

A Comparison Over Time of Two Virginia Populations of the Coquina Clam, *Donax variabilis*

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ABSTRACT

The coquina clam, *Donax variabilis*, is well known for its great variation in shell colors and patterns. This extensive polymorphism and a short life span make *Donax* an interesting organism for studies of genetic variation in natural populations. In order to assess the stability of the polymorphism, samples were collected over one growing season from two sites in Virginia Beach, VA, and compared for the distribution of shell lengths and for the frequencies of colors and patterns both within and between locations. Populations at the two locations differed in nearly all respects, both at any one time and in their patterns of change over time. The distribution of shell lengths indicated that length was related to the age of the clam and also to the colors and patterns of the shell. The frequencies of both shell colors and patterns differed at the two sites and changed over time in different ways.

Key Words: *Donax*, polymorphism.

INTRODUCTION

Species of *Donax* (Mollusca: Bivalvia), commonly known as coquina clams, are found on sandy beaches along the eastern and western coasts of the United States, on the coast of the Gulf of Mexico, and on many other warm-water beaches around the world (Wade, 1967; Leber, 1982). Their ideal habitat is the wash zone of a gently sloping beach, halfway between the high tide mark and the water's edge. In a favorable environment, populations of *Donax* have been observed to reach densities of over 20,000 clams per square meter. Such a population, in a strip 2 to 5 meters wide, extended with some interruptions for more than five miles along the beach (Coe, 1953). These clams have attracted the attention of several ecologists because of their ability to migrate up and down the beach with the stage of the tide (Turner and Belding, 1957; Leber, 1982) and because the continuous growth of their shells makes them suitable for size/age studies (Cerrato, 1980; Bayne and Newell, 1983; Wilbur and Owens, 1983).

Rates of Growth: Coe (1955) followed rates of growth as well as population densities in his study of the California Bean Clam, *Donax gouldi*. He determined that clams at one and two years of age averaged about 12 mm and 18 mm in length, respectively, and that their first spawning occurred at the age of one to one and a half years. In some years almost all breeding individuals died after the first spawning, while in other years most individuals survived to spawn in a second summer. The few individuals which survived to the third year were about 20 mm in length.

Wade, in his 1968 life history study of the West Indian beach clam, *Donax denticulatus*, collected data monthly on lengths of shells at two sites over a period of two years, the typical life span of the species. He found that the average shell length increased rapidly during the first seven months of life and then more slowly until the eleventh month. Thereafter, adults grew only when food supplies were abundant. The average rate of growth at one site was much greater than that at the other, and Wade concluded that the differences in the maximum sizes of clams on beaches in the West Indies resulted from this factor. Both Coe's and Wade's findings indicate that, when ample food is available, *Donax* species can grow throughout their life spans and that the rate of growth is specific to the site of the population.

In a study of two populations of *Donax variabilis* in Florida, Mikkelsen (1983, 1985) showed major differences in density, tidal migration patterns, and growth rates between the populations. He attributed these differences to dissimilarities in slope, wave action, and particle size between beaches and concluded that each population had site-specific characteristics.

Studies of Polymorphism: Shell colors of marine mollusks were once assumed to be controlled by the environment, but recent studies have shown that shell colors and patterns are often genetically determined. A polymorphism for shell color is under genetic control in the scallop *Argopecten* (Adamkewicz and Castagna, 1988), the snail *Cepaea* (Cain et al., 1960), and the blue mussel *Mytilus* (Innes and Haley, 1977; Newkirk, 1980), although the exact mechanism which produces shell colors has not been determined.

The possible adaptive value of such polymorphisms has seldom been investigated. Mitton (1977) for the mussel *Mytilus*, and Heller and Volokita (1981) for the snail *Xeropicta*, proposed that differences in color may influence an animal's internal temperature. Populations in warmer climates tend to have higher frequencies of banding and of white and other light colors which can reflect heat, while those living in cooler climates tend to have higher frequencies of darker colors, which enable the animals to absorb solar radiation faster (Cain et al., 1960; Cook and King, 1966; Jones, 1973).

Cain (1988) has also noted that bivalves which commonly live buried in sediments tend to be drably colored while those species which are occasionally or always exposed to light (and thus to both visual predation and solar heating) are often polymorphic for bright colors. Moment (1962) had *Donax* specifically in mind as a possible example of a genus whose extreme polymorphism was an adaptation to visual predators. Although *Donax* species do burrow in the sand, they are frequently exposed to light and to view as they migrate up and down the beach with the tides, and both absorption of solar heat and exposure to visual predators (Smith, 1975; Schneider, 1982) are potentially important to them.

Very few studies have compared frequencies of shell colors and patterns among populations of *Donax*. Mikkelsen's (1978) comparative study of *Donax variabilis* showed that the frequencies of colors were significantly different in two Florida populations. He found that the frequency of white shells was higher at the Gulf coast site, while the frequency of the darker forms was higher at the Atlantic coast site. He attributed the differences in the frequencies of colors to water temperatures, the Gulf of Mexico being warmer on average, and suggested that the

differences in frequencies of patterns were maintained by apostatic or reflexive selection as originally proposed by Moment (1962) and Clarke (1962).

Even rarer than studies of the frequencies of colors and patterns found on the outside of *Donax* shells are studies of frequencies of colors and patterns found on the inside. Adamkewicz (1989) compared both inner and outer shell characters, as well as shell lengths, in samples of *D. variabilis* taken at one time from four Atlantic coast sites in North Carolina. She found that mean shell lengths and the frequencies of various colors and patterns were significantly different among the sites but could not detect a consistent pattern of change. She attributed the differences among the samples to either the establishment of each population at a different time or to adaptation to the local environment.

The differences in the frequencies of colors and patterns among populations at different locations raises the question of whether the growth rates, colors, and patterns of shells also vary over time at one site. To answer this question, samples of *D. variabilis* were collected over one growing season from two beach sites with distinctively different physical characteristics. The frequencies over time of shell lengths, colors, and patterns were examined and compared within and between populations.

SAMPLING

Samples were collected periodically for one growing season, June through November, at two locations. After November, low water temperatures made sampling impractical. The first site was on the beach in front of the Ocean Island Motel at the entrance to Lynnhaven Inlet in Virginia Beach, VA. This site was inside the Chesapeake Bay, sheltered from the waves of the open ocean. Adequate samples were found there in June, the first month in which the site was visited, and from August to November, but virtually no clams were found there in July. The second site, visited for the first time in July, was located eight land miles southeast of Lynnhaven on the beach at the end of 33rd Street in the city of Virginia Beach. This site was on the ocean, exposed to more intense wave action. Samples were taken from this population from July to November, but the November sample was too small to be useful. Collections were always taken near the time of low tide. Animals might be found anywhere from the middle of the wash zone to below the water's edge under about 10 cm of water.

Sizes of samples collected ranged from 12 to 803 individuals, and the occasionally sparse populations made density determinations unfeasible. Animals were collected by scooping sand onto a 1 mm mesh and rinsing in the sea water. The sieve was capable of retaining individuals as small as 1.5 mm, although no individuals smaller than 3 mm were ever found. Each shell was cleaned and its left valve measured to the nearest millimeter. Then, using a system similar to that of Adamkewicz (1989), the shells were scored for five characters. For statistical analysis, it was usually necessary to pool several possible states of each character. The scoring system and pooling procedures were as follows:

1. Background (BKGD) was defined as the color on the outside surface of the shell. It could be purple, red, yellow, brown, or white (which is simply the absence of any pigment). For analysis, these colors were pooled into white versus any other color.

2. One to many concentric rings (RINGS), could be present on the outer surface of the shell. These rings probably formed when a clam's growth was interrupted by adverse environmental conditions (Gordon and Carriker, 1978; Crenshaw, 1980) and could be purple, red, yellow or the background color of the shell. If the latter, RINGS was scored as absent. Pooling was colored RINGS present versus absent.

3. Purple juvenile rays (PJR) were first defined by Mikkelsen (1978) as three thin, purple lines radiating from the umbo. If present, they were most conspicuous on small animals (3 to 5 mm), hence the term juvenile. Pooling was present versus absent.

4. The extent of purple pigment on the inner surface of the shell (INSIDE) ranged from a complete covering, through a partial covering, to one single posterior ray, and finally to a shell that was entirely devoid of pigment on the inside. It was pooled as present (any pigment present) versus absent (no pigment INSIDE the shell).

5. The shell's umbo (UMBO), the area between two sets of hinge teeth, could be distinctly colored with purple or red or it could show only the background color of the shell, in which case UMBO was scored as absent. Pooling was colored UMBO present versus absent.

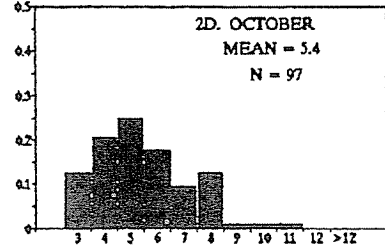
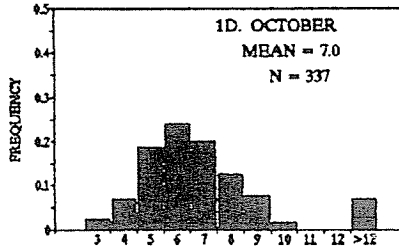
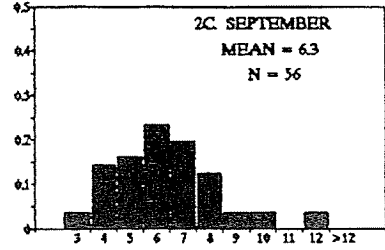
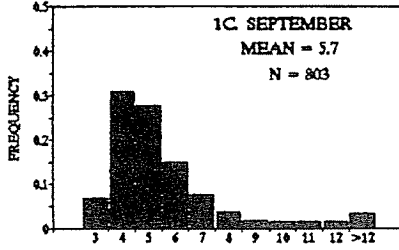
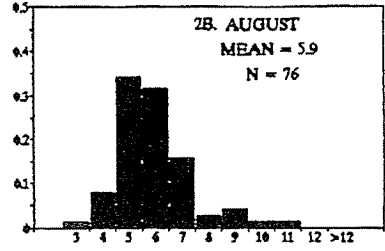
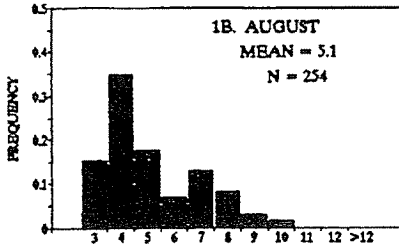
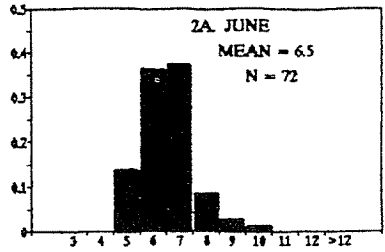
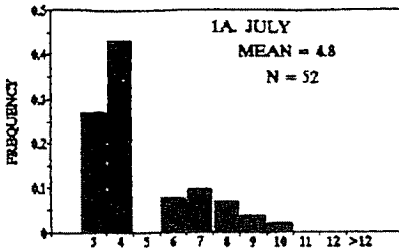
A total of 1,981 shells were examined: 1,482 from 33rd Street and 499 from Lynnhaven. During statistical analysis, the two samples with fewer than fifty individuals, November at 33rd Street and July at Lynnhaven, were simply dropped, and the first collections at the two sites were considered equivalent even though they were taken in different months. This treatment was judged to be superior to pooling successive months at one site because of the strong evidence for change over time. For data on the five patterns, using all possible variants for a character resulted in very small numbers for some categories. Numbers were therefore pooled as described above. Data were then analyzed with one-way analyses of variance to test means and contingency chi-squares to compare frequencies.

RESULTS

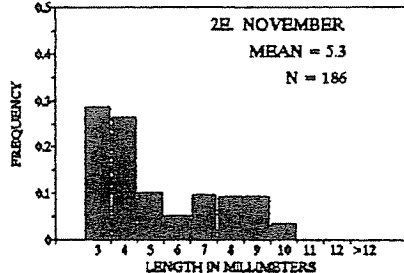
Shell Lengths: According to Chanley and Andrews (1971), *Donax* in the Virginia area complete their metamorphosis to the adult stage and begin settling into a population at about 3 to 4 mm in length, and the present results support their observation. Although smaller individuals could have been detected, the minimum shell length in any sample from either site was 3 mm.

The average shell length changed significantly over time at both sites, but the change was systematic and predictable only at 33rd Street, where, as expected during a growing season, the average shell length increased each month. A one-way analysis of variance for each site showed that the mean lengths of shells in the samples from the four months were significantly different. A similar comparison showed that mean lengths for any one month were significantly different between the two locations.

Figures 1 and 2 present the distribution of shell lengths for the collecting period. Early in the period, the population at 33rd Street had more small, newly recruited individuals than large ones, while the Lynnhaven population lacked these very small individuals. Clearly both the pattern of change and the distribution of shell lengths differed at the two sites, and these differences may well be attributed to the time



FIGS. 1 & 2
SHELL LENGTHS
OVER TIME



FIGURES 1 and 2. The distribution of shell lengths in samples at 33rd Street from July through October (Figures 1a - 1d) and at Lynnhaven from June through November (2a - 2e). Means are in millimeters and N = Sample size.

TABLE 1. A summary of the results from one-way analyses of variance on shell lengths in different color/pattern variants each month at each site. Variants were pooled as described in the methods. No symbol indicates that the result was not significant, * denotes $p < 0.05$, ** denotes $p < 0.01$, and na denotes a test that could not be performed. For every significant test except those for UMBO, the colored variant had a larger mean than the uncolored one.

| Character | 33rd Street | | | | Lynnhaven | | | | |
|-----------|-------------|----|----|----|-----------|---|---|---|----|
| | J | A | S | O | J | A | S | O | N |
| BKGD | ** | ** | ** | | | | | | ** |
| RINGS | | | | ** | | | | | ** |
| PJR | | | ** | ** | | | * | | * |
| INSIDE | ** | ** | ** | ** | | | | | * |
| UMBO | na | ** | ** | ** | | | | | ** |

of recruitment for each site. Accepting the presence of 3-4 mm clams as evidence of recent recruitment, 33rd Street was adding new individuals primarily in July and August, and probably earlier, while recruitment in Lynnhaven occurred mostly September through November.

Figures 1 and 2 also provide evidence for a relationship between shell length and age. Figure 1a-d shows the distribution of shell lengths over time at 33rd Street. The earliest sample (Fig. 1a) lacked a 5 mm size class, dividing the lengths into two discontinuous ranges which were probably year classes or cohorts. The clams in the 6 to 10 mm size range were probably breeding individuals that survived the winter, while those in the 3 to 4 mm size range were probably new recruits into the population. Recruitment, then, would have had to begin at least two or three weeks earlier, in June.

The distributions in August (Fig. 1b) and September (Fig. 1c) had a continuous range of sizes from 3 to 10 mm and from 3 to 15 mm respectively. The appearance of larger size classes indicates growth, and the reduction in frequency with increasing size suggests that some of the larger clams were lost from the population through predation or death. A reduction in the frequencies of the two smallest size classes (3 to 4 mm) could also be seen, indicating that fewer new individuals settled into the population with each succeeding month.

In October, (Fig. 1d) the last month for samples from 33rd Street, the sample was again divided into two discontinuous size ranges, a small cohort that had survived from the previous year and a large cohort recruited earlier in the summer and now adult.

Figure 2a-e displays the distributions of shell lengths over time at Lynnhaven, which was very different from the pattern at 33rd Street. In June (Fig. 2a), Lynnhaven had a continuous range of sizes from 5 to 10. These individuals must have survived the winter, and recruitment into the population has not yet started for the year. August and September (Fig. 2b-c) showed evidence of some recruitment of new individuals and growth of adults. During October and November (Fig.

2d-e), recruitment increased and larger individuals began to be lost from the population.

Shell color and length: The relationship between shell color and shell length was examined within each population. For each month at each site, a one-way analysis of variance was used to compare the mean lengths of shells with and without each pattern, pooled as described in the methods section. A summary of the results is presented in Table 1. The effect of shell characters on mean length was much more pronounced at 33rd Street, where more than half of the statistical tests were significant, than at Lynnhaven, where fewer than a quarter of the tests were significant. All significant tests for every character except UMBO showed the mean to be larger for shells with more colors present.

Colors and Patterns: As shown in Figures 3 and 4, the frequencies of colors and patterns also varied over time within each population and differed between sites. Alternative states of each pattern were pooled as described in the methods section and a contingency chi-square was used to compare the frequencies of each shell character both month by month between sites and within each site over the collection period. These differences were always significant over time at any one site and were usually significant between sites for any one month. The test of UMBO for July/June between sites could not be performed because some of the expected frequencies were less than three. The remaining comparisons between sites showed that frequencies of colors and patterns were similar in the two populations during June/July and August but differed significantly between populations after that time.

Some characters such as RINGS, PJR, and INSIDE at 33rd Street showed systematic changes, increasing throughout the study period (Fig. 3), while other characters changed without apparent pattern. However, as shown in Table 2, every character changed significantly in frequency over time at each site.

DISCUSSION

The distribution of shell lengths over time in these Virginia samples confirms the pattern observed in *D. variabilis* in Florida (Mikkelsen, 1981 and 1985). As at other locations, growth continued throughout the life span, which was about one year. The samples collected from 33rd Street showed a steady increase in both mean length and size range, with the largest size class, 17 mm, appearing in October, indicating that the clams were growing continuously. Two distinct size classes for the sample collected in July at the 33rd Street site represented at least two age groups or cohorts, with the survival over the winter of older individuals and the input in the spring of new ones. The observation that the frequencies of larger size classes were always much lower than those of smaller sizes indicates continuous growth with mortality at the larger sizes. This fact, along with the absence of clams larger than 10 mm at both sites in the beginning of the collecting period, suggests that larger clams must have died during the winter or after an early spawning in the spring.

The results of this study also demonstrate that, when sampling populations of *Donax*, both the location and the time of year are important. Comparisons should be made between locations only with great care and based only on data covering extensive periods of time, because the pattern of growth and recruitment is not the

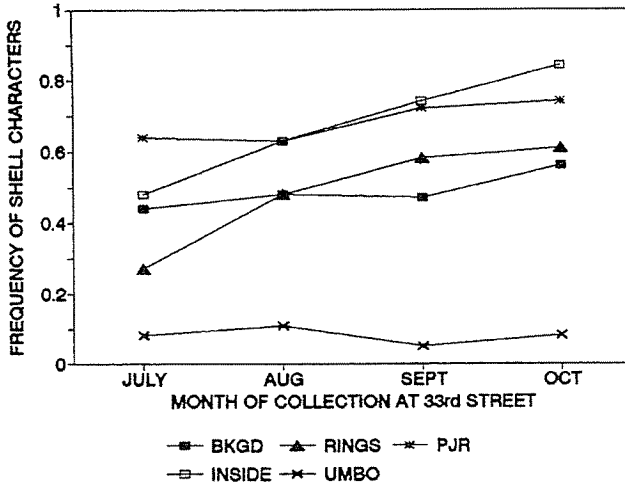


FIGURE 3. The frequencies of five shell characters in the samples from 33rd Street. Variants were pooled as described in the methods section and the values graphed are always for the colored variants as follows: BKGD, any color except white; RINGS, present; PJR, present; INSIDE, present; and UMBO, present.

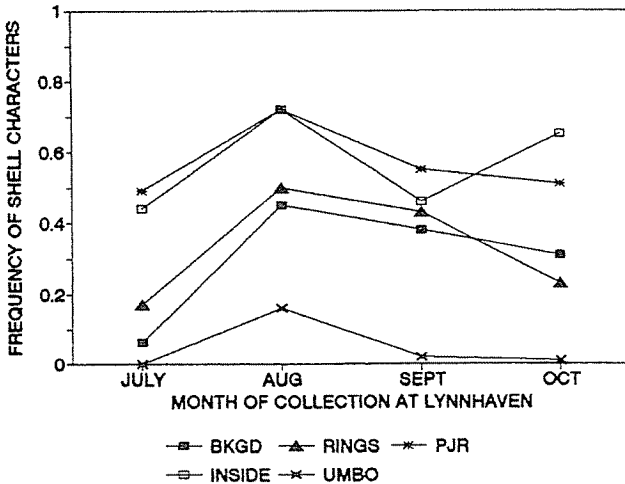


FIGURE 4. The frequencies of five shell characters in the samples from Lynnhaven. Variants were pooled as described in the methods section and the values graphed are always for the colored variants as follows: BKGD, any color except white; RINGS, present; PJR, present; INSIDE, present; and UMBO, present.

same at all locations. The contrast between the distribution of lengths at 33rd Street and the distribution at Lynnhaven showed that, while length was always a fair indicator of age, the association of a particular length with a particular age was site-specific. Clams at both sites showed continuous growth and mortality at larger sizes, but clams at Lynnhaven never reached as large a maximum length as clams at 33rd Street, and recruitment initiated much later at Lynnhaven.

The frequencies of the various polymorphic traits were also both time and site-specific, which will complicate efforts to discover the mechanism(s) that maintain the variation. The data cannot with certainty identify any one factor, but maintenance of the polymorphism for shell colors and patterns may depend at least in part on a mechanism already believed to act on the shells of other mollusks. Mitton (1977) proposed for the mussel *Mytilus edulis*, and Heller and Volokita (1981) proposed for the freshwater snail *Xeropicta*, that differences in color might affect the internal temperature of animals. Part of their evidence was that shells of animals in cooler climates had higher frequencies of darker colors, which would

TABLE 2. A summary of the results from the contingency chi-square analyses comparing the frequencies of the shell characters by site for any one month and by month for any one site. Variants were pooled as described in the methods. No symbol indicates that the result was not significant, * denotes $p < 0.05$, ** denotes $p < 0.01$, and na denotes a test that could not be performed. Actual frequencies over time are shown in Figures 3 and 4.

| Character | SAME SITE | | SAME MONTH | | | |
|-----------|-----------|------|------------|---|----|----|
| | 33rd | Lynn | J | A | S | O |
| BKGD | * | ** | ** | | | ** |
| RINGS | ** | ** | | | * | ** |
| PJR | * | ** | | | * | ** |
| INSIDE | ** | ** | | | ** | ** |
| UMBO | * | ** | na | | | * |

enable the mollusks to absorb solar radiation more readily. In *Donax*, which are exposed to the direct sun as they migrate with the tides, the addition of colors to the shell might allow the clams to accumulate and retain a higher body temperature, which in turn would allow them remain active and grow longer as water temperatures cooled.

The evidence is compatible with this possibility. As mean shell length increased over time at 33rd Street, so did the frequencies of colored shells, which would be predicted by the theory. The majority of shells at both sites had a colored BKGD, and the addition of the other characters (UMBO, RINGS, INSIDE, and PJR) to the colors of BKGD darkened the appearance and potentially increased the heat retention of the shell. The frequencies of all these shell patterns (except UMBO, which was rare but fairly constant) showed a steady increase over the four months of the collecting period at 33rd Street. The frequencies of colored shells also increased overall, but not steadily, at Lynnhaven. It was not possible from our data to determine directly whether colored shells grew faster than uncolored ones, but increases in the frequency of colored shells coincided with periods of increased growth, and this fact argues that they do.

An alternative explanation would be that shells simply add more pigments as they grow larger. Shell colors and patterns do develop and intensify in larger clams (presumably as the shell grows), and this relationship probably accounts for at least part of the association between shell color and increased length. It cannot be a complete explanation because, in any one sample, colored shells were usually significantly larger than uncolored ones even in samples (e.g. November at Lynnhaven) where the overall average shell length was small.

The differences observed between 33rd Street and Lynnhaven in mean shell length, in the frequencies of colors and patterns, and in recruitment times, are consistent with studies done by Mikkelsen on *D. variabilis* in Florida (1981, 1985) and by Wade (1967, 1968) on *D. denticulatus* in Jamaica. Both investigators found differences in samples taken from different sites, and both attributed these differen-

ces to environmental factors: the slope of the beach, the nature of the sand, and/or the wave action.

The two locations in the present study have several striking environmental differences. The 33rd Street site is located on the open ocean, while Lynnhaven is just inside the Chesapeake Bay in a much more protected situation. The wave action at Lynnhaven is usually gentle and slow compared to that at 33rd Street. While the slopes of the two beaches are both gentle, the sand is coarser at Lynnhaven and the condition of the beaches is not the same. Debris accumulates both along the beach and in the water at Lynnhaven, in contrast to the beach at 33rd Street, which is comparatively clean. Although no single environmental factor can be associated with any specific difference between the populations, the typical habitat of *Donax* in the wash zone suggests that the difference in exposure to the surf is probably critical. A systematic comparison of populations in sheltered versus highly exposed locations would be of great interest.

Other important questions also await study. Recruitment patterns in the two populations are different, and we need to know both where new recruits originate and whether the patterns of recruitment remain the same from year to year. The polymorphism of the shells was not constant over the study period; shells changed in appearance as they grew. We need to know whether this cycle of changes is repeated each year. Finally, it is important to discover which environmental factors are influencing the lengths, colors, and patterns of these shells.

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