Geographic Variation in Population Characteristics of an Intertidal Gastropod: Demographic Differences or Settlement History?

Russell J. Schmitt
Coastal Research Center, Marine Science Institute
University of California
Santa Barbara, California 93106

Abstract - Population characteristics of the littoral fringe periwinkle gastropod *Littorina keenae* were examined at two regions within its geographic range: Santa Catalina Island in southern California and Bodega Bay in northern California. Compared with Bodega Bay, populations at Santa Catalina Island were more dense and individuals had a smaller average body size. This pattern of latitudinal variation has been commonly observed among species of gastropods. Several lines of evidence suggest the pattern for *L. keenae* may be the result of settlement history and demography, and not caused primarily by genetic or phenotypic variation among regional populations. *Littorina keenae* was found to be a slow but variably growing, long-lived species with low per capita mortality. Mortality was independent of body size. No difference was found in growth rates between geographic regions. Females spawned thousands of planktonic egg capsules annually, but settlement of young appeared to be low and highly variable in time. Evidence suggests that settlement, when it occurs, tends to be spatially synchronous within a region but asynchronous among geographic areas. It appears that most local populations studied resulted from one (or a few closely timed) recruitment pulse(s). The interval between the last successful recruitment event appeared to be longer in the northern than southern region of California. This hypothesis was supported by a projection matrix model that simulated the frequency distribution of body sizes obtained in a local population under two extremes in temporal variability of recruitment: a single recruitment pulse and constant annual recruitment of the same magnitude. The results for the single recruitment pulse model matched well with observed population size structures.

Introduction

A commonly observed pattern among marine species is latitudinal variation in population characteristics. A typical pattern is for individuals at higher latitudes to have larger body sizes, reach older ages and have lower population densities than counterparts at lower latitudes. Such variation is prevalent among gastropod molluscs (*e.g.*, Newell 1964; Frank 1975; Fawcett 1984). While the pattern has been reported for a wide array of marine species, the underlying causal processes often remain unexplored.

There are several classes of mechanisms that can produce the latitudinal pattern described above. First, it can be genetically based, representing evolved adaptation to local conditions. Frank (1975) proposed the following scenario. Where reproductive success historically is uncertain and low, natural selection may have favored long-lived individuals. In turn, increased longevity may be made possible by a decreased reproductive effort per unit time. Conversely, where recruitment is high and predictable, selection may have favored adults that place maximal effort into making young, which is made possible by a lowered growth rate and reduced life span (*e.g.*, Murdoch 1966; Murphy 1968; Gadgil & Bossert 1970). Thus, for this mechanism to produce the observed geographic pattern, recruitment into populations must historically have been greater and temporally more constant at lower than higher latitudes (Frank 1975).

A second mechanism involves phenotypic responses to environmental conditions. For example, there could be geographic differences in factors that influence the nature of recruitment and/or subsequent growth and survivorship that are not due to genetic differentiation. These sources include geographic differences in food supply (*e.g.*, Sutherland 1970; Frank 1975), in the intensity of predation or competition (*e.g.*, Vermeij 1978; Fawcett 1984; Ortega 1985, 1986; Garrity *et al.* 1986), and in abiotic conditions (*e.g.*, Ebert 1968; Shirley *et al.* 1987). Clearly, genetic and phenotypic responses to local conditions are not mutually exclusive processes.

Recruitment history alone can result in geographic differences in characteristics of populations (*e.g.*, Ebert 1983). For example, if temporally varying settlement results in dominant year-classes, populations can differ in such attributes as age-structure, size-structure and density due solely to different intervals since the last major recruitment event. Variability in the supply of new individuals can have tremendous consequences with respect to the distribution, abundance, and dynamics of a population (*e.g.*, Doherty 1983; Ebert 1983; Keough 1984; Caffey 1985; Gaines & Roughgarden 1985; Connell 1985; Warner & Chesson 1985; Victor 1986; Jones 1987; Hughes 1990). Further, the magnitude, timing and spatial distribution of recruitment can determine the extent to which post-recruitment processes may play a significant role in shaping characteristics of adult populations (Keough 1984; Connell 1985; Gaines & Roughgarden 1985).

This paper concerns a species of gastropod, *Littorina keenae* (= *planaxis*), that occurs along the Pacific coast of North America from Baja California to Oregon (Ricketts *et al.* 1985), and is found on all California Channel Islands. The intent of the paper is to: 1) provide a description of the life history and population biology of *L. keenae* and 2) illustrate geographic differences in population features of this periwinkle with a view towards understanding the causal mechanism.

Natural History of *Littorina keenae*: *Littorina keenae* is a mesogastropod that occurs in the uppermost reaches (littoral fringe) of the rocky intertidal coast of Pacific North America and reaches its greatest abundance on California shores (Ricketts *et al.* 1985). As reported here, individuals, which can attain a maximum size of about 20 mm shell length, grow slowly (Chow 1987) and can live two decades or more. These periwinkles consume microalgae scraped from rock surfaces wetted by tidal action (Foster 1964). Sexes are separate and sex ratios in populations examined here were not statistically different from 1:1. Breeding is distinctly seasonal, lasting 5-6 months after starting in late spring (Schmitt 1979). Fertilization is internal but females are broadcast spawners (Ricketts *et al.* 1985). Mature females release gelatinous egg masses containing individual planktonic capsules on incoming spring tides during the breeding season (Schmitt 1979). Released egg masses are swept into the ocean where the gelatinous material dissolves within 24 hr (Schmitt 1979), freeing the planktonic capsules each of which contains a single small (<90 μm dia.) ovum (Murray 1973). A veliger develops and hatches from the capsule in about six days at the relatively small size of 140 μm (Murray 1973). The duration of the post-hatching planktonic phase is unknown, but other species of littorines hatching at a similar size require several months of further development to become competent to settle (Pilkington 1971; Struhsaker 1966; Struhsaker & Costlow 1968).

Sites and Methods

Local populations of *Littorina keenae* were examined at two geographic locations: Bodega Bay in northern California (38°15'N, 123°05'W) and Santa Catalina Island in southern California (33°27'N, 118°20'W). Within each region several sites were chosen to represent a range in variability of wave exposure regimes. At the (more wave exposed) northern location, five distinct local populations were observed; three were along a 2 km stretch of rocky shore at Dillon Beach (moderate wave exposure) and two on Bodega Head (highest wave exposure). At the less wave exposed Santa Catalina Island in southern California, six local populations were examined: five between Blue Caverns and Arrow Point on the north (leeward) side of the island and one at Ben Weston Beach on the more exposed south side.

Each population was observed monthly for one year. Field sampling was done from September 1973-August 1974 at Bodega Bay, and from January-December 1977 at Santa Catalina Island. Monthly sampling consisted of counts of gastropods in quadrats, measurement of a random collection of individuals from each population, and a thorough search of the shore for new recruits (defined here as individuals < 1.5 mm in shell length). If recruits were observed, additional quadrat counts were made and shell lengths of individuals were measured. The entire vertical range of distribution of *Littorina keenae* was examined by partitioning the shore into six 0.67 m tidal height intervals, then sampling three randomly placed quadrats 0.25m^2 in area within each stratum (for a total of 18 quadrats month^{-1} local population^{-1}). The shell lengths of all individuals from one randomly selected quadrat per tidal interval were measured in the field with vernier calipers.

Reproductive state and size-specific fecundity (females only) of *Littorina keenae* were determined by collecting a wide size range of gastropods every two weeks, sexing them using a dissecting microscope (males have a penis on their cephalic tentacle), and placing females in individual Stender dishes filled with filtered seawater. Small individuals of both sexes were dissected during the breeding season to further establish size at maturity. Females, which spawned if ready, were kept for 14 days (*i.e.*, a tidal series); random dissections at the end of each 14 day spawning period revealed virtually no mature eggs remained. Spawned eggs were collected daily and counted, and the number of eggs spawned per female was regressed against shell length. Mark and release studies indicate that individual females spawn approximately eight times during the year (Schmitt 1979). For more methodological details, see Schmitt (1979).

Change in shell length over a year was used to measure growth rates of individuals. To examine geographic differences in growth, 600 snails were collected, marked and released in one population at Dillon Beach and one at Santa Catalina Island (Ben Weston Beach). Growth of approximately 200 snails from additional populations within each region also was determined to explore potential local variation. No variation in growth was found within geographic locations, although the ability to detect such variation was diminished because additional populations were represented by a narrow range of body sizes (large in the north and small in the south) and growth rates in general were highly variable. Snails were marked with sequential numbers inscribed on their shell with India ink (northern site) or by gluing numbered Brady wire tags using Dekophane (southern site). Growth was determined by remeasuring marked snails after a year. The growth rate during breeding and non-breeding periods was estimated separately by measuring individuals at approximately six month intervals. Differences in growth between geographic regions and between reproductive seasons were analyzed by ANCOVA.

To estimate the degree to which observed size-frequency distributions of local populations may reflect variability in growth rate of individuals following recruitment, a projection matrix model was developed using the measured level of variation in growth within snail size-classes (for a general explanation of the technique, see Hughes 1984). Size categories were 1 mm shell length intervals between 7-14 mm; sizes below 7 mm and above 14 mm were grouped into their own categories because of limited growth data for these sizes. The size distribution of a model population was obtained by multiplying the number of individuals within each size category by the transition probability of growing to larger size classes in one year (*i.e.*, one iteration of the model); the transition probability for each initial size-class was obtained from the actual growth data. Since survivorship of *Littorina keenae* approximates Type II (*i.e.*, mortality constant among age/size classes; see Results), no mortality function was included. Two forms of the model were run to incorporate extremes in variability of new recruitment: 1) initial settlement of a cohort that grows without further recruitment and 2) initial recruitment followed by annual recruitment of identical magnitude. The model output (*i.e.*, size-frequency distributions) is presented for various intervals from initial settlement.

Mortality rates of individuals in the field were not estimated directly. A strong negative relationship existed between mean age of a population (estimated from size-age analyses) and its density. This relationship can be used to obtain an estimate of the survivorship curve by regressing the log(density) against mean age. A critical assumption is that the principal source of variation in density among populations is mortality of a single aging cohort. Clearly other factors can and will influence variation in density among populations. These include different initial cohort sizes (*i.e.*, settlement intensity), populations composed of different numbers of cohorts and local conditions affecting growth and mortality that are not spatially and temporally similar among sites.

To verify whether mortality rates were independent of body size, size-specific frequencies of recapture of marked snails (used to measure individual growth rates at Dillon Beach) were examined. A goodness of fit test was calculated using the proportion of individually marked snails in each of nine size categories that were recaptured six months after release to establish whether the proportion recovered differed among size classes. Since no effort was made to relocate every surviving marked snail (*i.e.*, those overlooked or migrated away), the absolute proportion that survived cannot be accurately determined.

Results

Geographic Variation in Population Characteristics: Average shell length of *Littorina keenae* was significantly larger overall at the northern (site mean = 12.4 mm) than southern location (site mean 5.6 mm; $t = 5.88$, $P < 0.001$). Mean shell length for individual populations ranged between 10 and 15 mm at Bodega Bay (Table 1), whereas it varied from 3-9 mm for populations at Santa Catalina Island (Table 1). There was virtually no change in mean body size over the year of observation (Fig. 1), although southern populations tended to be slightly more variable in this respect.

Size-frequency distributions (Fig. 2) show that perhaps as many as eight of the 11 populations examined were unimodal; one population that clearly had a polymodal body size distribution was observed in the north (Bodega Bay 2) and one in the south (Ben Weston Beach). In addition to these two sites, populations at Dillon Beach 3 (Fig. 1) and Big Fisherman Cove (Fig. 2) might also be bimodal, although these populations were certainly dominated by a single mode.

Sites with polymodal size-structures were areas most exposed to wave activity within a geographic location. However, there was no consistent relationship between size-structure and exposure gradient since most northern sites, which all had greater exposure than populations at Santa Catalina, had size-structures dominated by a single mode. Populations with reasonably unimodal size-frequencies, especially those in the north, typically had a steep decline in sizes larger than the mode and relatively long left tails. As might be expected from the data on mean body size, size-frequency distributions were more similar within a geographic location than between regions.

Table 1. Average shell length of *Littorina keenae* in local populations at study sites in northern and southern California. Data are the mean ± 1 SE shell length (mm) at the initial (month 1) and final (month 12) sampling date; number of individuals measured is given in parentheses.

	Mean Initial		Mean Final	
Study Site	Length	*n*	Length	*n*
Northern California				
Dillon Beach 1	11.1 ± 0.1	(579)	11.8 ± 0.3	(160)
Dillon Beach 2	12.4 ± 0.2	(331)	12.2 ± 0.5	(90)
Dillon Beach 3	12.3 ± 0.3	(62)	11.9 ± 0.6	(23)
Bodega Bay 1	15.1 ± 0.2	(84)	14.8 ± 0.6	(43)
Bodega Bay 2	10.7 ± 0.4	(78)	10.8 ± 0.3	(99)
Southern California				
Ben Weston Beach	8.4 ± 0.1	(769)	9.4 ± 0.3	(216)
Intake Pipes	6.1 ± 0.1	(512)	4.9 ± 0.1	(401)
Pin Rock	2.8 ± 0.1	(853)	3.0 ± 0.1	(759)
Big Fisherman Cove	4.5 ± 0.1	(285)	3.9 ± 0.1	(405)
Emerald Bay	4.6 ± 0.1	(214)	4.3 ± 0.1	(559)
Indian Rock	7.0 ± 0.1	(130)	6.1 ± 0.4	(55)

Snails smaller than 5 mm shell length were rarely observed in the north (Fig. 1), whereas most southern populations had many individuals in the smallest size classes (Fig. 2). By contrast, snails as large as 15 mm were common in all northern populations but individuals larger than 10 mm were rare in the south. The one exception was Ben Weston Beach, the most exposed site at Santa Catalina Island. The occurrence of large snails at Ben Weston Beach indicates that *Littorina keenae* can obtain large body size in the southern region.

Population densities were significantly lower overall in the north than in the south ($t = 3.13$; $P < 0.02$). Populations at Bodega Bay varied between 10-55 snails m^{-2} (Fig. 3), whereas densities at Santa Catalina Island ranged between 50-300+ m^{-2} (Fig. 4). As with mean body size, no consistent pattern of change in density was detected over the year long course of study (Figs. 3 & 4). There was a strong negative correlation between density of a population and the average body size of its members ($r^2 = 0.734$; $P < 0.001$); populations composed mostly of small snails were dense whereas those composed mostly of large individuals were sparse.

Patterns of recruitment (*i.e.*, appearance of 1 mm snails), shown in Figure 5, indicate that northern populations did not receive any recruits during the year studied. Five of the six populations at Santa Catalina Island received some recruits, but the greatest density observed was less than 5% of the standing stock of adults. These data suggest that recruitment success is variable and failure can occur over an entire geographic region or for a subset of sites within a region. However, the data suggest that when recruitment occurs, its magnitude is most similar for populations close to one another.

Demography of *Littorina keenae*: Examination of gonadal material, field observations of copulation and laboratory spawning trials revealed that *Littorina keenae* reaches sexual maturation at a minimum shell length of about 4-5 mm, corresponding to about 2-3 years of age (see below). Female fecundity was great and size-related (Fig. 6). For example, a female 13 mm in length released on the average 12,000 eggs per spawning event (*i.e.*, one spring tidal cycle; see Schmitt 1979). Since there are about eight spring tidal cycles in a breeding season (Schmitt 1979), the annual fecundity of a 13 mm female was on the order of 100,000 eggs. Large females (18+ mm shell length) can have

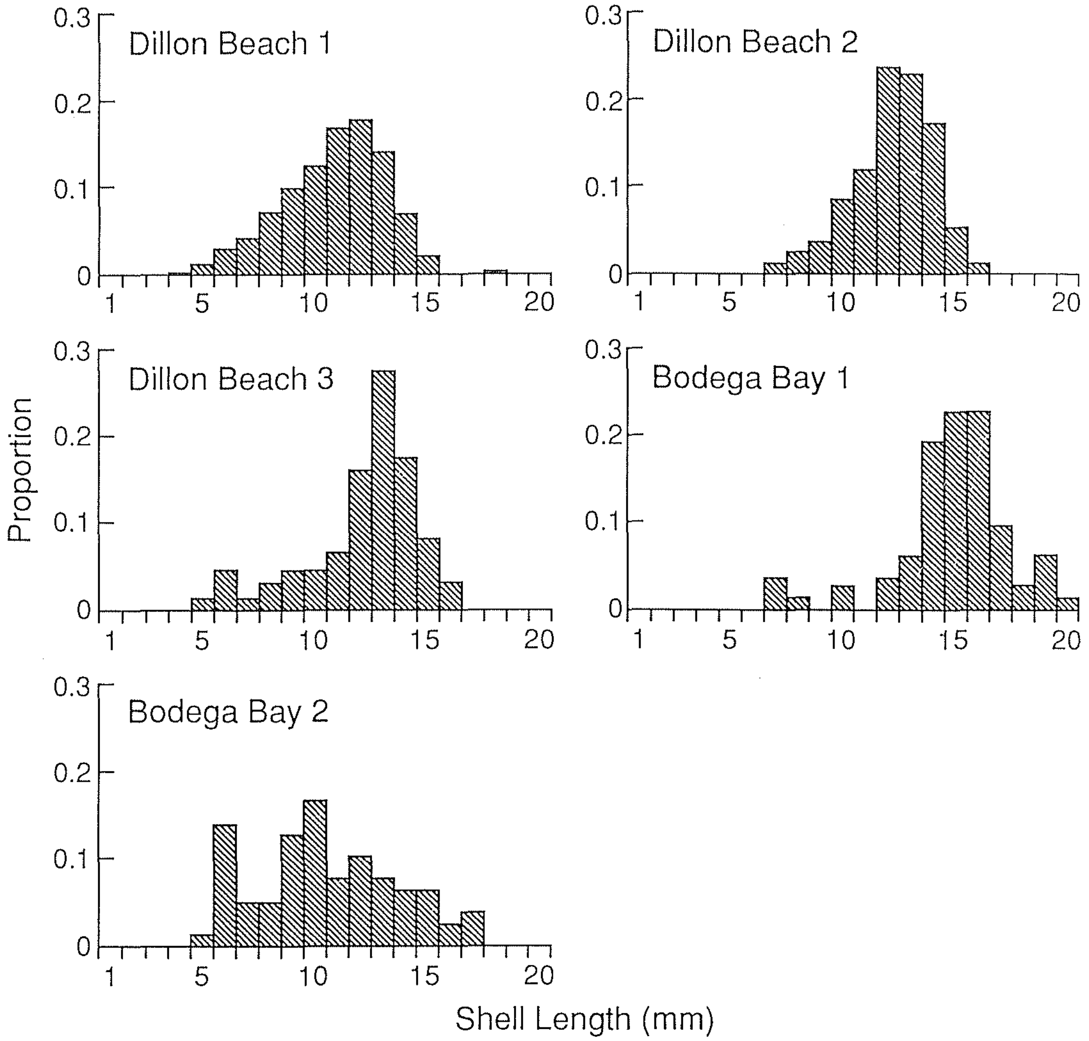

Figure 1. Population size-structure of local populations of *Littorina keenae* at Dillon Beach and Bodega Bay in northern California. Data are the proportion of individuals in each size class on the initial sampling date (see Table 1 for sample sizes); no qualitative change in the size-frequency distribution of any population occurred during the year of observation.

an annual fecundity in excess of 400,000 eggs. New recruits appear in the adult habitat following a planktonic larval stage of unknown duration.

Growth rates of individuals on the shore were low and size-dependent (Fig. 7). As expected, fastest growth was observed for the smallest size classes, with shell growth decreasing with increasing size and ceasing at approximately 15-17 mm. The growth data revealed several important features. First, there was no significant difference in the size-specific growth rates of *Littorina keenae* in northern and southern populations (ANCOVA with initial shell size as covariate: $F_{(1,172)} = 0.83$; $P > 0.35$). Virtually all annual increase in shell length occurred during the non-breeding season (Fig. 8; $P < 0.001$). Second, the amount of variance in growth explained by initial snail size was low (45%) but similar for individuals in both northern and southern populations. Size-specific growth of *L. keenae* varied greatly among individuals of the same initial size.

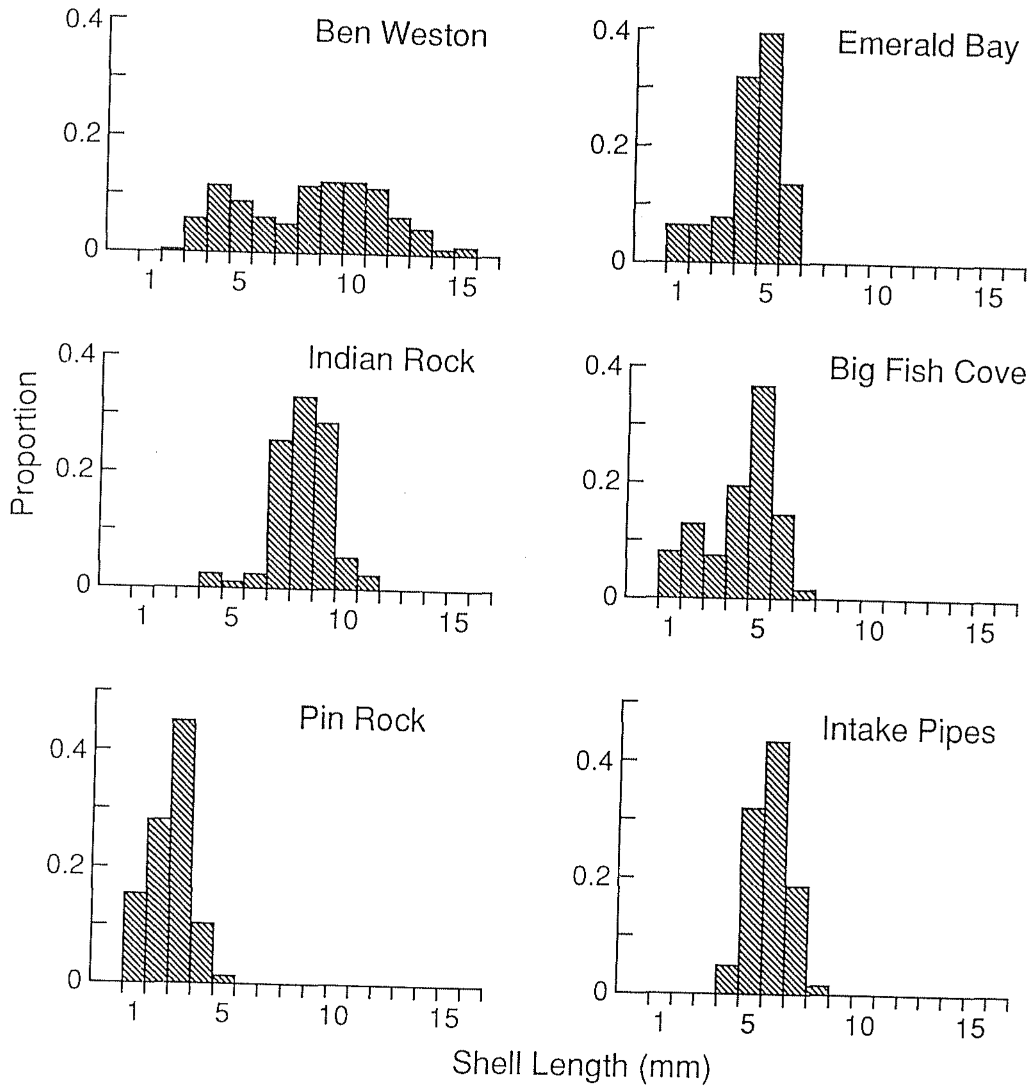

Figure 2. Population size-structure of local populations of *Littorina keenae* at Santa Catalina Island in southern California. Data are the proportion of individuals in each size class on the initial sampling date (see Table 1 for sample sizes); no qualitative change in the size-frequency distribution of any population occurred during the year of observation.

An idealized relationship between shell length and age was constructed based on the average annual growth rate within a size-class (Fig. 9). Mean ages in northern populations were estimated to be on the order of 12-20 years, whereas those at Santa Catalina Island (with the exception of Ben Weston Beach) were less than five years (Fig. 9).

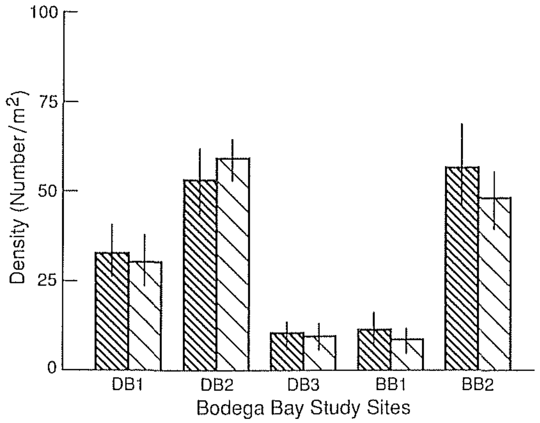

Figure 3. Population densities of *Littorina keenae* at northern California study sites. Data are the mean number per m^2 (± 1 SE) during the initial sampling date (dark hatch) and 12 months later (light hatch). DB = Dillon Beach; BB = Bodega Bay.

While mortality rates were not measured directly, several lines of evidence suggest that they are relatively low for post-recruitment life stages. Population sizes did not vary to a detectable degree over the year of study even at sites that did not receive recruits during the study. With a number of assumptions, the relationship between population density and mean age can be used to approximate mortality rate. The assumptions include similar growth rates and recruitment patterns among sites and regions. The analysis suggests that adult *Littorina keenae* has a survivorship curve that approximates a Type II (*i.e.*, constant among age/size classes) with 7.6% annual mortality (Fig. 10; r^2 = 0.818; $P < 0.001$). Mortality rates of *L. keenae* probably do vary somewhat in space and time; however, this analysis suggests that mortality may be independent of body size. This assertion is bolstered by the proportion of marked snails that were recaptured. All size classes were recaptured with nearly the same frequencies (Table 2) and no statistical differences were detected (X^2 = 2.226, 8 df; $P > 0.9$), indicating that loss rates (mortality plus migration) were roughly equal among size classes of *L. keenae*.

Spatial Variation in Population Features: a Hypothesis and Projection Model: The data presented above suggest that many populations of *Littorina keenae* examined primarily were established by one or a few successive pulses of high annual recruitment, preceded and followed by long periods of little or no recruitment. Here I develop the hypothesis that such populations may be composed of a dominant settlement cohort characterized by variable growth rates of individuals. By this hypothesis, most similarities and differences in characteristics among populations and between geographic locations reflect recruitment history.

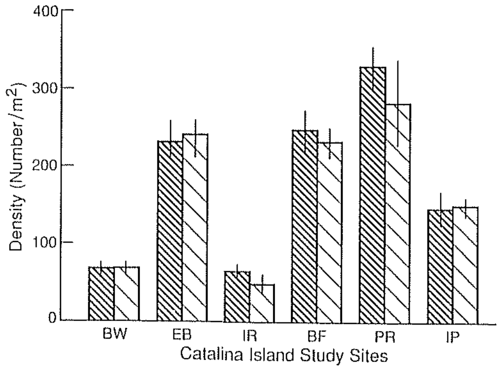

Figure 4. Population densities of *Littorina keenae* at southern California study sites. Data are the mean number per m^2 (± 1 SE) during the initial sampling date (dark hatched) and 12 months later (light hatch). BW = Ben Weston Beach; EB = Emerald Bay; IR = Indian Rock; BF = Big Fisherman Cove; PR = Pin Rock; IP = Intake Pipes.

Table 2. Proportion of individually marked *Littorina keenae* recaptured after 6 months as a function of size class (shell length). Snails were used to estimate size-specific growth rates at Dillon Beach 1. The number of snails released in each size category is given. There was no statistical difference in the recapture frequency among size-classes (X^2 = 2.226; df = 8; $P > 0.9$), indicating that loss rates (mortality plus migration) were independent of snail size.

Snail Size Class	Number Released	Proportion Recaptured
4 - 7	58	0.64
8	44	0.68
9	57	0.77
10	74	0.78
11	99	0.72
12	103	0.68
13	79	0.76
14	38	0.53
15 - 17	22	0.64

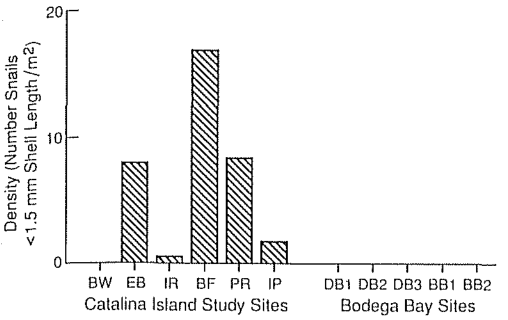

Figure 5. Density of new recruits (individuals < 1.5 mm shell length) at study sites in southern and northern California. Data are the mean number of recruits observed during 12 monthly observations at each site. Site abbreviations are given in Figures 3 and 4.

The size-frequency distributions and measured rate of appearance of new individuals indicate that recruitment varied greatly through time and space. The data support the hypothesis that, when a recruitment event occurred, it tended to be spatially synchronous on a regional scale, but relatively asynchronous across geographic regions. Once a population was established, survivorship was relatively high and individual growth rates low but highly variable. It appears that a population can persist for a decade or more without another recruitment event. Over this period, mortality lowers population abundance and growth of survivors leads to larger mean body size.

It is notable that large, old individuals were absent from five of the six populations at Santa Catalina Island, which suggests that recruitment may have failed at these sites for many previous years. The lack of very small individuals (<4 mm) at Bodega Bay sites, together with the observed recruitment failure during the year of observation, suggests that these populations received few or no recruits subsequent to establishment.

For the recruitment-pulse hypothesis to be tenable, the broadly skewed right shape of the unimodal size-frequency distributions (Figs. 1 & 2), especially those in the north, must be explained. It is conceivable that the observed range of body sizes within a population could reflect the highly variable individual growth rate (Fig. 7). This possibility was explored with a projection matrix model. The annual transition probability of an individual of a given size growing into the next larger size-class(es) was taken directly from the growth data (Fig. 7). Two forms of the model were run to encompass the endpoints of temporal variability in recruitment: 1) an initial settlement pulse without any further recruitment and 2) constant annual recruitment. The model was run for 25 iterations (years) to simulate population size-structures under the two recruitment regimes.

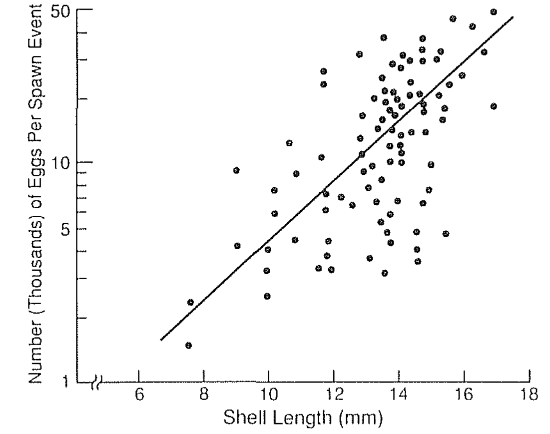

Figure 6. Size-specific fecundity of female *Littorina keenae*. Data are the number of eggs spawned by an individual during one 14 day spawning cycle during the breeding season. The regression, which was highly significant (r = 0.59), is log[number eggs spawned] = 13.35[shell length] + 5.06.

Results of the growth projections for the two recruitment patterns are presented in Figure 11 for certain years after initial recruitment. The qualitative shapes of the size-frequency distributions that result from a single recruitment event fit remarkably well with those observed (Figs. 1 & 2). In particular, the model size distributions produced by a single recruitment cohort were skewed right (especially as the cohort aged). Thus, the variable pattern of individual growth within a single recruitment

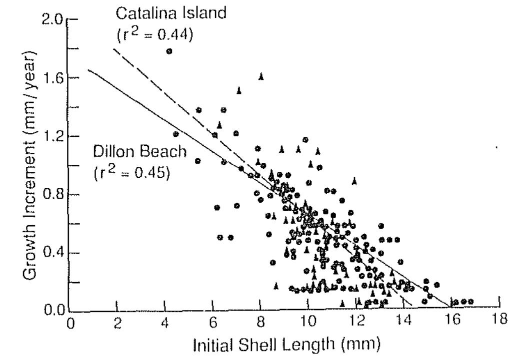

Figure 7. Size-specific annual growth of *Littorina keenae* in northern (circles) and southern (triangles) California. No statistical difference in growth rates was detected between geographical regions.

cohort can produce the broadly right skewed unimodal distributions of body sizes observed for many populations of *Littorina keenae.* Finally, the constant recruitment model produced a size-structure (Fig. 11; iteration 13) that was qualitative similar to that observed at Ben Weston Beach (Fig. 2), suggesting that occasional populations of *Littorina keenae* may receive new recruits regularly.

Discussion

Often populations of marine organisms at higher latitudes are composed of fewer, older individuals of larger body size relative to counterparts at lower latitudes. Geographic variation in these aspects of the littoral fringe periwinkle, *Littorina keenae*, is typical of the latitudinal pattern; populations in northern California were less dense and composed of larger, older individuals compared with those at Santa Catalina Island. Data gathered by other workers on this periwinkle appear to fit this qualitative pattern (North 1954; Bock & Johnson 1967).

Few studies have established the causal mechanisms producing latitudinal variation in life history features (Frank 1975; Garrity *et al.* 1986; Shirley *et al.* 1987). One well studied example involves the intertidal gastropod *Tegula funebralis*, which lives longer and obtains larger body size at higher latitudes in its geographic range (Frank 1975; Fawcett 1984). Frank (1975) found that variation in growth rates of individuals, which were slower to the north, had a genetic component. Based on population size-structures, Frank (1975) concluded that recruitment was less predictable at higher latitudes. Fawcett (1984) found that, due to size-selective predation on *T. funebralis*, populations subject to intense predation were composed of smaller, younger individuals with lower survivorship relative to less exploited populations, regardless of latitude. However, the degree to which populations were subject to predation tended to increase with decreasing latitude. Increasing consumer pressure has been invoked as an explanation for latitudinal variation in such characteristics of gastropods as shell morphology and species diversity (*e.g.*, Garrity *et al.* 1986; Ortega 1986; Vermeij 1978). Experimental transplants of *T. funebralis* indicated that observed geographic differences in behavioral responses to certain species of predator had a genetic basis (Fawcett 1984). Taken together, these data suggest that an element of geographic variation in the demographic characteristics of *T. funebralis* includes evolved, genetically-based adaptations to local environmental conditions.

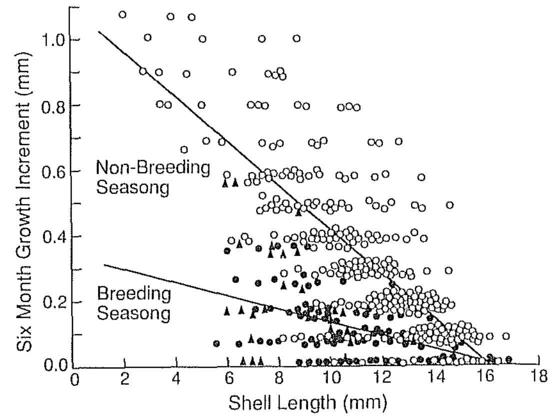

Figure 8. Size-specific growth of *Littorina keenae* during the six month breeding season (closed symbols) and the six month non-breeding season (open symbols). Growth rates differed significantly between seasons (F = 19.99; P <0.001).

The underlying mechanism producing geographic variation in populations of *Littorina keenae* may not involve a significant genetic component or grossly different phenotypic responses to dissimilar local conditions. For example, I detected no significant difference in size-specific growth rate between geographic regions or among populations within a region, although growth rates within each size class were highly variable (also see Chow 1987). This suggests that geographic differences in genetic and environmental influences on growth rate were relatively weak, which is surprising given the distance between regions and the range in such parameters as wave exposure, substrate composition, and slope of shore. The mortality rate of post-recruitment size-classes appears to be reasonably low and independent of body size (age). For local adaptation to have produced the observed geographic pattern (*i.e.*, increased adult longevity as an evolved response to a decreased probability of successful recruitment), recruitment of young must have been historically more variable at higher latitudes (see Frank 1975). While recruitment of *L. keenae* appears to be highly variable in time, at present there is no evidence to assess whether recruitment success is any more variable in northern than southern populations.

The observed geographic variation in population features of *Littorina keenae* can be explained by recruitment history. This is not to suggest that genetic or environmentally induced differences in life history attributes do not contribute, only that the recruitment history hypothesis is a sufficient and plausible explanation for the observed patterns. Population size-structures support the contention that many populations of this long-lived species were composed of a few cohorts or less. The growth model indicates that the measured level of variation in size-specific growth within just a single cohort can account for the observed distribution of body sizes within many of the populations examined. The recruitment event(s) that founded most populations at Santa Catalina Island appears to have been preceded, and those at Bodega Bay followed, by long periods of recruitment failure. Because of low individual growth and death rates, a single cohort population of *L. keenae* can persist for longer than a decade, during which time another recruitment event may or may not occur.

It is quite conceivable that populations of *Littorina keenae* with unimodal body size frequencies were composed of more than a single recruitment cohort. A population may have two (or more) age modes that recruited a number of years apart, yet the population could display a reasonably unimodal size distribution because highly variable growth rates can result in broadly overlapping body sizes among the cohorts. Nonetheless, it is doubtful that most populations examined had even an approximation of constant annual recruitment. The population at Ben Weston Beach in the south, and perhaps Bodega Bay 2 in the north, may be exceptions to this general pattern.

By the recruitment history hypothesis, geographic patterns in population features simply reflected different elapsed intervals from successful recruitment events. This hypothesis was suggested by North (1954) to explain spatial variability between two populations of *Littorina keenae* in southern California. Mean body size and size-frequency distributions differed between the sites but varied little over the two-year span of his study. However, North (1954) argued against the hypothesis that the among-site patterns resulted from areas receiving "a favorable spawn" at different times in favor of the view that the variation in population characteristics reflected dissimilar local environmental conditions (*i.e.*, wave exposure and substrate heterogeneity) that in turn affected growth rates and mortality. Results of the present study lend credence to the "favorable spawn" hypothesis and suggest that such local environmental differences may not set body size and population density to the degree suggested by North (1954).

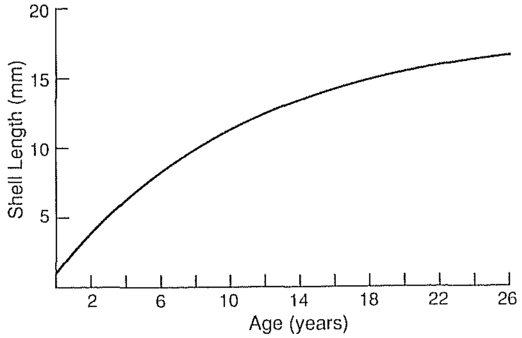

Figure 9. Idealized plot of the relationship between shell length and age (years) of *Littorina keenae*. The relationship is based on the average growth rate of each size-class; metamorphosis was assumed to occurred at 1 mm shell length.

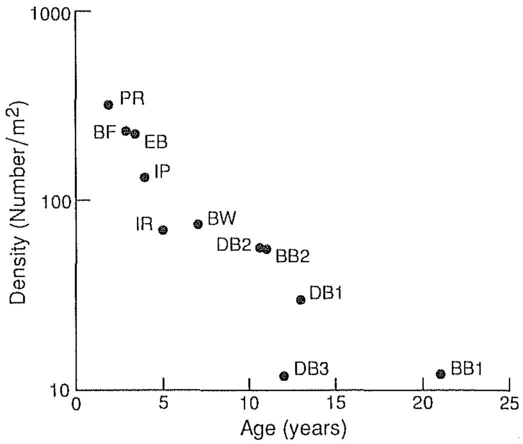

Figure 10. An approximation of the survivorship curve of *Littorina keenae*. Data are the (log) density of each local population plotted against its estimated mean age ($r^2 = 0.82$).

There is growing awareness that the nature of recruitment of new individuals to a population can have a fundamental role in setting patterns of: 1) distribution (*e.g.*, Strathmann *et al.* 1981; Grosberg 1982; Gaines & Roughgarden 1985; Victor 1986); 2) abundance (*e.g.*, Vance 1980; Doherty 1983; Caffey 1985; Connell 1985; Gaines *et al.* 1985; Victor 1986; Underwood & Denley 1984; Roughgarden *et al.* 1988; Underwood & Fairweather 1989; Hughes 1990); 3) size structure (*e.g.*, Ebert 1983); 4) dynamics (*e.g.*, Roughgarden *et al.* 1985; Warner & Chesson 1985; Roughgarden *et al.* 1988; Underwood & Fairweather 1989; Hughes 1990) and 5) stability (*e.g.*, Roughgarden 1977; Vance 1980; Warner & Chesson 1985). Patterns of recruitment are of particular importance to populations of marine benthic organisms because the preponderance of species have a planktonic larval stage (Underwood & Fairweather 1989). Connell (1985) found that population density of adult barnacles can be set by larval limitation when settlement is light, or by space limitation on the shore when settlement is heavy (for reef fishes, see Jones 1987). Thus, the importance of more traditionally studied processes, those that occur after settlement, depends on the rate of supply of new individuals to a population (Keough 1984).

Local populations of *Littorina keenae* were characterized by marked annual constancy in density, body size and age-structure (also see North 1954). This constancy could be mistaken for some sort of population "stability," but was simply a demographic consequence of slow growth and low mortality (Frank 1968). Local populations of *L. keenae* may have a relatively high probability of eventually declining to extinction because successful recruitment events appear to be uncommon. This does not necessarily imply the system is unstable (Warner & Chesson 1985). Although dispersal is generally believed to increase stability (Roughgarden 1977; Vance 1980), Vance (1980) showed theoretically that temporal variability can decrease the stability of a local population. Long life enhances the probability that a population with highly variable recruitment will persist (*e.g.*, Murphy 1968; Warner & Chesson 1985). For species such as *L. keenae*, it perhaps is more fruitful in this context to consider the regional population, which is the collection of local patches of adults in a geographic region that result from the same pool of planktonic larvae (for a barnacle example, see Roughgarden *et al.* 1988). Thus, while a particular patch of adult *L. keenae* on the shore (a local population) may go extinct, the regional population may persist.

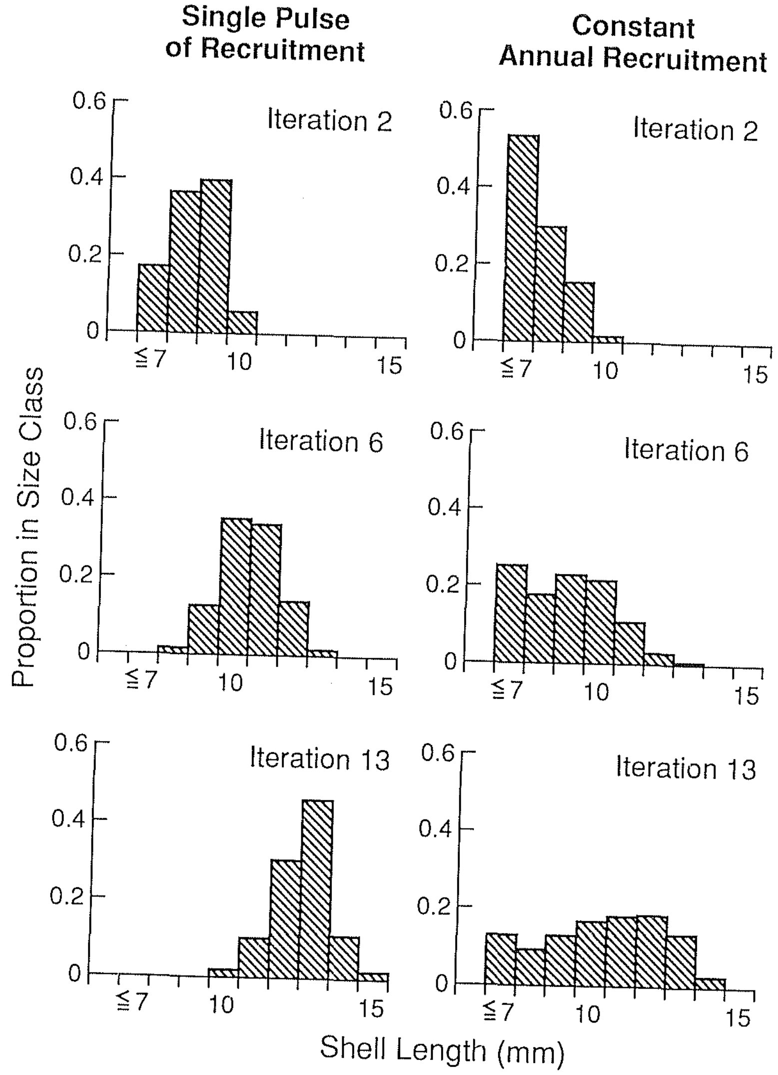

Figure 11. Results of a projection matrix model to simulate body size-structures of populations with different recruitment dynamics. Data are the proportion of individuals in each size class for various annual intervals (model iterations) following establishment of a population. Two forms of the model examined extremes in temporal variability of recruitment: the "single-pulse" model had no recruitment after the initial recruitment event, and the "constant recruitment" model had annual settlement of the same magnitude as the initial event.

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