 4. Size distribution of *Cittarium pica* obtained in belt transects. Only individuals $\geq$ 62 mm shell width (harvest-size) are presented. Belt transect data were pooled by island group. **A.** Southern island of St. Croix (19 surveys). **B.** Northern islands of St. Thomas, St. John, and associated cays (26 surveys).

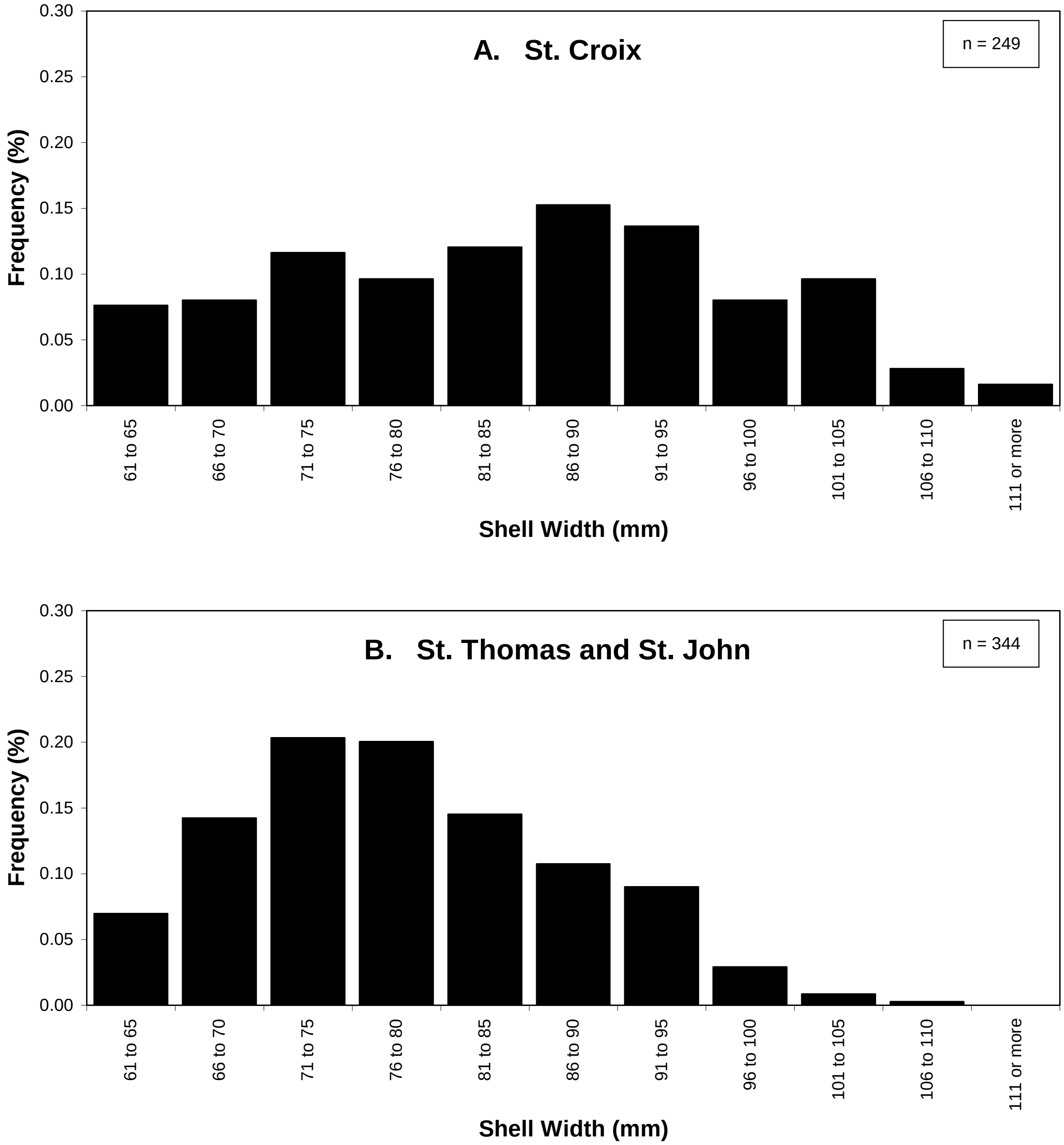
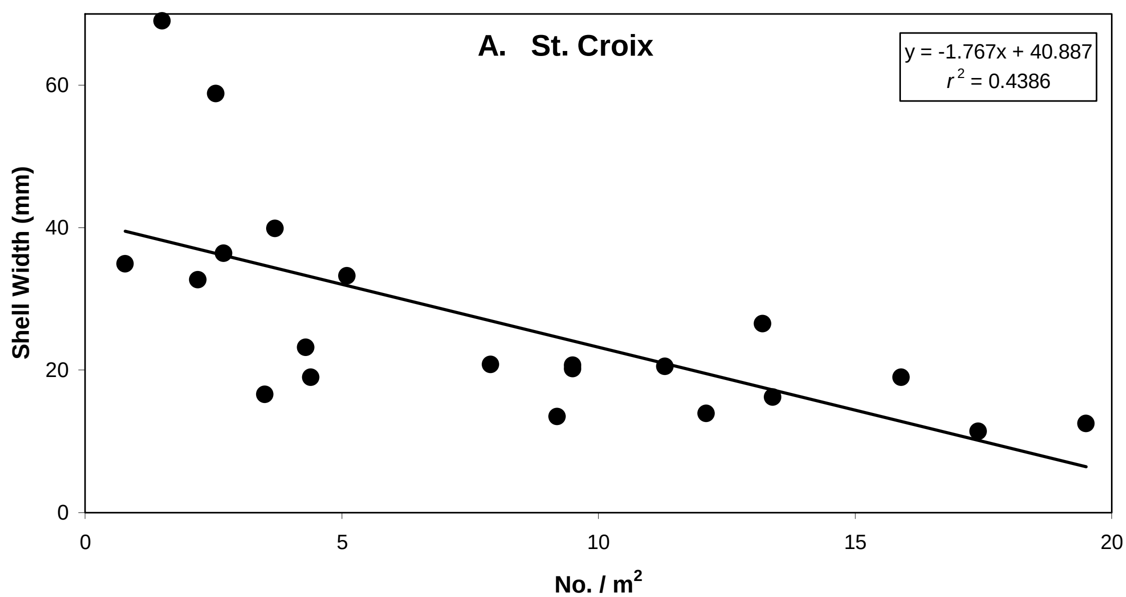


Figure 5. Relationship between size and abundance as observed for *Cittarium pica* in the USVI. Average abundance (number per m^2) is plotted against average shell width. Data are from quadrat surveys. Results from linear regression are shown with r^2 values. **A.** St. Croix. **B.** St. Thomas and St. John.



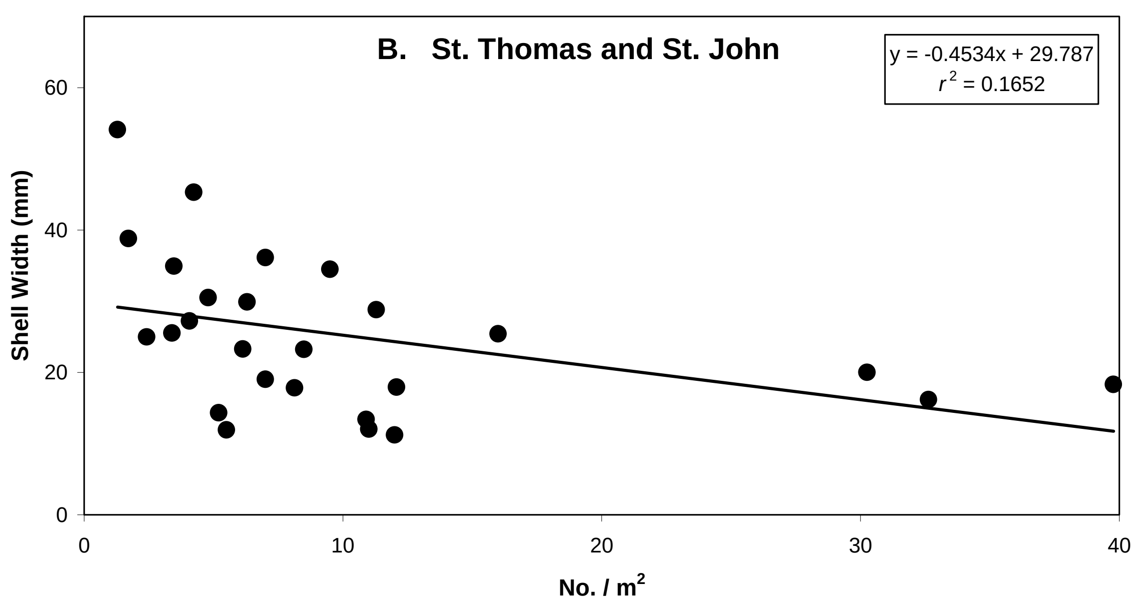


Figure 6. Differences in *Cittarium pica* populations between exposed and protected sites. Data are from six different areas in the USVI where paired-site surveys were conducted on the relatively exposed (windward) and relatively protected (leeward) stretches of the same coastline (see text). Presented data are from quadrat surveys, error bars represent standard deviation. **A.** Average abundance (number per m^2). **B.** Average size (shell width in mm).

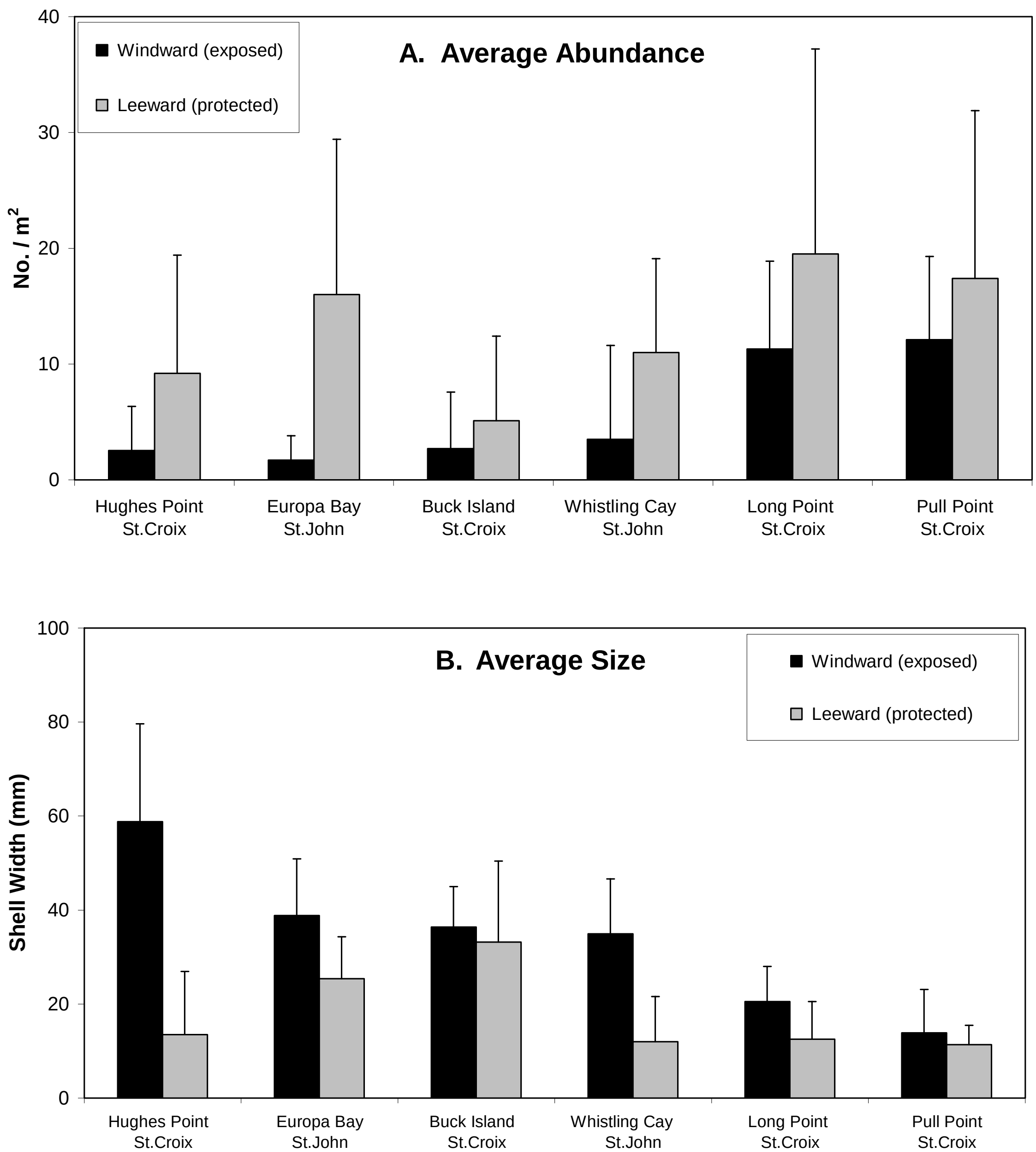
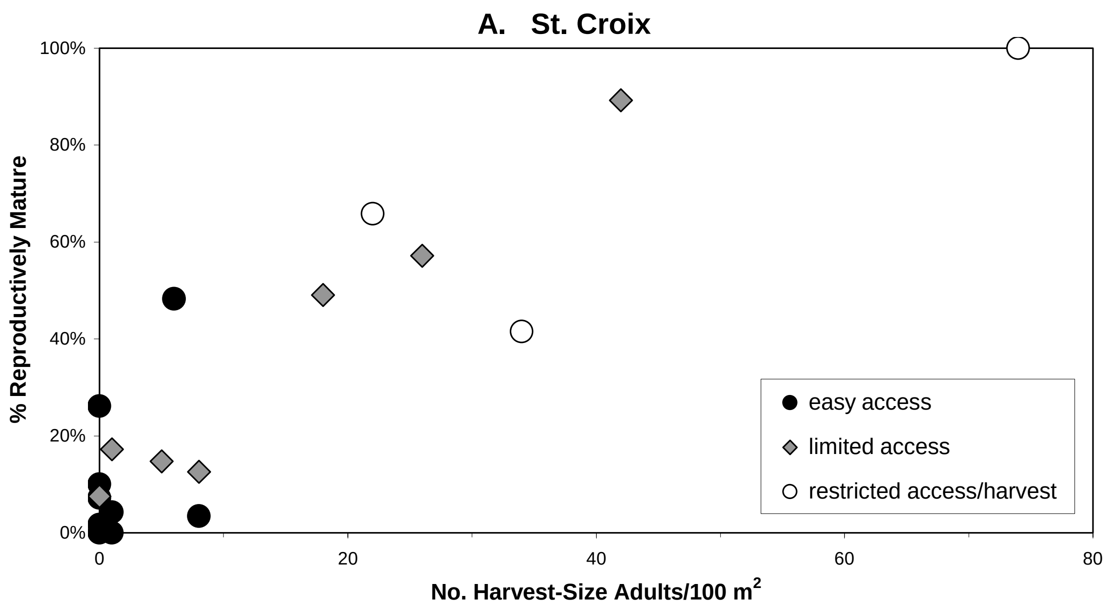


Figure 7. Accessibility of sites compared to reproductive attributes of *Cittarium pica* populations. Data for abundance of harvest-size adults (≥ 62 mm shell width) are from belt transects. Data for percentage of reproductively mature individuals are from quadrats surveys done at the same sites, and assume that *C. pica* reaches reproductive maturity at 31 mm. Sites are classified as easy access (black circles), limited access (gray diamonds) or restricted access (white circles). **A.** St. Croix. **B.** St. Thomas and St. John.



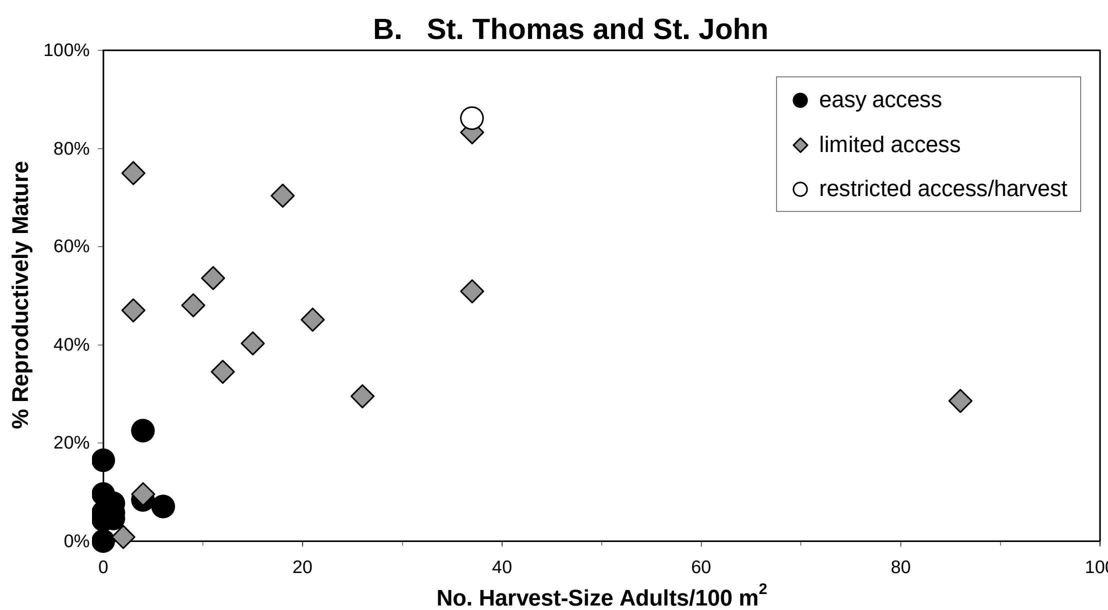
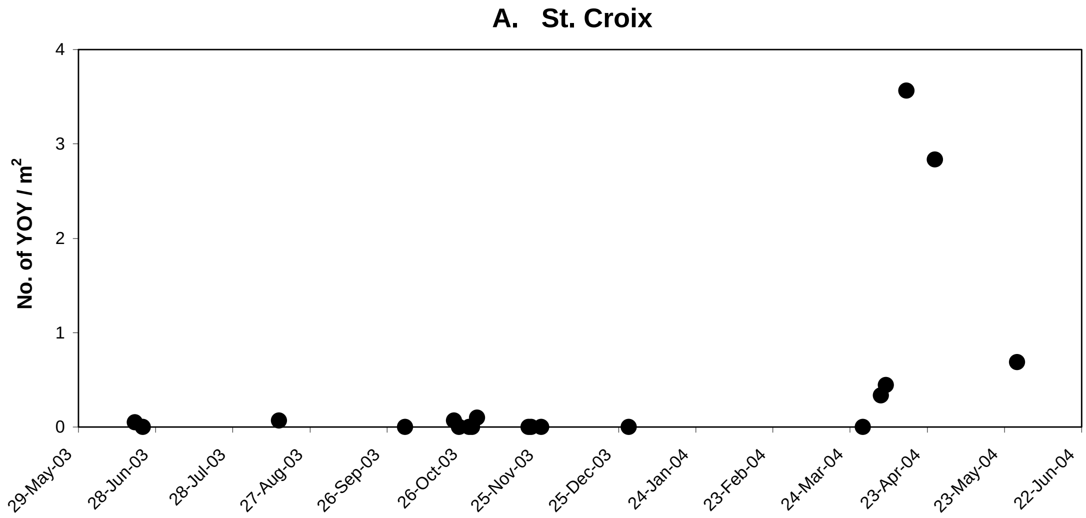


Figure 8. Variation in the density of *Cittarium* young-of-the-year (YOY; ≤ 5 mm shell width) during 2003-2004 surveys at 41 areas in the USVI. Values are reported as the average number of YOY per m^2 observed during quadrat surveys. **A.** St. Croix (17 survey areas). **B.** St. Thomas and St. John (24 survey areas). Note the different scales used for y-axes.



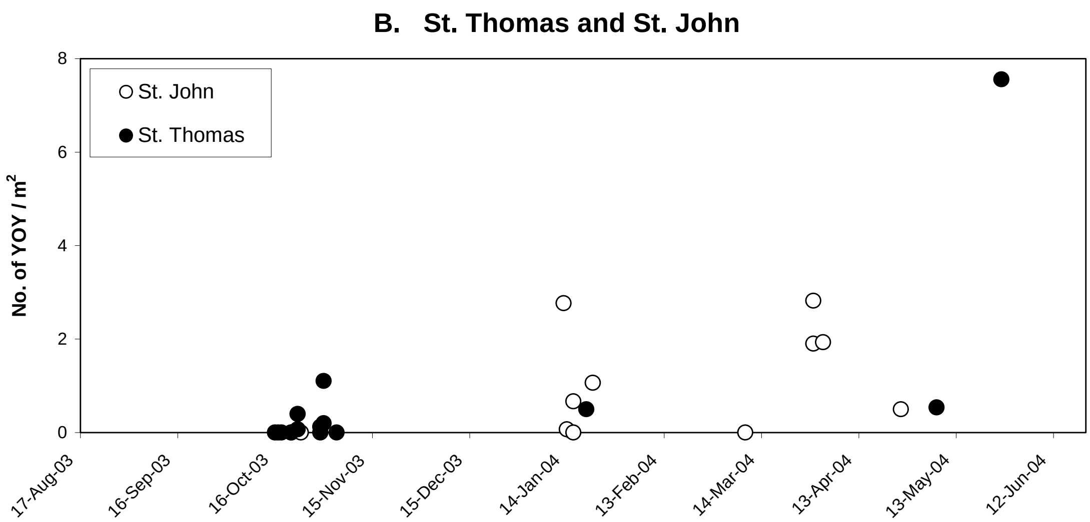
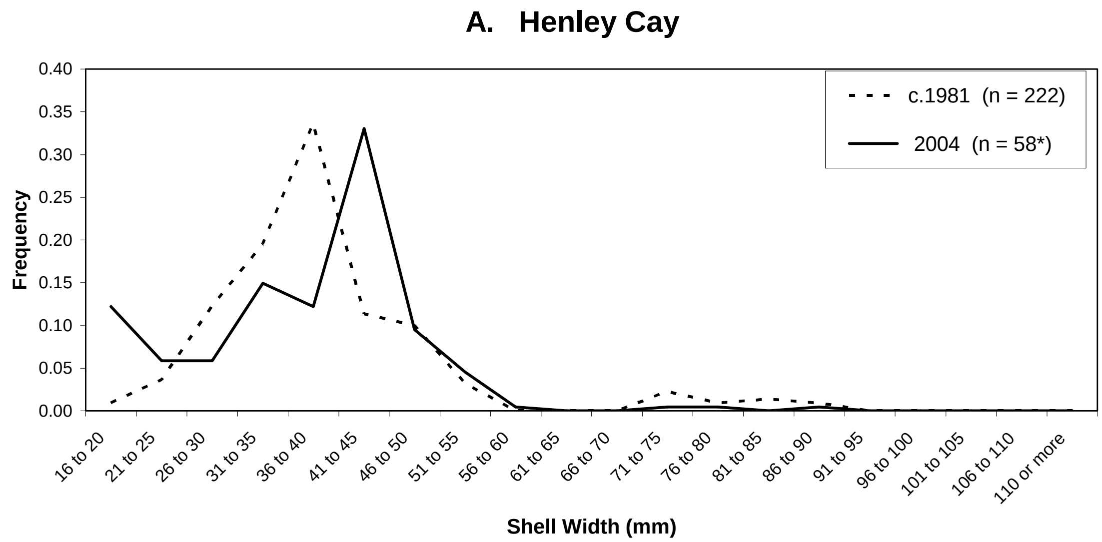
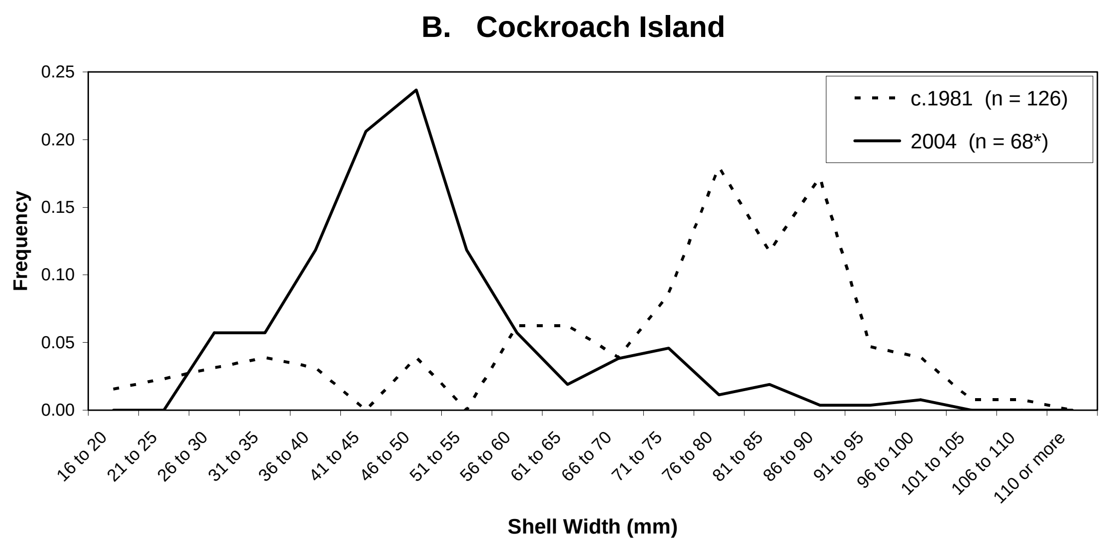


Figure 9. Historic data for *Cittarium pica* size distribution compared to results obtained in this study. Data from quadrats and belt transects were combined (see text) **A.** Henley Cay, St. John. **B.** Cockroach Island, St. Thomas.





Appendix 1. *Cittarium pica* survey results using the quadrat method.

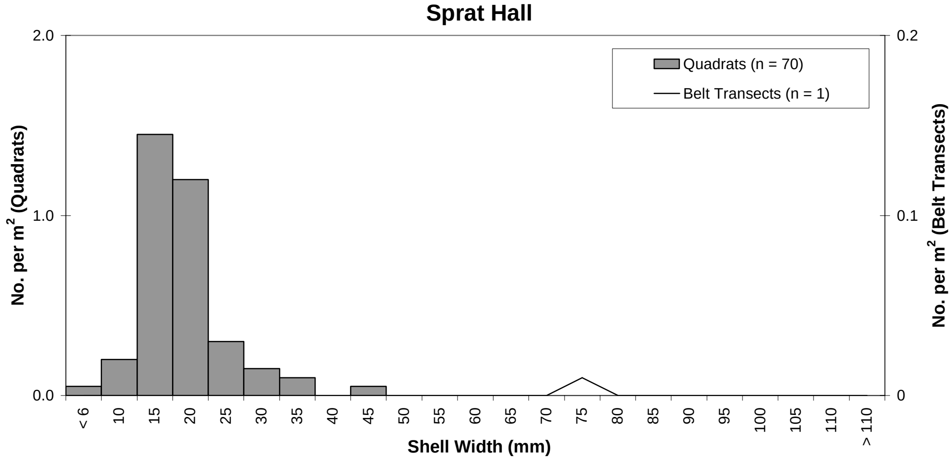
Site Name (code)	No. Quads	Total No.	Topshell Density (No./m2) Avg	StDev	Max	Min.	Topshell Size (mm) Avg.	StDev	Max	Min
St. Croix										
Sprat Hall (SPH)	20	70	3.5	5.2	19	0	16.6	6.1	41	3
Hams Bay (HAM)	15	65	4.3	4.7	20	0	23.2	8.4	37	8
Barons Bluff (BRB)	15	118	7.9	4.9	18	0	20.8	14.1	59	4
Long Point, East (LPE)	15	201	13.4	7.7	25	1	16.2	8.8	78	8
Annaly Bay (ANB)	15	143	9.5	6.0	25	2	20.2	9.2	56	4
Knights Bay (KNB)	11	175	15.9	8.6	28	0	19.0	4.8	48	11
Grassy Point (GRP)	15	55	3.7	4.9	15	0	39.9	23.8	105	17
Grapetree Point (GTP)	13	29	2.2	4.1	15	0	32.7	13.5	60	17
Watch Ho (WHP)	10	95	9.5	6.6	20	0	20.7	7.5	41	5
East Point (EPT)	9	7	0.8	1.3	4	0	34.9	14.1	64	22
Buck Island-1 (BI-1)	15	41	2.7	4.9	15	0	36.4	8.6	57	25
Buck Island-2 (BI-2)	15	77	5.1	7.3	24	0	33.2	17.2	92	12
Hovensa (HOV)	8	12	1.5	2.5	6	0	69.0	13.6	93	53
Hughes Point-1 (HP-1)	11	28	2.5	3.8	13	0	58.8	20.8	78	6
Maroon Hole (MAH)	12	53	4.4	3.5	14	1	19.0	12.2	55	4
NW Tidepools (NTP)	9	119	13.2	10.1	33	2	26.5	11.7	80	3
Long Point, West-1 (LP-1)	8	90	11.3	7.6	25	4	20.5	7.5	37	3
Long Point, West-2 (LP-2)	8	156	19.5	17.7	58	1	12.5	8.0	29	2
Hughes Point-2 (HP-2)	12	110	9.2	10.2	27	0	13.5	13.4	55	3
Pull Point-1 (PP-1)	8	97	12.1	7.2	24	6	13.9	9.2	57	3
Pull Point-2 (PP-2)	8	139	17.4	14.5	45	0	11.4	4.1	22	3
St. Thomas										
Rotto Cay (ROT)	17	72	4.2	5.4	16	0	45.3	15.5	97	17
Dog Island (DGI)	16	18	1.1	1.8	6	0	54.1	21.3	85	15
Secret Harbor (SEC)	8	261	32.6	18.1	68	9	16.2	6.9	57	6
Thatch Cay (THC)	12	29	2.4	2.4	7	0	25	13.2	47	6
Salt Cay (SLT)	15	72	4.8	7.2	20	0	30.5	15.9	64	4
Stumpy Bay (STB)	10	55	5.5	4.8	15	0	11.9	6.6	29	4
Water Island (WAT)	8	242	30.3	26.2	71	5	20	6.3	57	5
Hassel Island (HAS)	14	119	8.5	10.2	27	0	23.2	6.5	58	6
L. Hans Lollick (LHL)	10	120	12.0	11.2	34	0	11.2	4.6	36	5
Inner Brass (IBR)	10	52	5.2	8.3	25	0	14.3	11.3	58	5
Saba Island (SAB)	12	84	7.0	8.6	20	0	36.1	12.8	64	19
Lovango (LOV)	10	113	11.3	10.3	27	0	28.8	10.6	56	3
Cockroach Island (CRI)	13	53	4.1	5.6	21	0	27.2	19.8	58	3
Mandal (MAN)	9	358	39.8	33.9	93	0	18.3	11.9	55	2
St. John										
Turner Bay (TUR)	13	91	7.0	5.9	19	0	19.0	5.9	41	8
Flanagan Island (FLA)	10	63	6.3	13.8	45	0	29.9	11.0	62	11
Reef Bay (RFB)	13	157	12.1	14.5	45	0	17.9	9.5	42	2
Round Bay (RND)	15	92	6.1	10.3	42	0	23.3	5.1	34	3
Europa Bay-1 (EU-1)	14	24	1.7	2.1	7	0	38.8	12.1	57	12
Henley Cay (HEN)	15	51	3.4	5.3	15	0	25.5	16.6	52	2
Waterlemon Cay (WLM)	16	152	9.5	11.2	47	0	34.5	15.5	60	2
Whistling Cay-1 (WST-1)	14	52	3.7	8.1	29	0	34.9	11.7	58	10
Whistling Cay-2 (WST-2)	11	121	11.0	8.1	25	0	12.0	9.6	51	2
America Point (AMP)	10	109	10.9	6.1	19	0	13.4	8.8	51	2
Rams Head (RAM)	15	122	8.1	6.2	18	0	17.8	15.7	52	3
Europa Bay-2 (EU-2)	10	160	16.0	13.4	33	0	25.4	8.9	52	3

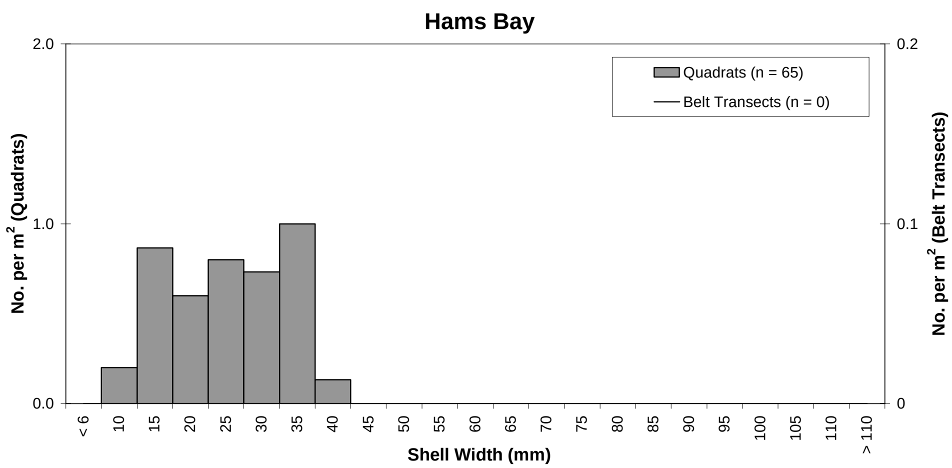
Appendix 2. *Cittarium pica* survey results using the belt transect method.

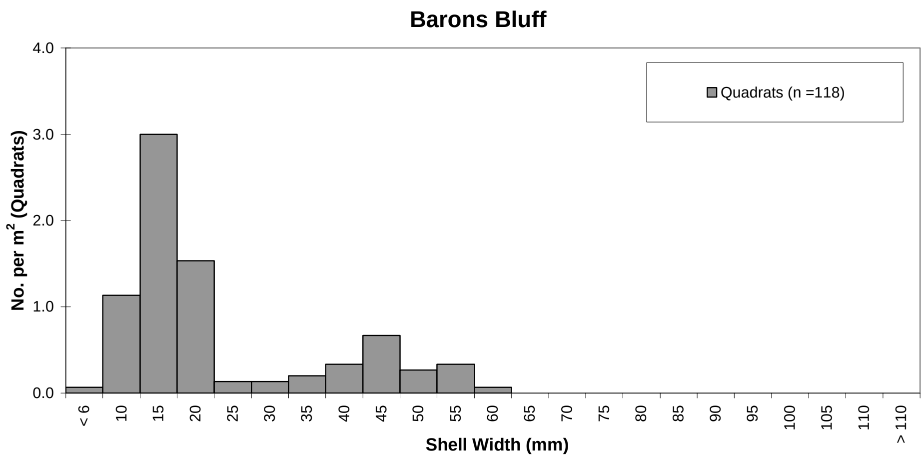
Site Name (code)	No. Belts	Total No. All	Total No. (≥62)	Total No. (<62)	Avg Density (No./m2) All	Avg Density (No./m2) (≥62)	Size (mm) Avg	Size (mm) StDev	Size (mm) Max	Size (mm) Min
St. Croix										
Sprat Hall (SPH)	2	1	1	0	0.01	0.01	72	-	72	72
Hams Bay (HAM)	2	0	0	0	0.00	0.00	-	-	-	-
Long Point, East (LPE)	2	8	8	0	0.08	0.08	70.1	4.9	79	64
Annaly Bay (ANB)	2	10	9	1	0.10	0.09	69.0	10.1	94	61
Knights Bay (KNB)	2	0	0	0	0.00	0.00	-	-	-	-
Grassy Point (GRP)	2	18	18	0	0.18	0.18	99.2	10.4	114	73
Grapetree Point (GTP)	2	8	6	2	0.08	0.06	72.3	15.4	87	46
Watch Ho (WHP)	2	5	5	0	0.05	0.05	101.4	11.6	111	83
East Point (EPT)	2	27	26	1	0.27	0.26	80.7	13.3	105	60
Buck Island-1 (BI-1)	2	22	22	0	0.22	0.22	95.0	7.1	109	83
Buck Island-2 (BI-2)	2	34	34	0	0.34	0.34	93.6	6.2	105	82
Hovensa (HOV)	2	74	74	0	0.74	0.74	86.0	10.6	108	65
Hughes Point-1 (HP-1)	2	45	44	1	0.45	0.44	74.1	8.1	92	59
Maroon Hole (MAH)	2	0	0	0	0.00	0.00	-	-	-	-
Long Point, W-1 (LP-1)	1	0	0	0	0.00	0.00	-	-	-	-
Long Point, W-2 (LP-2)	1	0	0	0	0.00	0.00	-	-	-	-
Hughes Point-2 (HP-2)	2	1	1	0	0.01	0.01	84.0	-	84	84
Pull Point-1 (PP-1)	1	1	0	1	0.02	0.00	56.0	-	56	56
Pull Point-2 (PP-2)	1	1	1	0	0.02	0.02	83.0	-	83	83
St. Thomas										
Rotto Cay (ROT)	2	38	37	1	0.38	0.37	73.6	6.7	84	56
Dog Island (DGI)	2	41	37	4	0.41	0.37	77.8	9.6	99	58
Secret Harbor (SEC)	2	1	1	0	0.01	0.01	77.0	-	77	77
Thatch Cay (THC)	2	15	13	2	0.15	0.13	70.6	12.1	88	40
Salt Cay (SLT)	2	20	15	5	0.20	0.15	73.3	14.9	103	52
Stumpy Bay (STB)	2	0	0	0	0.00	0.00	-	-	-	-
Water Island (WAT)	2	17	6	11	0.17	0.06	58.4	17.2	94	37
Hassel Island (HAS)	2	12	4	8	0.12	0.04	56.4	17.8	92	35
L. Hans Lollick (LHL)	2	2	2	0	0.02	0.02	79.0	12.7	88	70
Inner Brass (IBR)	2	32	5	27	0.32	0.05	50.9	11.3	80	32
Saba Island (SAB)	2	14	12	2	0.14	0.12	67.7	6.3	77	55
Lovango (LOV)	2	26	21	5	0.26	0.21	78.4	13.8	96	50
Cockroach Island (CRI)	2	39	38	1	0.39	0.38	74.2	8.7	97	61
Mandal (MAN)	2	0	0	0	0.00	0.00	-	-	-	-
St. John										
Turner Bay (TUR)	2	1	1	0	0.01	0.01	76.0	-	76	76
Flanagan Island (FLA)	2	92	86	6	0.92	0.86	82.3	10.3	109	52
Reef Bay (RFB)	2	0	0	0	0.00	0.00	-	-	-	-
Round Bay (RND)	2	0	0	0	0.00	0.00	-	-	-	-
Europa Bay-1 (EU-1)	2	5	4	1	0.05	0.04	72.0	13.2	86	55
Henley Cay (HEN)	2	8	3	5	0.08	0.03	63.5	14.3	90	50
Waterlemon Cay (WLM)	2	34	18	16	0.34	0.18	64.9	11.1	94	49
Whistling-1 (WST-1)	2	10	9	1	0.10	0.09	85.4	13.5	105	61
Whistling-2 (WST-2)	2	0	0	0	0.00	0.00	-	-	-	-
America Point (AMP)	2	1	1	0	0.01	0.01	98.0	-	98	98
Rams Head (RAM)	2	34	26	8	0.34	0.26	72.4	10.5	87	47
Europa Bay-2 (EU-2)	2	5	5	0	0.05	0.05	72.8	10.5	85	62

Note: Belt transect surveys were not conducted at Barons Bluff (BRB) and Northshore tidepools (NTP).

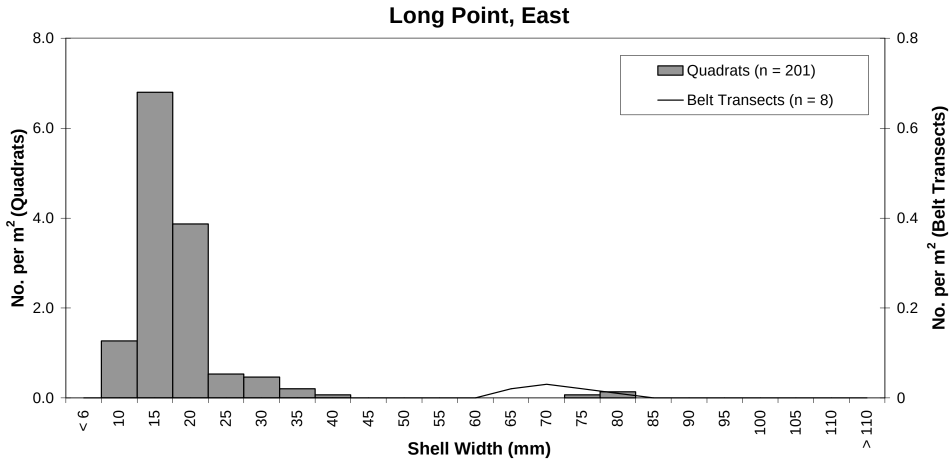
Appendix 3. Size distribution of *Cittarium pica* at St. Croix sampling sites as determined from quadrat sampling (columns) and belt transect sampling (lines).

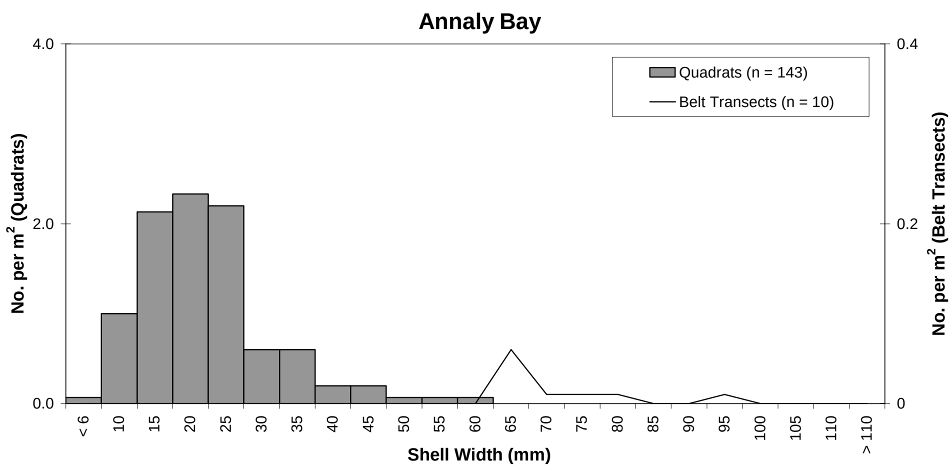


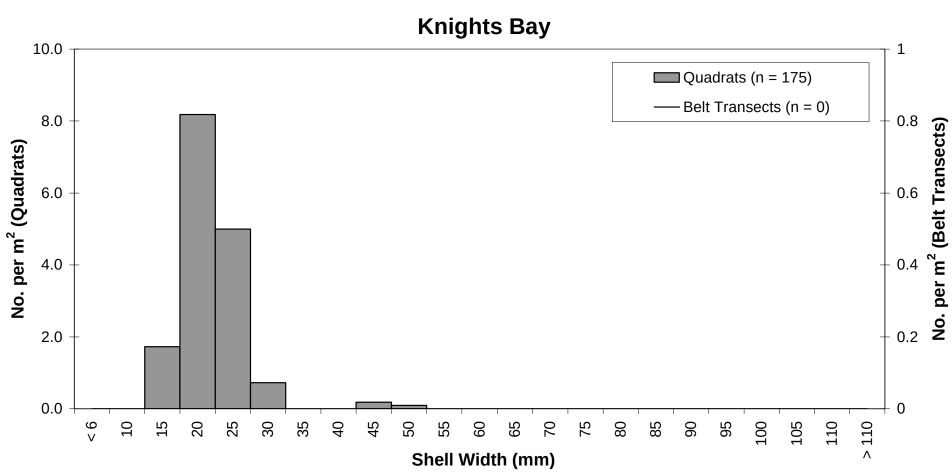




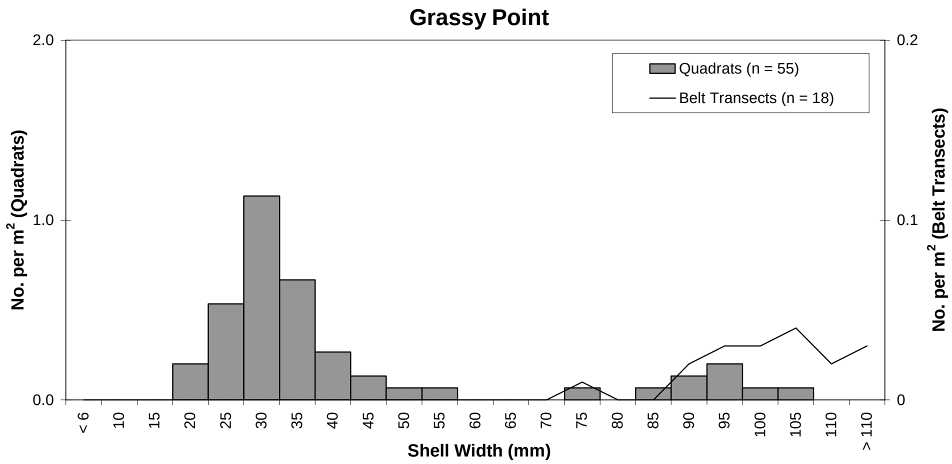
Appendix 3 continued. Size distribution of *Cittarium pica* at St. Croix sampling sites as determined from quadrat sampling (columns) and belt transect sampling (lines).

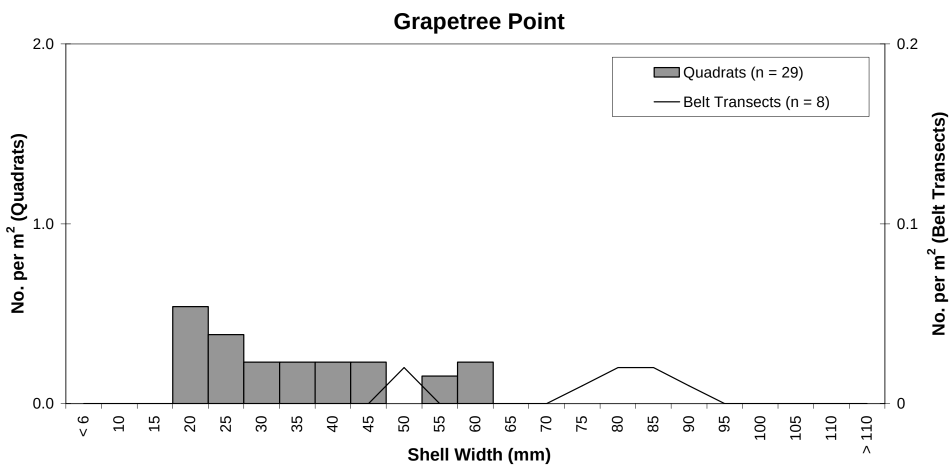


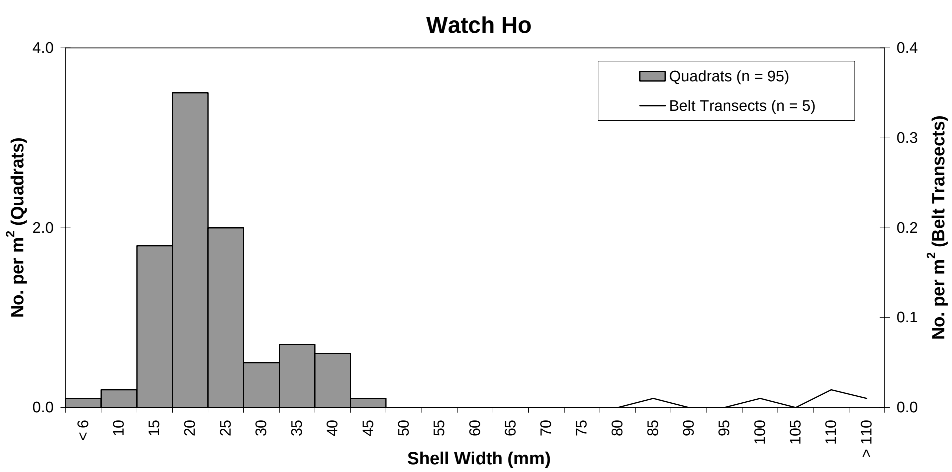




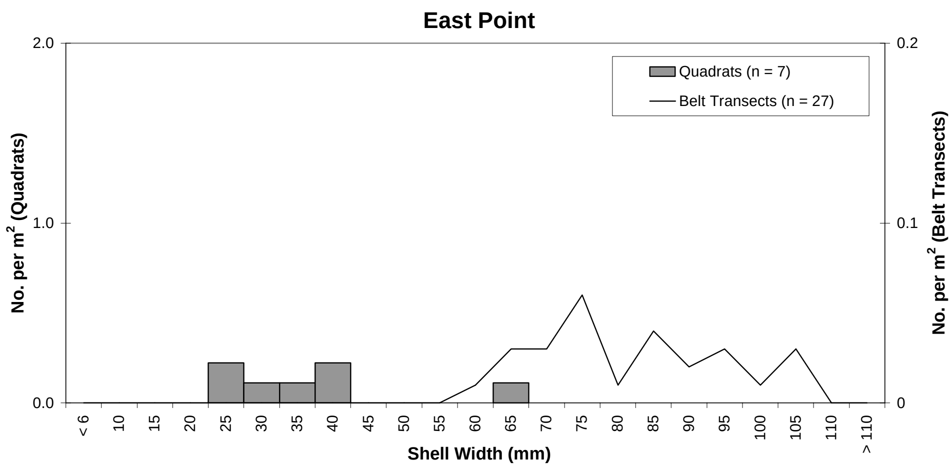
Appendix 3 continued. Size distribution of *Cittarium pica* at St. Croix sampling sites as determined from quadrat sampling (columns) and belt transect sampling (lines).

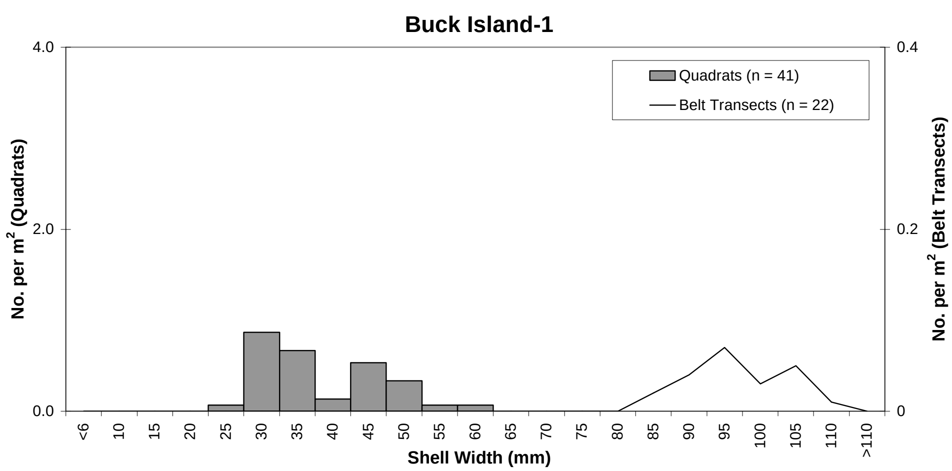


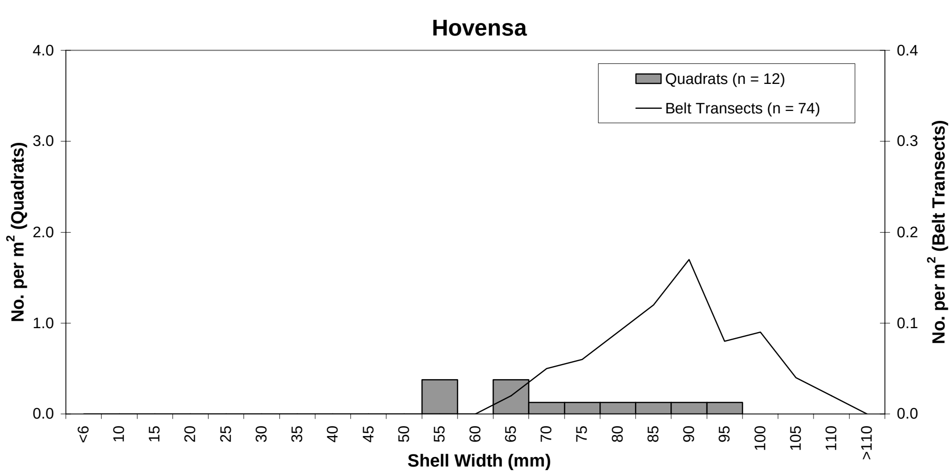




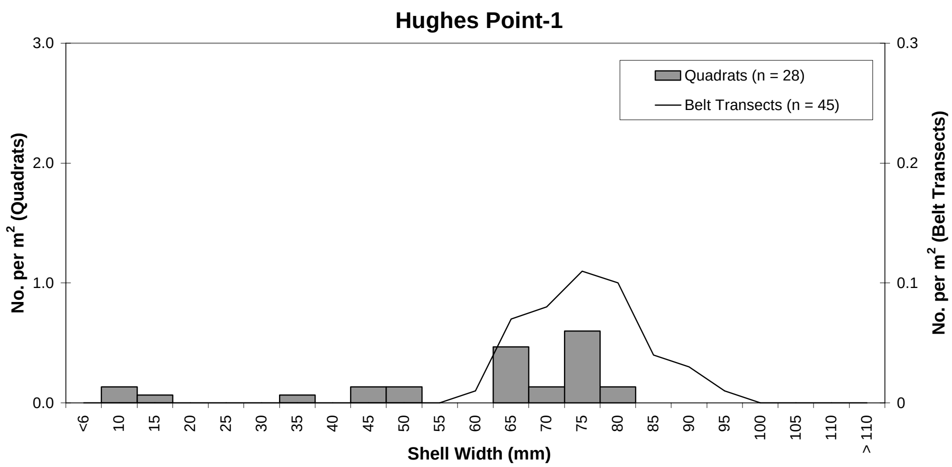
Appendix 3 continued. Size distribution of *Cittarium pica* at St. Croix sampling sites as determined from quadrat sampling (columns) and belt transect sampling (lines).

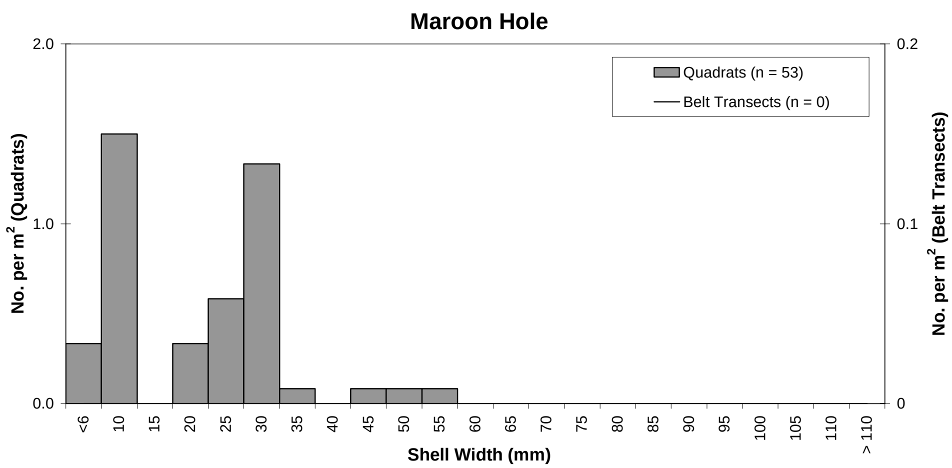


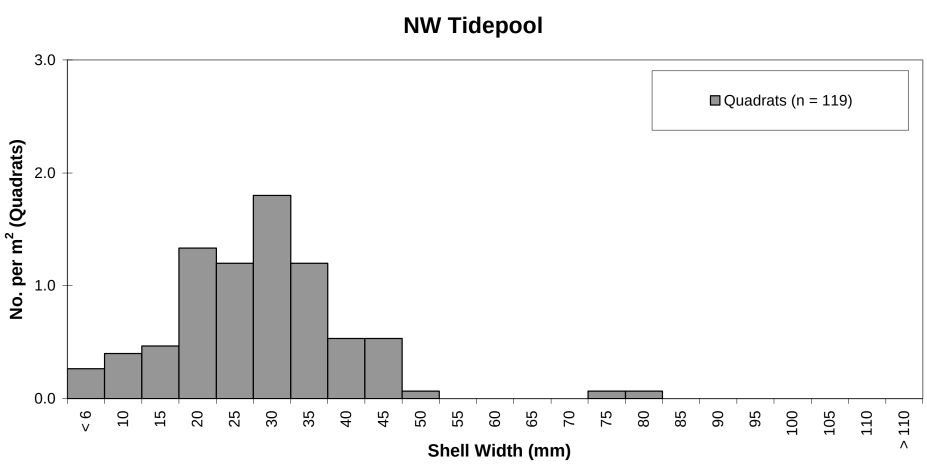




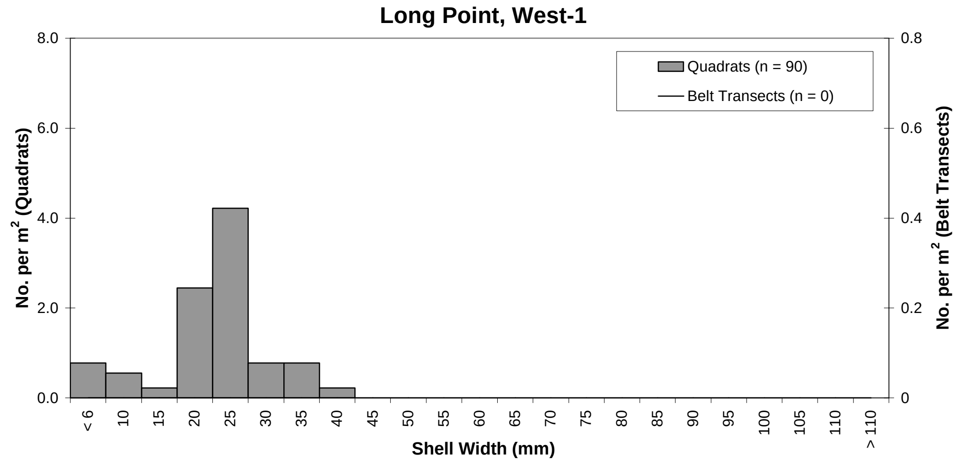
Appendix 3 continued. Size distribution of *Cittarium pica* at St. Croix sampling sites as determined from quadrat sampling (columns) and belt transect sampling (lines).

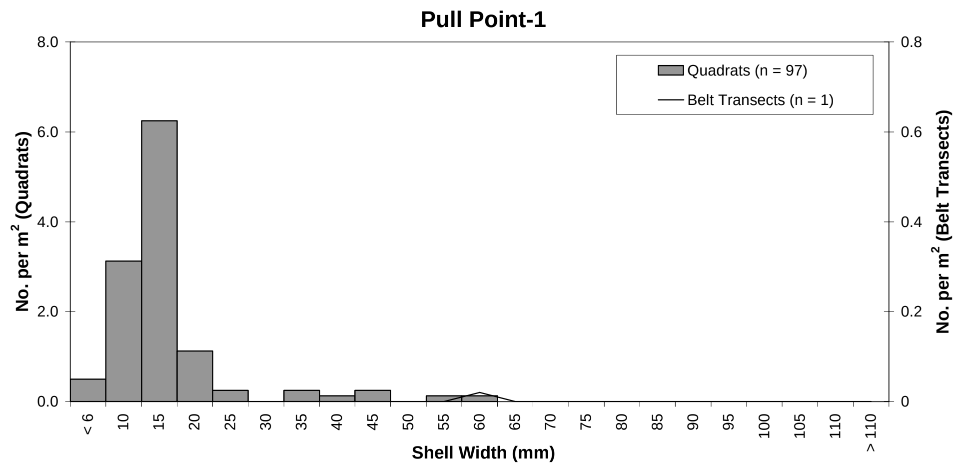




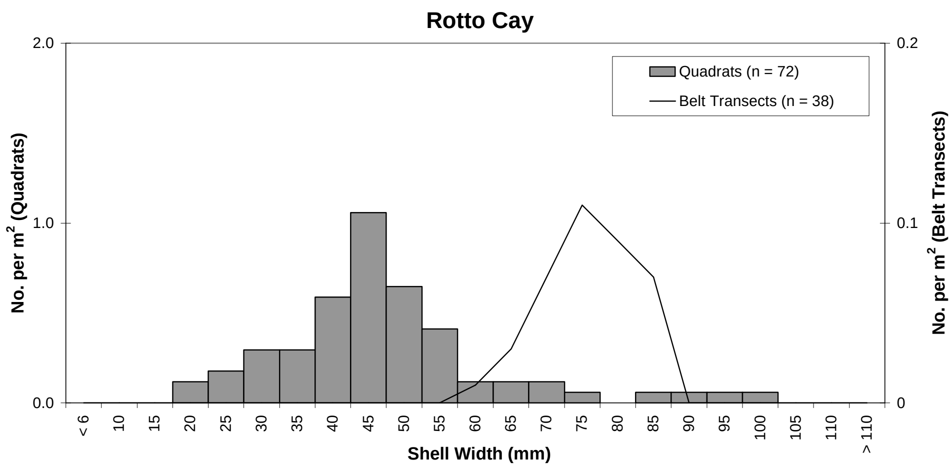


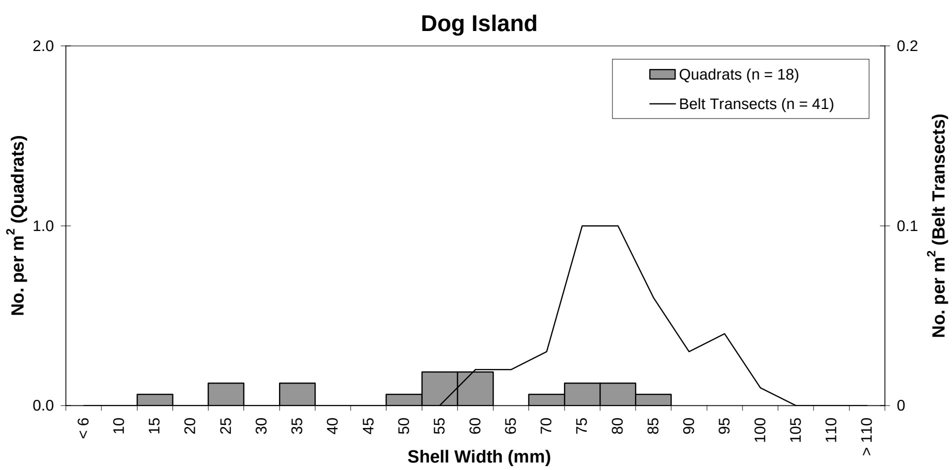
Appendix 3 continued. Size distribution of *Cittarium pica* at St. Croix sampling sites as determined from quadrat sampling (columns) and belt transect sampling (lines).

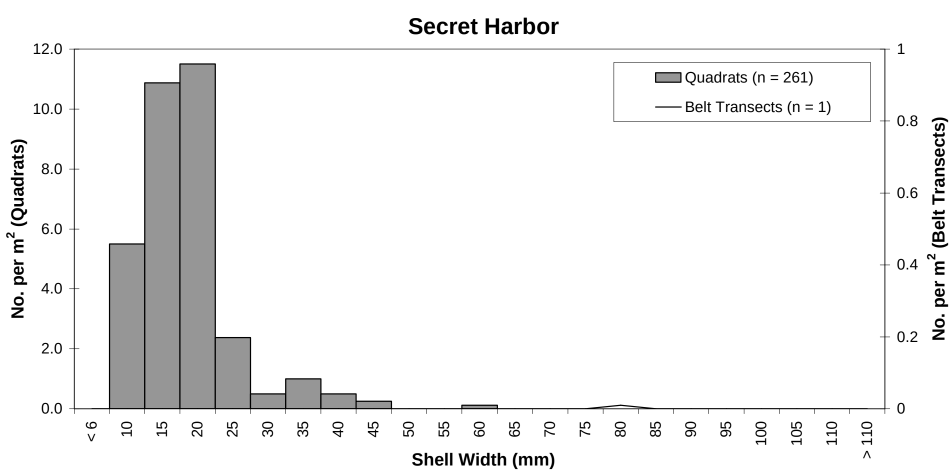




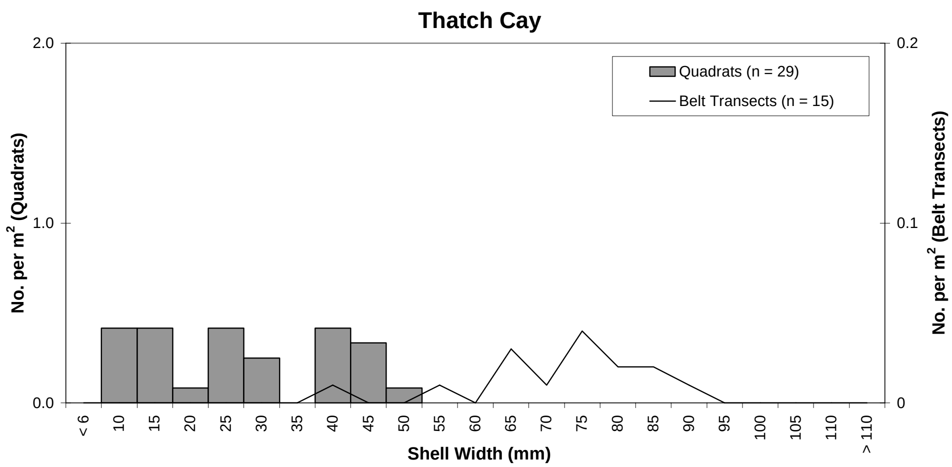
Appendix 4. Size distribution of *Cittarium pica* at St. Thomas sampling sites as determined from quadrat sampling (columns) and belt transect sampling (lines).

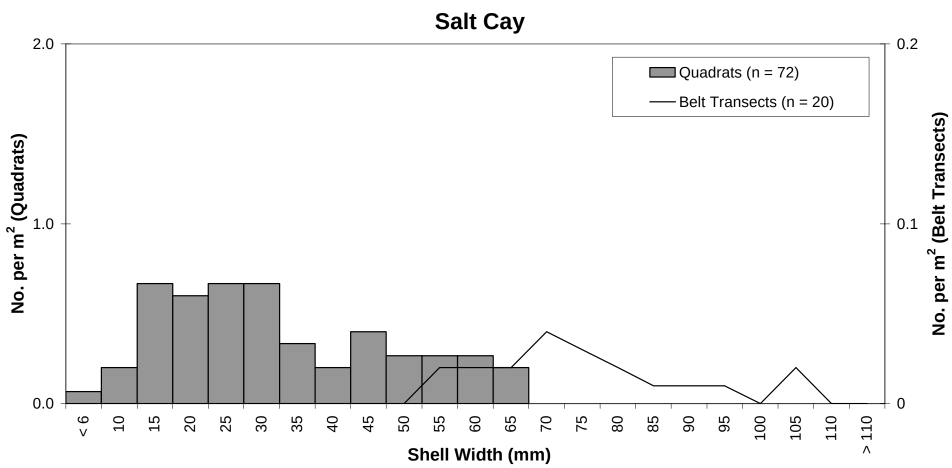


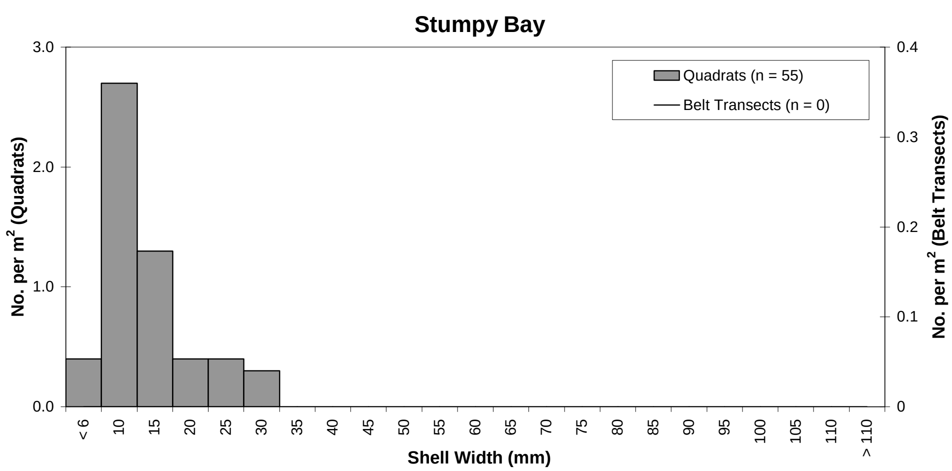




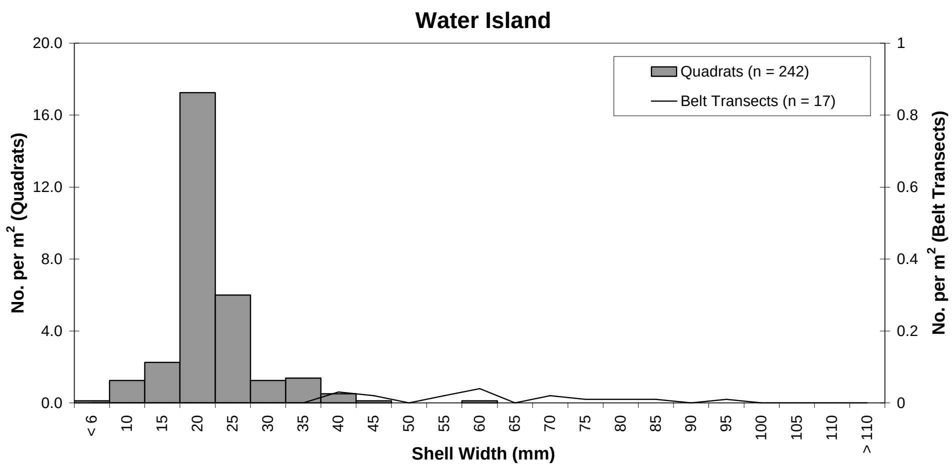
Appendix 4 continued. Size distribution of *Cittarium pica* at St. Thomas sampling sites as determined from quadrat sampling (columns) and belt transect sampling (lines).

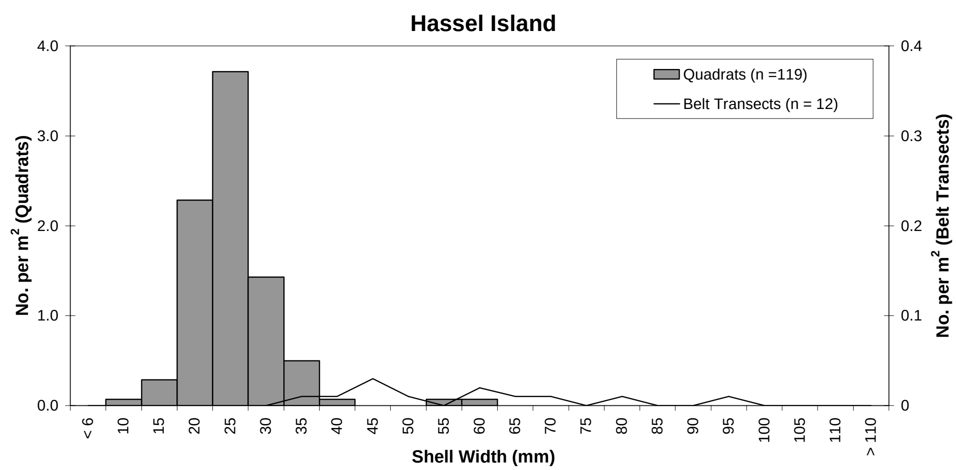


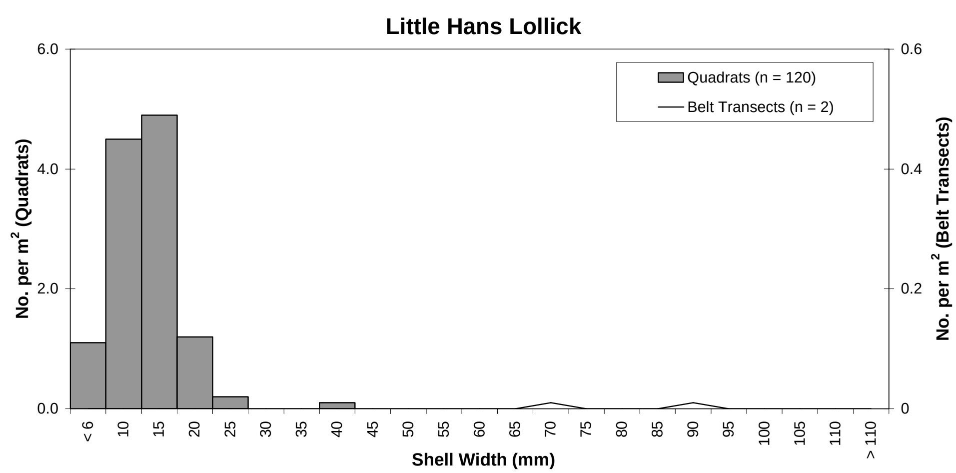




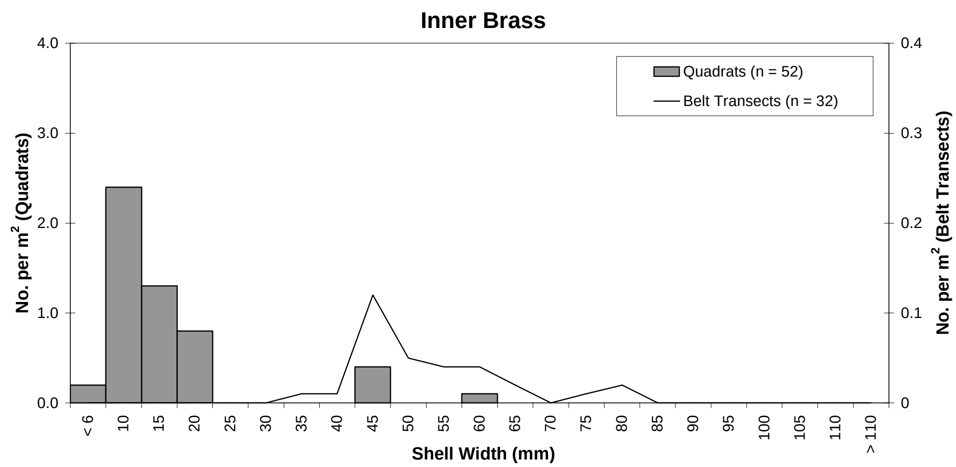
Appendix 4 continued. Size distribution of *Cittarium pica* at St. Thomas sampling sites as determined from quadrat sampling (columns) and belt transect sampling (lines).

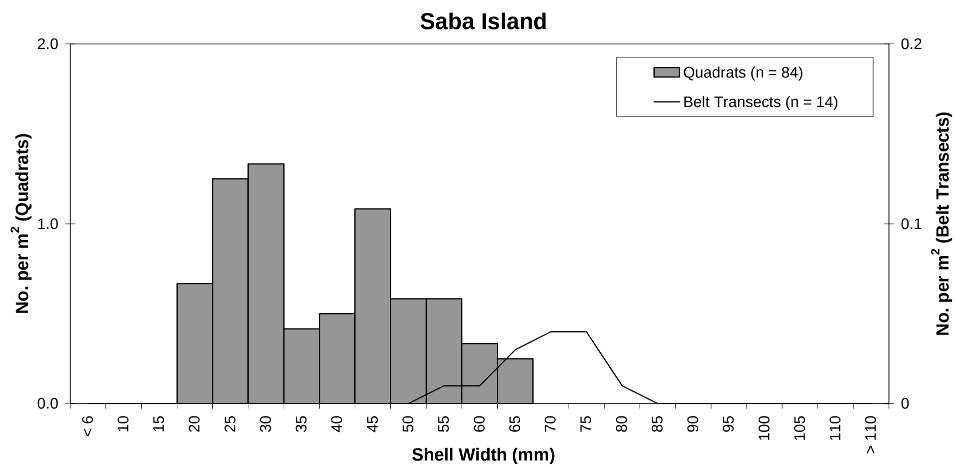


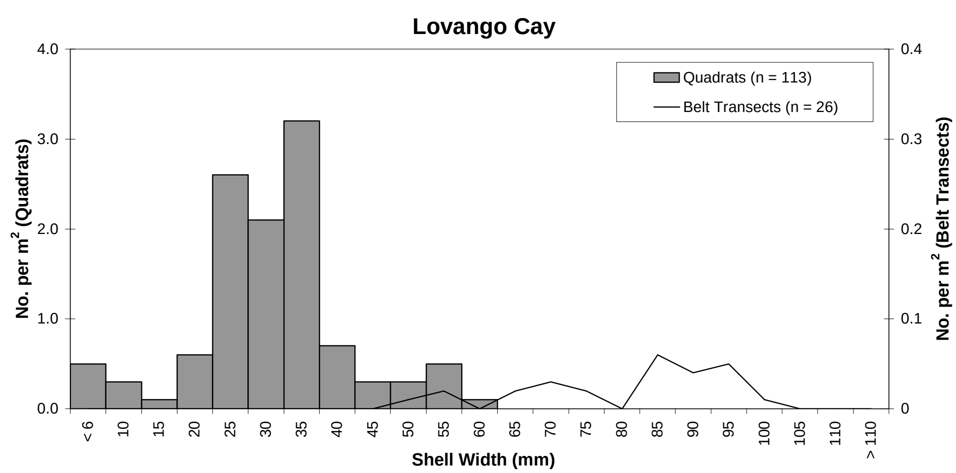




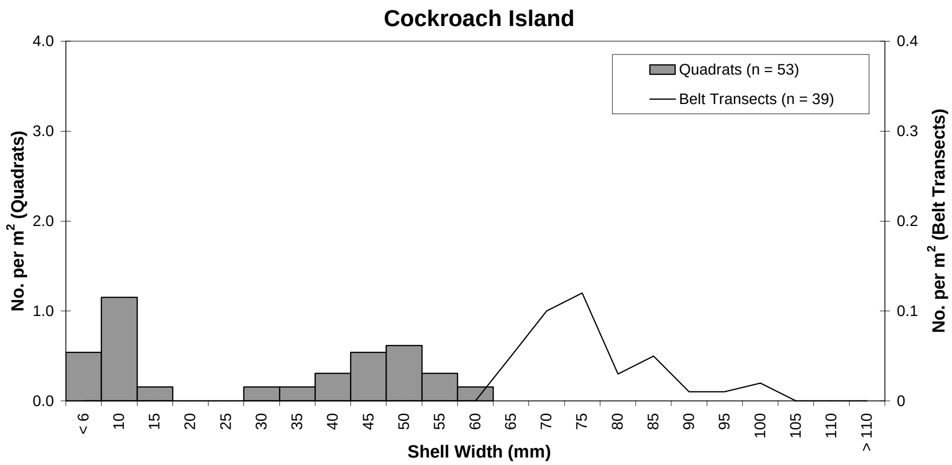
Appendix 4 continued. Size distribution of *Cittarium pica* at St. Thomas sampling sites as determined from quadrat sampling (columns) and belt transect sampling (lines).

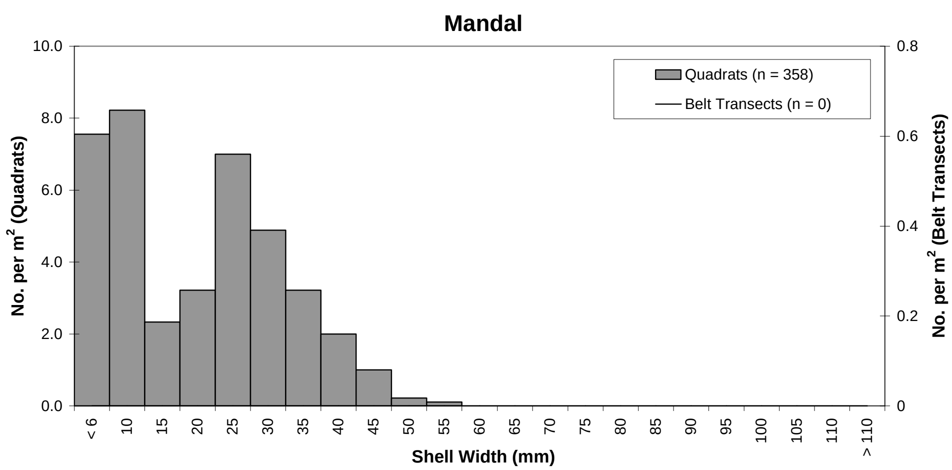




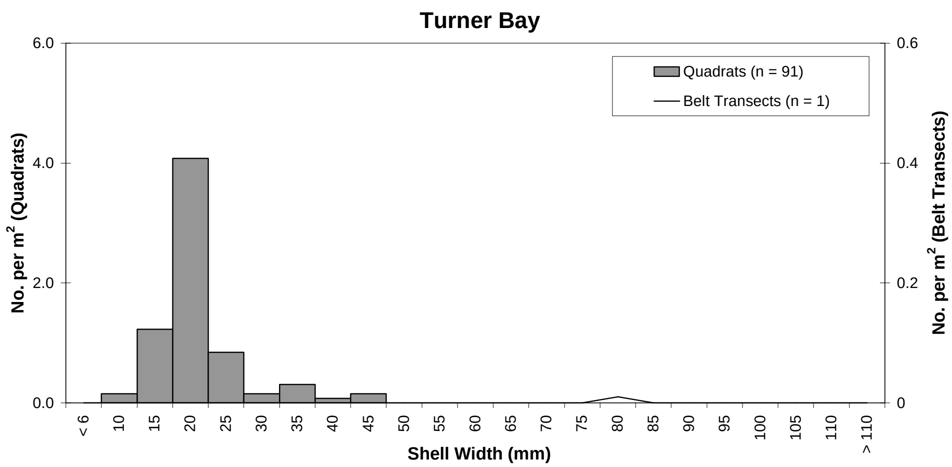


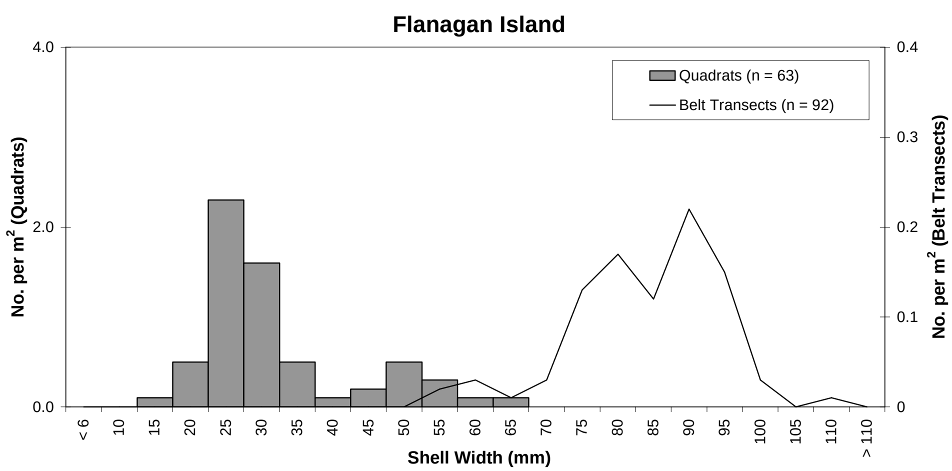
Appendix 4 continued. Size distribution of *Cittarium pica* at St. Thomas sampling sites as determined from quadrat sampling (columns) and belt transect sampling (lines).

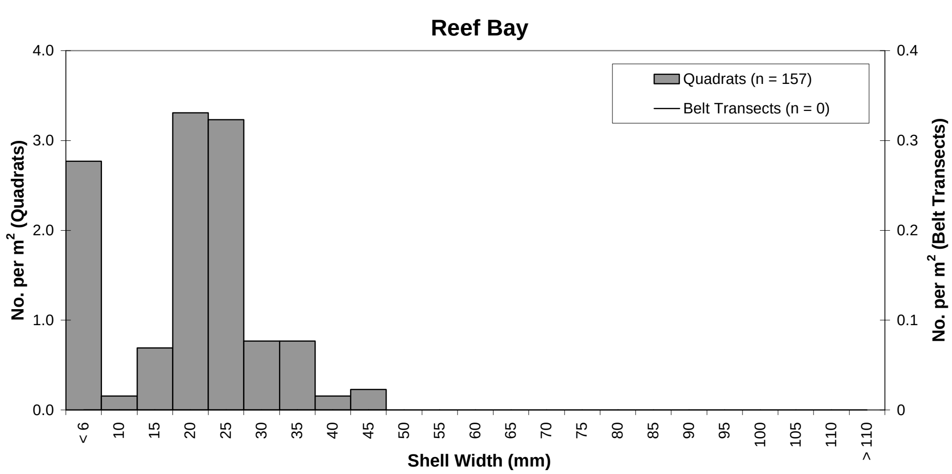




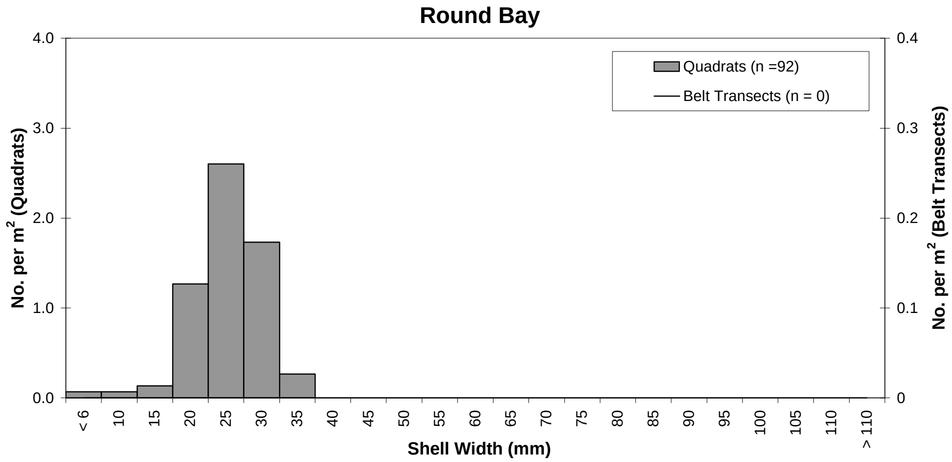
Appendix 5. Size distribution of *Cittarium pica* at St. John sampling sites as determined from quadrat sampling (columns) and belt transect sampling (lines).

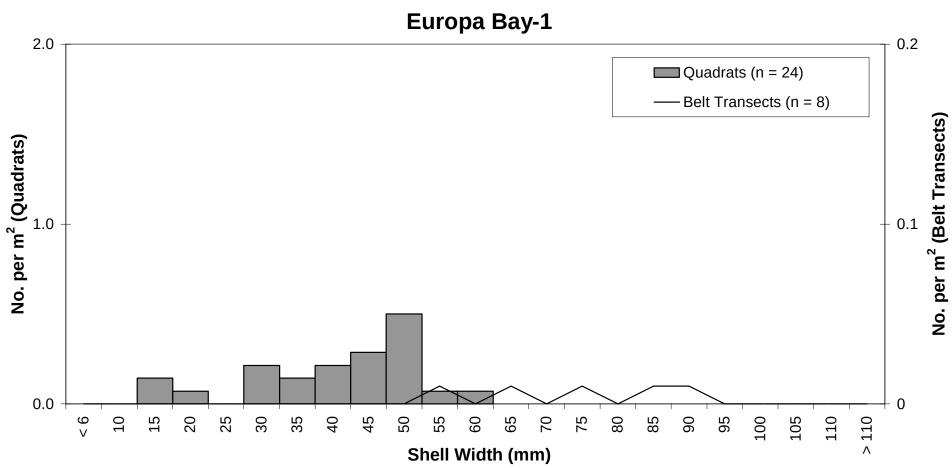


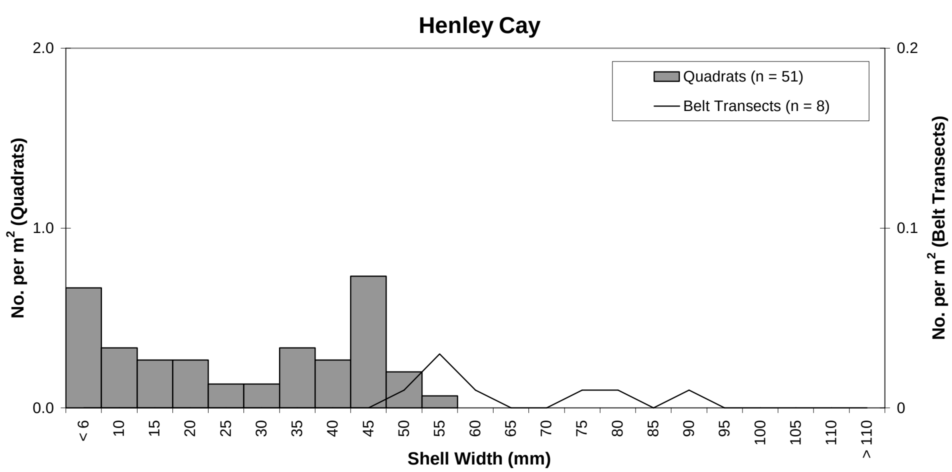




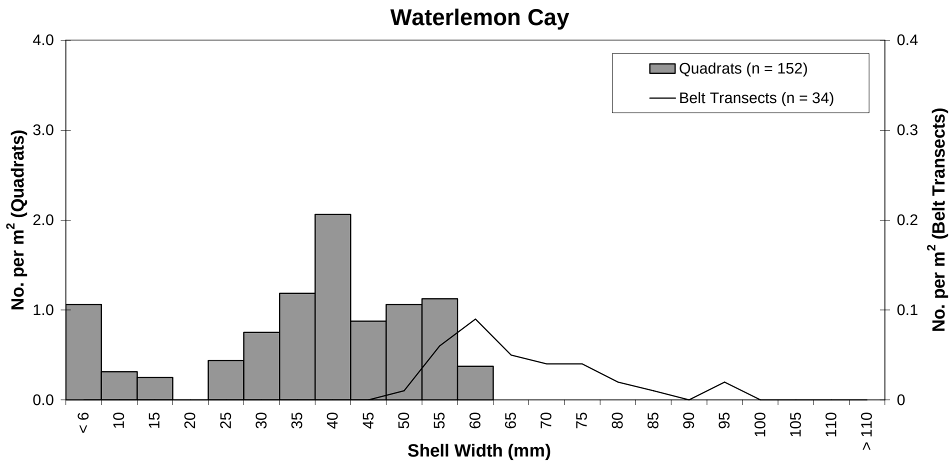
Appendix 5 continued. Size distribution of *Cittarium pica* at St. John sampling sites as determined from quadrat sampling (columns) and belt transect sampling (lines).

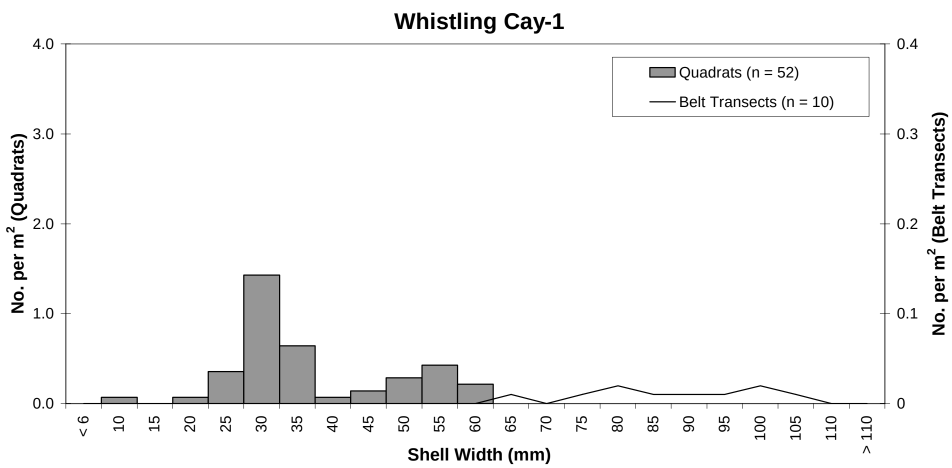


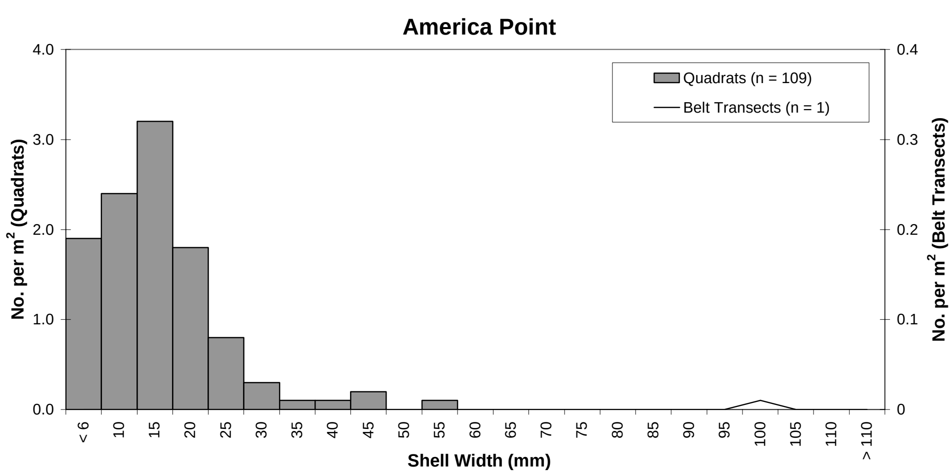




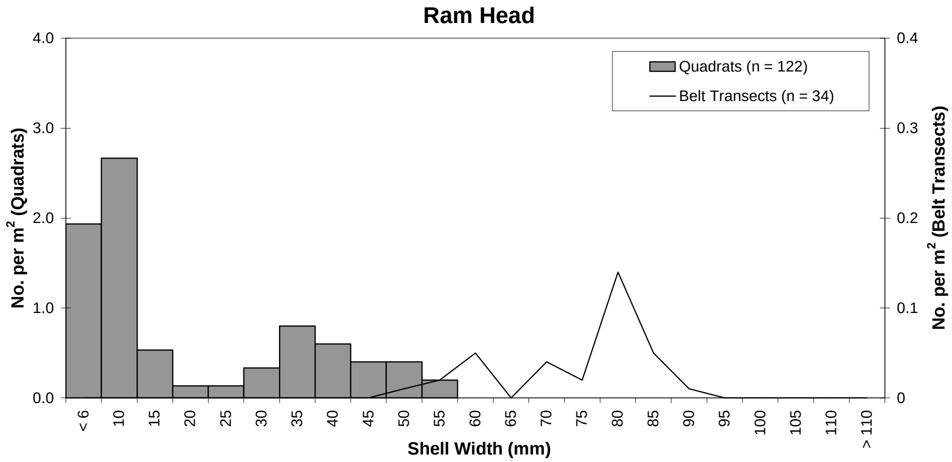
Appendix 5 continued. Size distribution of *Cittarium pica* at St. John sampling sites as determined from quadrat sampling (columns) and belt transect sampling (lines).



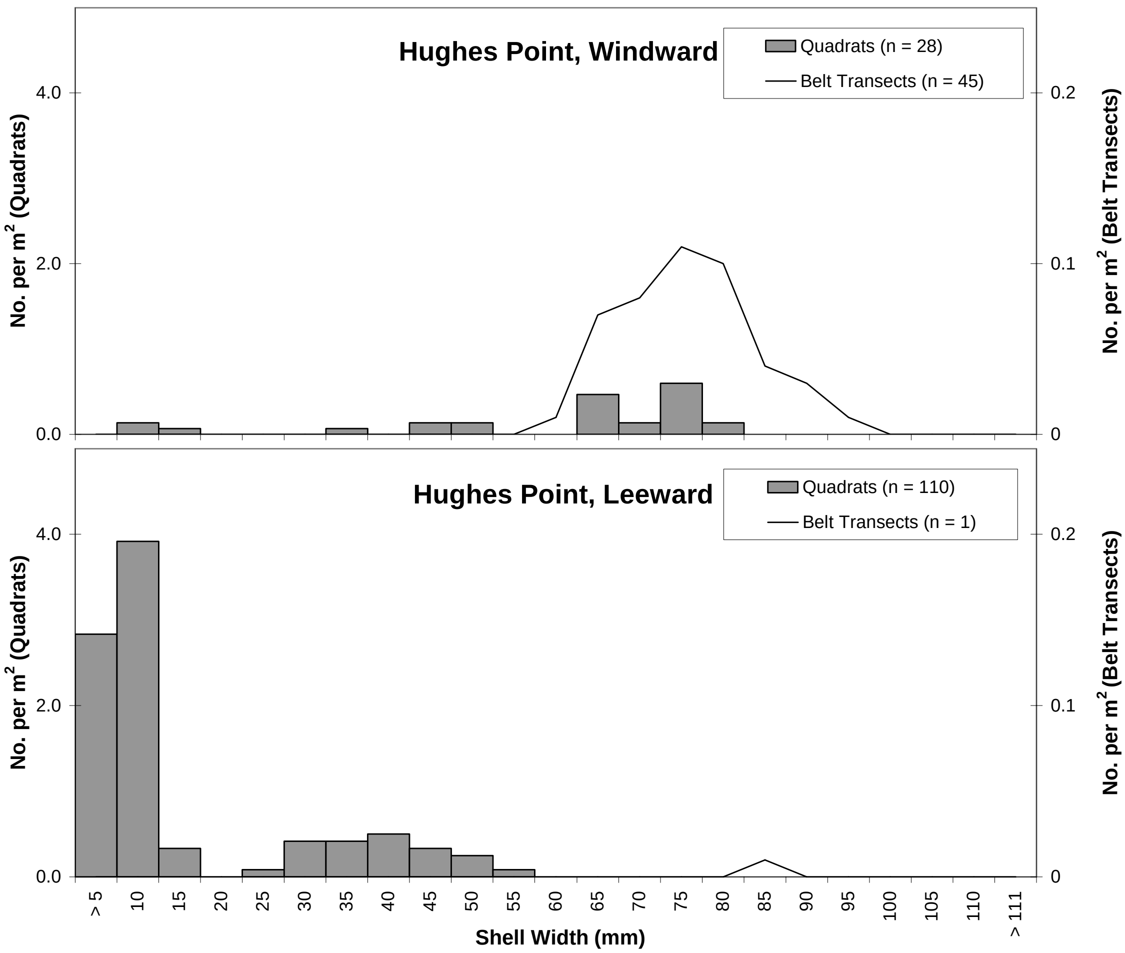




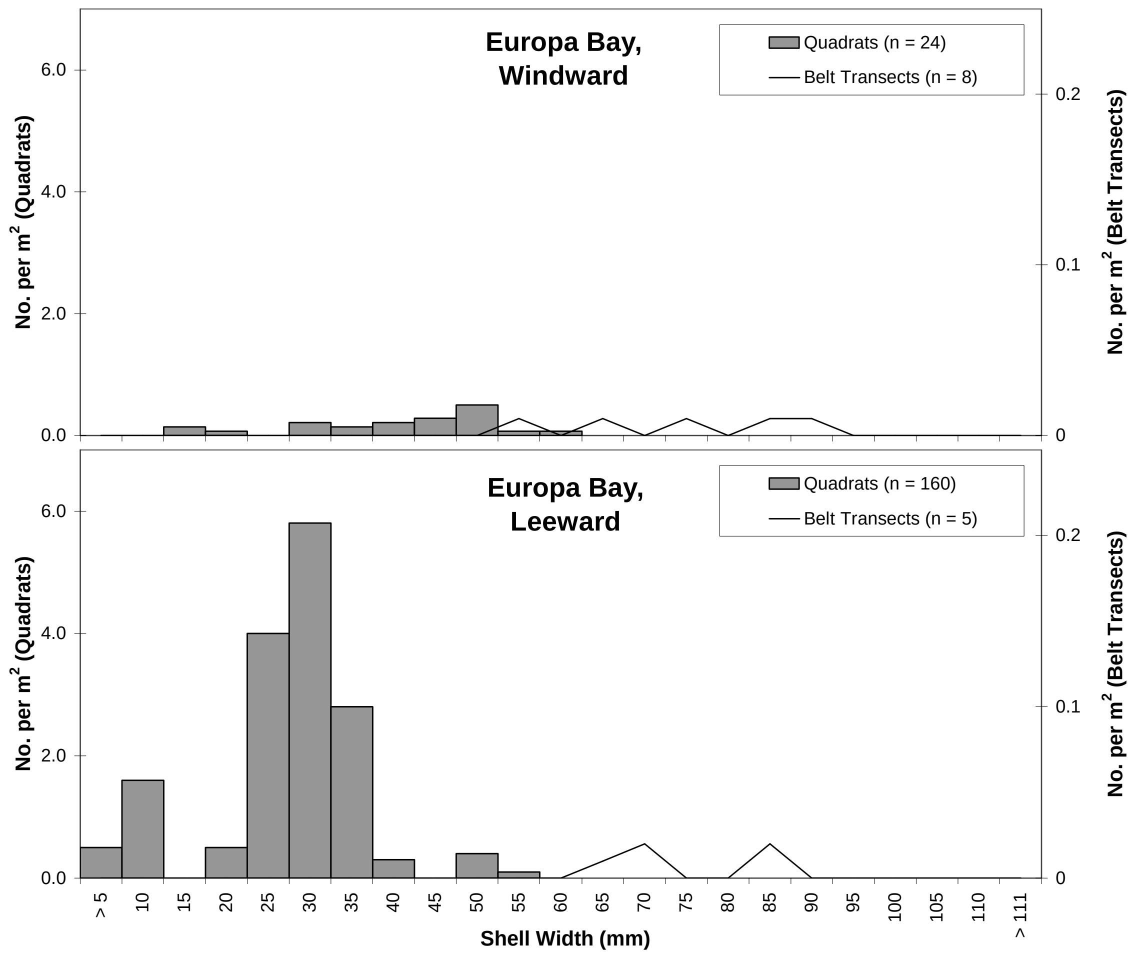
Appendix 5 continued. Size distribution of *Cittarium pica* at St. John sampling sites as determined from quadrat sampling (columns) and belt transect sampling (lines).



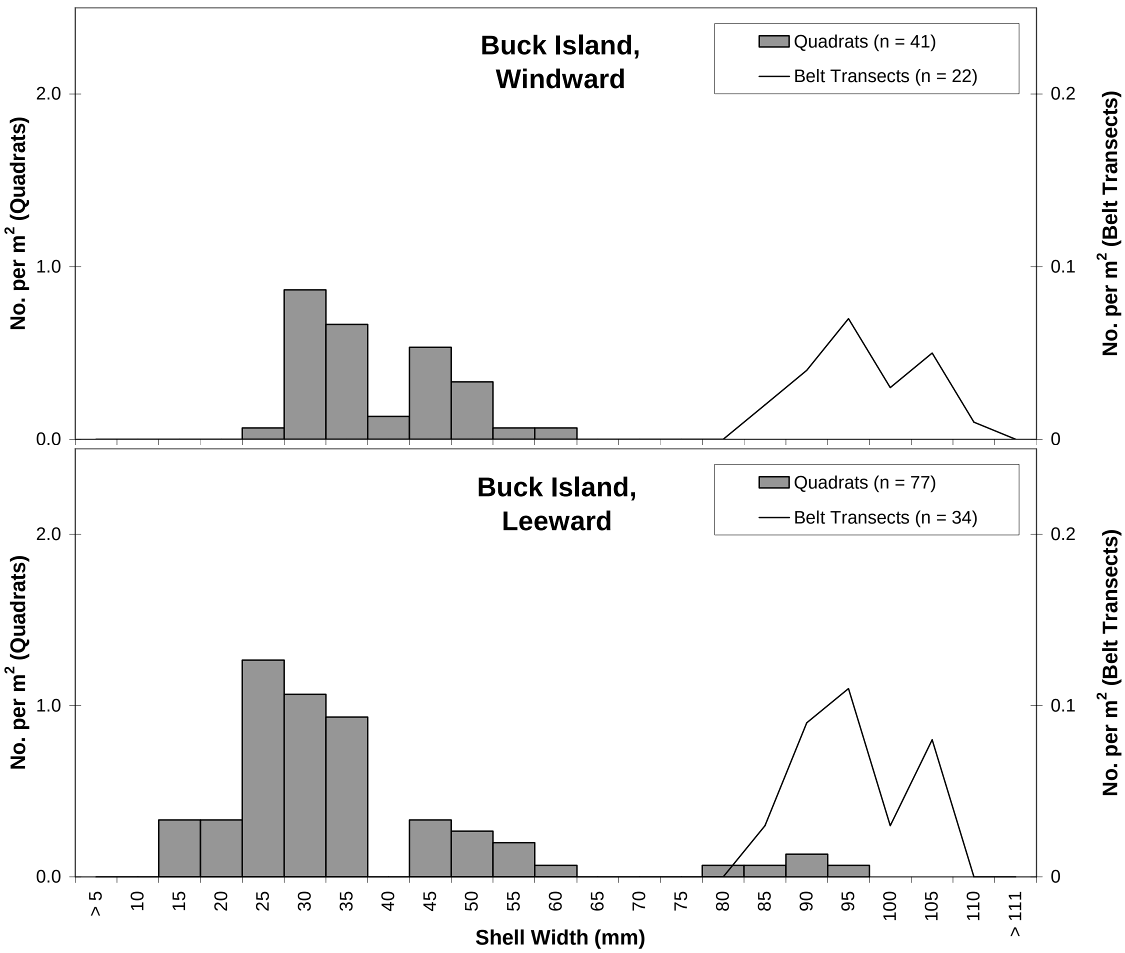
Appendix 6A. Size distribution of *Cittarium pica* at windward (exposed) and leeward (protected) paired-sample sites at Hughes Point, St. Croix. Data are from quadrat sampling (columns) and belt transect sampling (lines).



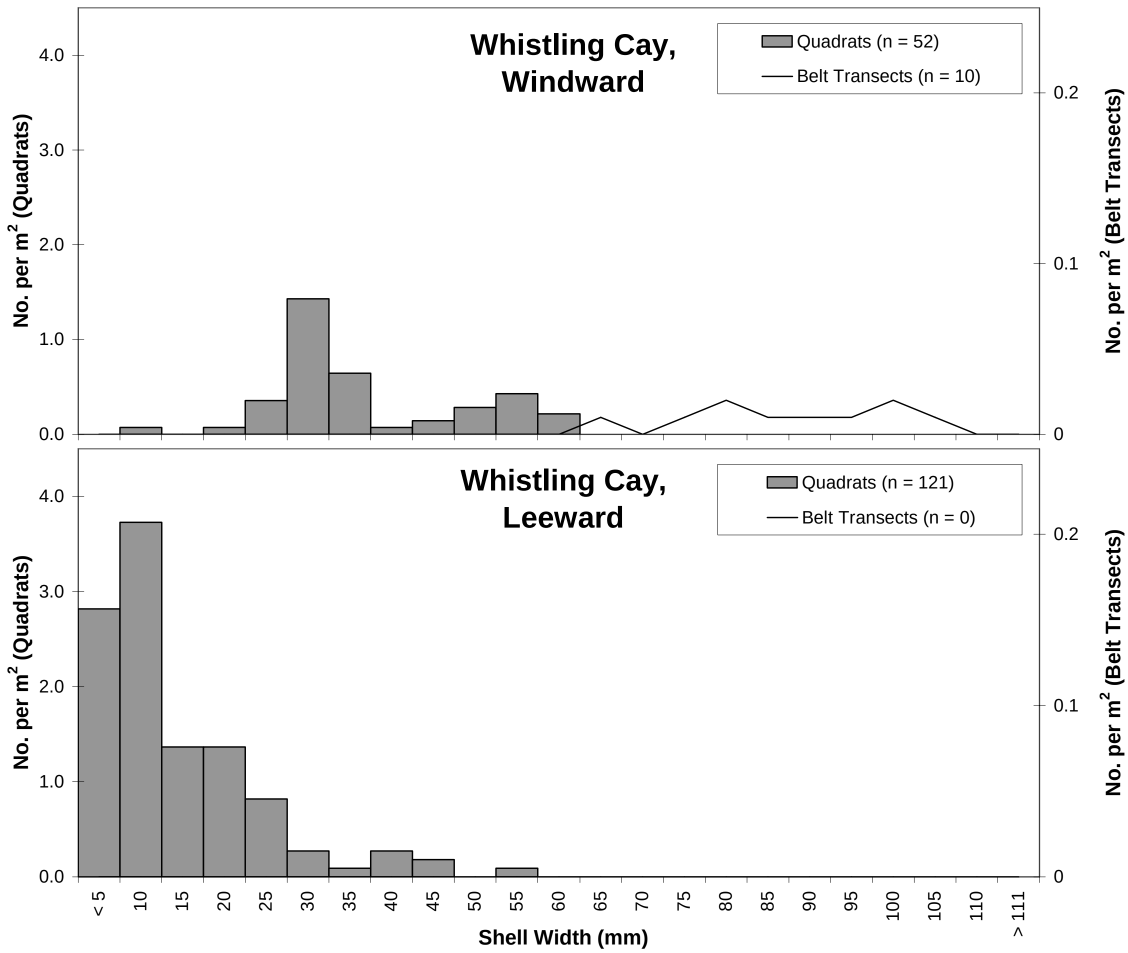
Appendix 6B. Size distribution of *Cittarium pica* at windward (exposed) and leeward (protected) paired-sample sites at Europa Bay, St. John. Data are from quadrat sampling (columns) and belt transect sampling (lines).



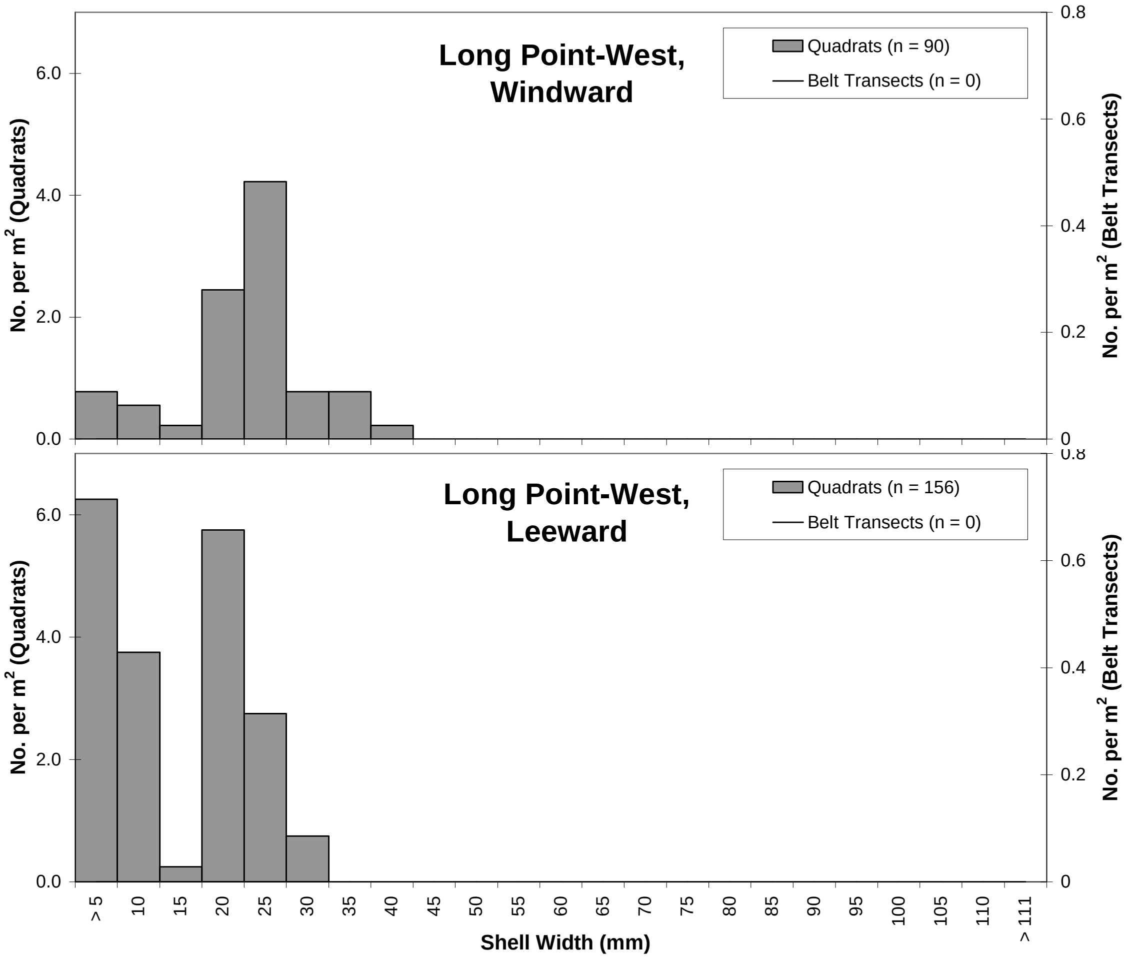
Appendix 6C. Size distribution of *Cittarium pica* at windward (exposed) and leeward (protected) paired-sample sites at Buck Island, St. Croix. Data are from quadrat sampling (columns) and belt transect sampling (lines).



Appendix 6D. Size distribution of *Cittarium pica* at windward (exposed) and leeward (protected) paired-sample sites at Whistling Cay, St. John. Data are from quadrat sampling (columns) and belt transect sampling (lines).



Appendix 6E. Size distribution of *Cittarium pica* at windward (exposed) and leeward (protected) paired-sample sites at Long Point-West, St. Croix. Data are from quadrat sampling (columns) and belt transect sampling (lines).



Appendix 6F. Size distribution of *Cittarium pica* at windward (exposed) and leeward (protected) paired-sample sites at Pull Point, St. Croix. Data are from quadrat sampling (columns) and belt transect sampling (lines).