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Growth and Longevity of the Mud Snail *Batillaria attramentaria*

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Abstract

Batillaria attramentaria (Sowerby), a recent introduction to North America from Japan, occurs on tidal mudflats from California to British Columbia. A population of this deposit-feeder was followed for 10 yr on Galiano Island, British Columbia by recovering marked individuals and by following shifts in size-frequency distributions. Growth as well as erosion pattern and age class analysis indicate that the average size of *B. attramentaria* in the first 6 yr of life is 3, 9, 12, 15, 17, and 18 mm in length and that longevity falls between 6 and 10 yr. Recruitment of young *B. attramentaria* occurred every year. The key to *B. attramentaria's* success must lie in its combination of both a relatively predictable annual recruitment and a moderately long longevity.

Introduction

The deposit-feeding mud snail *Batillaria attramentaria* occurs throughout the Strait of Georgia and Puget Sound in Western Canada and Washington, and in two localities in California, Tomales Bay and Elkhorn Slough (Hanna, 1966; Carlton, 1979). Originally a native of Japan, *B. attramentaria* was introduced to North America with the Japanese oyster *Crassostrea gigas* (Quayle, 1964). Previously known as *B. zonalis* (Bruguière), *B. attramentaria* is now the accepted name for the only representative of its genus in the eastern north Pacific Ocean, (Carlton and Roth, 1975).

Batillaria attramentaria is abundant on mud flats in many areas where Japanese oysters were planted, but has not spread to other suitable habitats. The absence of a pelagic dispersal stage appears to be responsible in part for this restricted distribution (Behrens Yamada and Sankurathri, 1977).

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Whitlatch (1974), using mark-recapture studies and size-frequency analysis, estimated that *Batillaria attramentaria* in Tomales Bay, California, grew to a length of 35 mm in about 8 yr. The present study, spanning 10 yr, examines growth and longevity of this species at Galiano Island, British Columbia.

Materials and Methods

The study site at Montague Harbour, Galiano Island (123°26′W Long.; 48°51′N Lat.) consists of a high tidal marsh connected to the sea by a narrow drainage channel. *Batillaria attramentaria* (Sowerby) is patchily distributed along the gently sloping edges of drainage channels and in marsh pans, flat areas with standing water and fine silt (Whitlatch, 1974 and personal observations). The size-frequency distributions of *B. attramentaria* in both habitats are identical with the exception that individuals smaller than 7 mm are absent from drainage channel sites. Growth studies were done along a 10-m stretch of drainage channel close to the mouth of the tidal marsh and on two marsh pan sites. Growth data were obtained by following shifts in size-frequency distributions and by recovering marked individual snails. Annual growth data were used in determining growth parameters and in estimating longevity. Longevity was also estimated using erosion pattern analysis and age class analysis.

Size-Frequency Distributions

Since *Batillaria attramentaria* is patchily distributed, no attempt was made to choose random quadrats. Instead, permanent quadrats were chosen for the abundance and representative size distribution of *B. attramentaria.* One drainage channel quadrat was sampled 6 times from 1970 to 1976; one marsh pan quadrat 12 times from 1976 to 1979.

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All *Batillaria attramentaria* within 50×50 cm quadrat samples were collected and measured. Individuals from drainage channel quadrats were picked out of the gravel substrate by hand; those from marsh pan quadrats were extracted by washing mud samples through a 1-mm sieve. All the mud within the quadrat, down to the black anoxic layer was spooned into the sieve. The smallest size picked up by the sieving method was 2 to 3 mm in length.

Mark and Recapture

From 200 to 500 *Batillaria attramentaria* from both sites were collected on 7 occasions between 1970 and 1976. Snails smaller than 3 mm were discarded. Sediment and algae were wiped off the shell lips with paper towels. After shells had dried, the whole outer lip was marked with cellulose base model paint. A different colour was used at each marking date. After the paint dried, snails were returned to their site of collection. The whole marking procedure from collection to release took no longer than 2 h.

On subsequent visits the release site was searched for marked individuals. Length at release and new length were noted for all snails. For those individuals that had grown more than a whorl, width at release was measured and transformed to the corresponding length using length $=4.53+1.74$ width ($r=0.90$). Length at recapture was plotted against length at release for short term and annual growth.

Growth Parameters

As an individual ages it grows progressively less. This growth process is described by the von Bertalanffy curve, a curve of the decaying exponential type:

$$L = L_\infty (1 - ae^{-kt}),$$

where L = length; L_∞ = growth parameter, maximum length; a = growth parameter; e = base of natural logarithms; k = growth paramter, instantaneous growth rate; and t = age. By plotting the length at release of a marked snail along the x-axis and the length of that same snail at recovery 1 yr later along the y-axis, one gets a Walford plot (Walford, 1946) (Fig. 3). The growth parameters L_∞ and k can be directly extracted from the plot. L_∞ is that length at which the average individual ceases to grow, the point of intersection between the regression line with the line of no growth. The instantaneous growth rate, k, $=-\log_e$ slope of the regression line.

Fabens (1965) describes a computer program which fits the von Bertalanffy growth curve to recapture data. When length of individuals at release and at recapture at yearly intervals is fed into the program, it will produce growth parameters a, k and L_∞. The most useful feature of this program, however, is its capacity for estimating age from size information.

Age

The older a snail gets the more difficult it becomes to age. This is especially true for long-lived, slow growing species. Fabens (1965) circumvents this aging problem by introducing the concept of the chron. One chron is defined as the period, ln 2/k, in which an individual achieves half its remaining linear growth toward an asymptote. This concept, analogous to that of the half-life for describing the age of a radioactive element, is useful in comparing the growth of organisms at the same physiological age, irrespective of differences in taxon or age in years. Individuals of the same age in chrons are at corresponding points along their respective growth curve: at 2 chrons they have reached ¾ of their linear growth, at 3 chrons, ⅞ etc. By knowing the size of an individual at 1 and 2 yr of age and by using the conversion 1 chron = ln 2/k age in years, Fabens' program will generate age at various sizes.

Age Class Analysis

Schnute and Fournier (1980) devised a computer program for sorting out overlapping year classes from size frequency distributions. The program, based on the von Bertalanffy relationship of decreasing growth with age, requires initial guesses of values of k, L_∞ and the possible number of age classes represented. As long as the first two classes are well defined, the program will pick out the most likely modes for the year classes represented. The agreement of the final k and L_∞ values with those observed from growth data offers some measure of the goodness of fit. Schnute and Fournier's program was applied to the July 8, 1978 frequency data.

Erosion Pattern Analysis

All the *Batillaria attramentaria* sampled July 1, 1976 were sorted into size classes and examined under a microscope. The number of eroded whorls and the number of non-eroded whorls were recorded. The assumption was made that the number of eroded whorls represented the size of the snail at the end of the winter and that the number of non-eroded whorls represented spring and summer growth.

Results

Recruitment

Young *Batillaria attramentaria,* 2 to 4 mm in length, first appear in sieved marsh pan samples from March to early July (Fig. 1). Oviposition also occurs during this time (Behrens Yamada and Sankurathri, 1977), and this suggests that these juvenile snails are one year old. Shell erosion patterns also indicate that these individuals spent a winter in the marsh (Table 1).

Table 1. *Batillaria attramentaria.* Analysis of shell erosion patterns of snails collected at Montague Harbour on July 1, 1976. Modal size class is indicated by an asterisk. p: designates that a category was present, but due to erosion of whorls in most individuals, its abundance could not be scored

Total number of whorls	Number of eroded whorls	Number of new whorls	Number of snails in size class									Deduced year class
			0–1	2–3	4–5	6–7	8–9	10–11	12–13	14–15	16–17	
7, 8	5, 6	1–2½		19*	7							75
8, 9	7, 8	¼–1¼			2	5	12*	6				74
9	8, 9	1/16–½					2	7	8*	p		73
9, 10	8½–10	1/32–½								p	p	72 and older

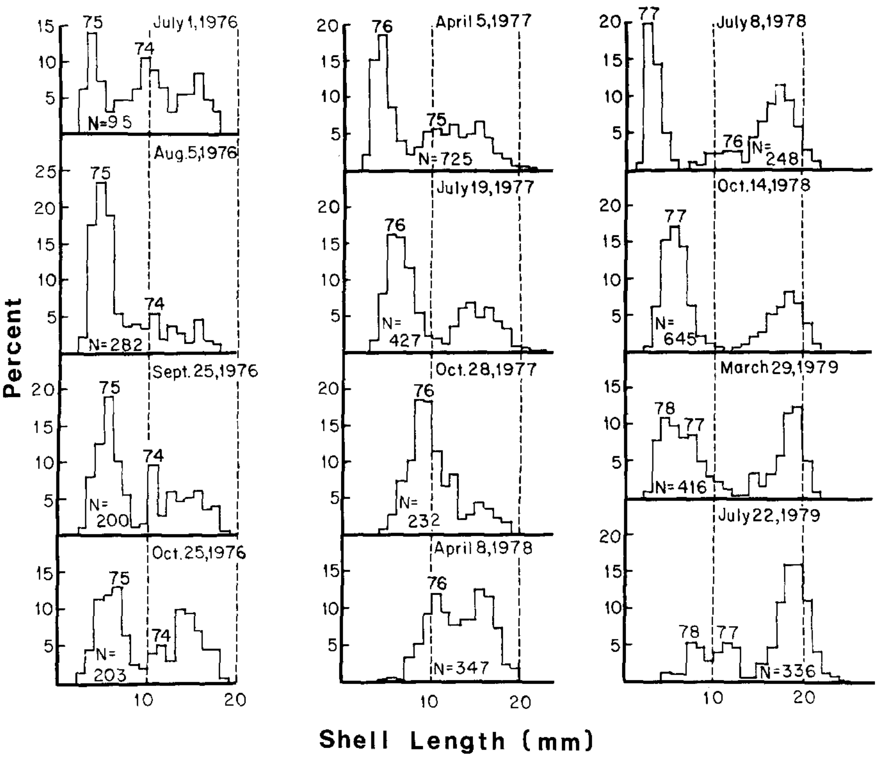

Fig. 1. *Batillaria attramentaria.* Percent in each size class for marsh pan samples. Numbers above modes indicate year classes; N: designates the sample size

Table 2. *Batillaria attramentaria.* Recruitment patterns correlated with deviations from the 30-year mean monthly air temperatures during development. Recruitment patterns were derived from Fig. 1; temperature data, from a weather station on nearby Salt Spring Island. A 1.5 C° deviation from the 30-year mean monthly air temperature is indicated by + or –; a 3.0 C° deviation by ‡ or =

Year class	Recruitment		Long term mean monthly air temp. (°C) and deviation from mean											
	timing	abundance	J 15.0	J 17.2	A 16.7	S 15.0	O 10.5	N 6.1	D 3.9	J 2.8	F 4.4	M 5.5	A 8.9	M 12.2
1975	late	good								+				
1976	early	good	–						+		‡			
1977	very late	good			‡			–				+		
1978	early	poor	+	+						–	–	+		

Recruitment of young *Batillaria attramentaria* occurred in all the years that marsh pan samples were taken (Table 2). The timing and strength of the new year class, however, varied greatly from year to year. Winter temperatures prior to recruitment may play a role in explaining this variation. An unusually mild winter in 1976/77 was correlated with an early and strong recruitment of the 1976 year class, whereas cold winters were correlated with weak or late recruitment (Table 2).

Growth

The two methods for detecting growth in *Batillaria attramentaria* complement each other. Shifts in size-frequency distributions provided growth data for the first two year classes; marked and recaptured individuals provided growth data for older snails. Later year classes blended into one another (Fig. 1, Table 1), and thus became progressively more difficult to distinguish. Although snails between 3 and 8 mm were marked, they were never recovered.

Growth in *Batillaria attramentaria* is extremely variable from individual to individual. During the late summer of 1976, individuals in the 15-mm size class grew between 0 and 2 mm in length in 6 wk (Fig. 2). Body growth during such a warm, calm period may not keep pace with shell growth; however, the great variation in shell growth does indicate that not all individuals in a particular size class are at the same physiological state. Since annual shell growth includes periods of shell deposition as well as periods of shell erosion during winter, it

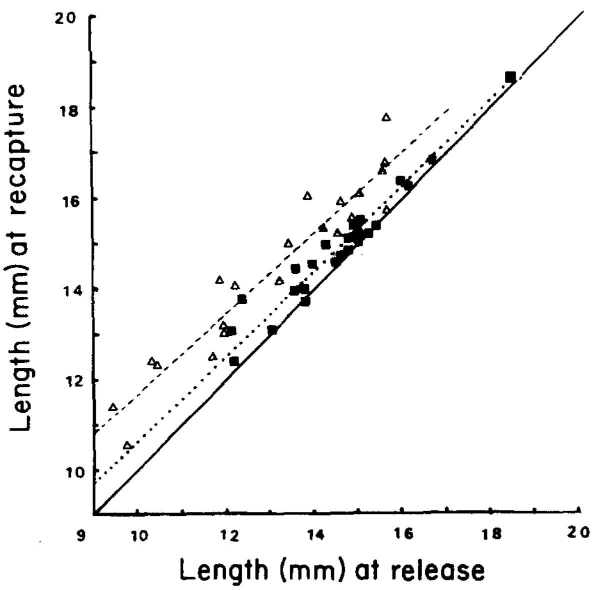

Fig. 2. *Batillaria attramentaria.* Individual variation in growth of marked *B. attramentaria* grown at Montague Harbour. ■ N = 24, 6 wk of growth from April 11 to May 15, 1976. △ N = 21, 6 wk of growth from August 11 to September 25, 1976. Regression lines and line of no growth are indicated

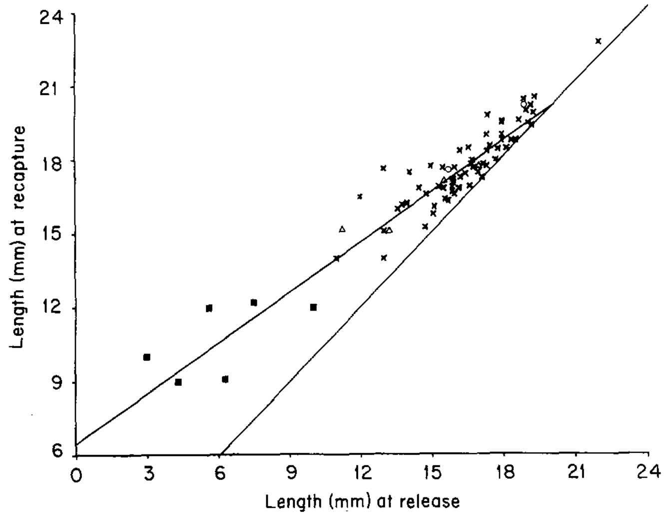

Fig. 3. *Batillaria attramentaria.* Walford plot of *B. attramentaria* from Montague Harbour. The regression $y = 6.5 + 0.67x$ intersects the line of no growth at $L_\infty = 20$ mm.

× N = 62, 1 yr of growth } determined by mark and recapture studies
△ N = 4, 2 yr of growth
○ N = 2, 3 yr of growth

■ N = 6, 1 yr of growth determined by following shifts in size-frequency distribution

is a better estimator of body growth. Annual growth also shows great individual variation. Some individuals grow less in 3 yr than others do in one (Fig. 3).

By pooling annual growth data from mark-recapture studies and from shifts in size-frequency distributions, Fabens' program yielded the following growth parameters for *Batillaria attramentaria* grown at Montague Harbour: $L_\infty = 20$ mm; $k = 0.40$; and $a = 1.3$. These parameters are resilient in that deleting the growth data from small individuals, obtained from shifts in size-frequency distributions, had no effect on their values.

Size-Frequency Distributions

Neither the size-frequency distributions taken in the drainage channel nor those taken in the marsh pan remained stable from year to year (Fig. 1). The first year class in marsh pan samples varies from as little as 20% to as much as 70% of the total. Snails 3 years old and older vary in relative abundance from 20 to 60%.

Longevity

Given the growth data and size at age 1 and age 2, Fabens' program produced the size-age relationship for *Batillaria attramentaria* at Montague Harbour (Fig. 4). These size relationships agree with those deduced from erosion pattern analysis (Table 1) and age class analysis

Table 3. *Batillaria attramentaria.* Mean size of age classes on July 8, 1978 as predicted by Schnute and Fournier's program

Year class	77	76	75	74	73	72
Length (mm)	3	9	12	15	17	18

sample size = 246
final k = 0.37
final L_∞ = 21

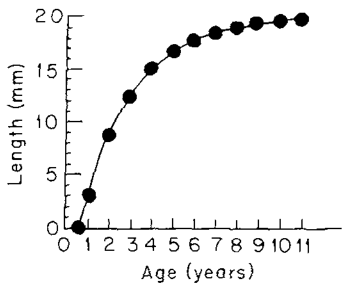

Fig. 4. *Batillaria attramentaria.* Size-age relationship of *B. attramentaria* from Montague Harbour as determined by Fabens' program

(Table 3), in that the average sizes for the first 6 yr of life are: 3, 9, 12, 15, 17, 18 mm in length. Great size overlap exists between snails of adjacent age classes (Table 1). One *B. attramentaria,* 15 mm long or 4 years old at release on April 24, 1973, was 17 mm at recovery on May 15, 1976 (Fig. 2). This observation indicates that at least some slow growing individuals in the 17-mm size category are 7 years old.

Fabens' size-age relationship suggests that, on the average, *Batillaria attramentaria* at Montague Harbour reach L_∞ of 20 mm in 10 yr. This information combined with the recovery of a 7 year old snail and the presence of at least 6 year classes on July 8, 1978, suggests that the life span of *B. attramentaria* at Montague Harbour is between 6 and 10 yr.

Discussion

Even though the age/size structure of *Batillaria attramentaria* at Montague Harbor did not remain stable, the population did persist through a decade of varying weather conditions. Since *B. attramentaria* lacks a planktonic dispersal stage (Behrens Yamada and Sankurathri, 1977), recruitment from other sites was not a factor in this persistence. Continual introduction of adults via seed oyster transplants, likewise, did not occur between 1968 and 1979. *B. attramentaria* at Montague Harbor represent a well established, self-perpetuating population of an introduced species.

The fact that *Batillaria attramentaria* has direct development may have contributed to its establishment on the North American west coast. Direct development assures that offspring will stay within the same suitable habitat as that of the parents. This feature may be an advantage on this coastline where suitable mudflat habitats are rare and are separated by vast areas of rocky and sandy shores. In this case planktonic development would be extremely wasteful since most larvae would settle in unfavorable habitats and die.

Although direct development, on the average, is more costly to the parent than is planktonic development, it is also less risky (Thorson, 1950; Vance, 1973). In some years planktonic recruitment fails altogether in certain populations of *Tivela stultorum, Tegula funebralis,* and *Patella vulgata* (Coe and Fitch, 1950; Frank, 1975; Bowman and Lewis, 1977). By by-passing the hazardous planktonic stage, recruitment would tend to be more predictable. Recruitment patterns in *Batillaria attramentaria* at Montague Harbor were predictable in that juveniles entered the population every spring and in that size-frequency data taken over 10 yr did not suggest the total failure of any one year class.

The timing of the appearance and the strength of the new year class, however, varied from year to year. Warm winter temperatures were linked with good recruitment; unusually cold winter temperatures with poor or late recruitment. The findings of Bowman and Lewis (1977) suggest that frost kills newly settled *Patella vulgata.* Frost occurring at the time of settlement of juveniles from the plankton always resulted in poor recruitment the next spring. Unsually cold winter temperatures in December 1978 and January 1979 may have had a similar effect on the 1978 year class of *Batillaria attramentaria.*

Batillaria attramentaria at Montague Harbor, British Columbia, on the average, grew to a size of 20 mm in about 10 yr. Whitlatch (1974) estimates that *B. attramentaria* at Tomales Bay, California grows to about twice this size in the same amount of time. A longer growing season, greater food abundance or genetic factors may account for this difference.

The most interesting feature of the *Batillaria attramentaria* growth data is the variability within a population growing under the same weather conditions. Great individual variation in growth would be expected if organisms were sessile and food abundance were to vary from patch to patch; however, it is difficult to imagine how adjacent, mobile detritus feeders such as *B. attramentaria* could experience different levels of food abundance. Since territorial behavior does not play a role, it is possible that the variability in growth rate may reflect great genetic variability. Singh and Zouros (1978) demonstrated that growth in the American oyster *Crassostrea virginica* has a genetic component. Unfortunately the genetic structure of *B. attramentaria* populations has not been looked at.

Regardless of the causes, variation in the growth rate of molluscs appears to be a widespread phenomenon (Coe and Fitch, 1950; Seed, 1968; Frank, 1969; Behrens, 1971; Hall *et al.,* 1974). As a rule, fast growing individuals have a greater turnover rate than slow growing individuals (Seed, 1968; Frank, 1975). An energetic tradeoff between growth and reproduction on the one hand and longevity on the other may play a role here. A population made up of slow growing but long-lived and fast growing but short-lived individuals would tend to be more resilient in that not all individuals would be equally susceptible to perturbations.

Batillaria attramentaria's life span of 6 to 10 yr is moderately long for a marine mollusc (Comfort, 1957; Frank, 1969). Longevity estimates for the other two gastropods found on Montague Harbor mudflat are 2 yr for *Littorina sitkana* and at least 7 yr for *L. scutulata* (Behrens, 1971). Some higher longevity estimates for other northeastern Pacific molluscs include 15 yr for *L. planaxis* (Schmitt, 1975), 19 to 25 yr for *Siliqua patula* (Weymouth *et al.*, 1931) and 6–30 yr for *Tegula funebralis* (Frank, 1975).

Murphy (1968) suggests that length of life is correlated with variation in breeding success. Frank (1975) finds this generalization to hold for the turban snail *Tegula funebralis* in which California populations with longevities of about 6 yr receive a greater and more predictable recruitment than do more northern populations with longevities of about 15 yr. Age class distributions suggest that in some years recruitment of British Columbia and Oregon populations fails altogether. Such unpredictable recruitment in combination with a short life span would increase the chances of local extinction, but would not be critical to population persistence when it is combined with longevity. The key to *Batillaria attramentaria's* success must lie in the combination of both a relatively predictable annual recruitment and a moderately long longevity.

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Literature Cited

Behrens, S.: The distribution and abundance of the intertidal prosobranchs *Littorina scutulata* and *L. sitkana*, 175 pp. M. Sc. thesis, Zoology Department, University of British Columbia 1971

Behrens Yamada, S. and C. S. Sankurathri: Direct development in the intertidal gastropod *Batillaria zonalis* (Bruguière, 1792). Veliger *20(2)*, 179 (1977)

Bowman, R. S., J. R. Lewis: Annual fluctuations in the recruitment of *Patella vulgata* L. J. mar. biol. Ass. U.K. *57*, 793–815 (1977)

Carlton, J. T. and B. Roth: Phyllum mollusca: shelled gastropods, pp 467–514, *In:* R. I. Smith and J. T. Carlton, Light's manual, intertidal invertebrates of the central California coast, Third Edition, 716 pp. Berkeley and Los Angeles: University of California Press 1975

Carlton, J. T.: History, biogeography, and ecology of the introduced marine and estuarine invertebrates of the Pacific coast of North America, 904 pp. Ph. D. dissertation, University of California, Davis, Ecology 1979

Coe, W. R. and J. E. Fitch: Population studies, local growth rates and reproduction of the Pismo clam (*Tivela stultorum*) J. mar. Res. *9(3)*, 188–210 (1950)

Comfort, A.: The duration of life in molluscs. Proc. Malacol. Soc. London *32*, 219–241 (1957)

Fabens, A. J.: Properties and fitting of the von Bertalanffy growth curve. Growth *29*, 265–289 (1965)

Frank, P. W.: Growth rates and longevity of some gastropod mollusks on the coral reef at Heron Island. Oecologia (Berl.) *2*, 232–250 (1969)

Frank, P. W.: Latitudinal variation in life history features of the black turban snail *Tegula funebralis* (Prosobranchia: Trochidae). Mar. Biol. *31*, 181–192 (1975)

Hall, C. A., W. A. Dollase and C. E. Cobrató: Shell growth in *Tivela stultorum* (Mawe, 1823) and *Callista chione* (Linnaeus, 1758) (Bivalvia): annual periodicity, latitudinal differences, and diminution with age. Palaeogeogr., Palaeoclimatol., Palaeoecol., *15(1)*, 33–61 (1974)

Hanna, G. D.: Introduced mollusks of western North America. Occ. Pap. Calif. Acad. Sci. *48*, 108 pp. (1966)

Murphy, G. I.: Pattern in life history and the environment. Am. Nat. *102*, 391–403 (1968)

Quayle, D. B.: Distribution of introduced marine Mollusca in British Columbia waters. J. Fish. Res. Bd Can. *21(5)*, 1155–1181 (1964)

Schmitt, R. J.: Population ecology of the littoral fringe gastropod *Littorina planaxis* in northern California, 107 pp. M. Sc. thesis Faculty of the Dept. of Marine Sciences, University of the Pacific 1975

Schnute, J. and D. Fournier: A new approach to length-frequency analysis: growth structure. Can. J. Fish. Aquat. Sci. *37(9)*, 1337–1351 (1980)

Seed, R.: Factors influencing shell shape in the mussel *Mytilus edulis*. J. mar. Biol. Ass. U.K. *48*, 561–584 (1968)

Singh, S. M. and E. Zouros: Genetic variation associated with growth rate in the American oyster (*Crassostrea virginica*). Evolution *32(2)*, 342–353 (1978)

Thorson, G.: Reproductive and larval ecology of marine bottom invertebrates. Bio. Rev. *25*, 1–45 (1950)

Vance, R. R.: On reproductive strategies in marine benthic invertebrates. Am. Nat. *107*, 339–352 (1973)

Walford, L. A.: A new graphical method of describing the growth of animals. Biol. Bull. mar. biol. Lab., Woods Hole *90*, 141–147 (1946)

Weymouth, F. W., H. C. McMillin and W. Rich: Latitude and relative growth in the razor clam, *Siliqua patula*. J. exp. Biol. *28*, 228–249 (1931)

Whitlatch, R. B.: Studies on the population ecology of the salt marsh gastropod, *Batillaria zonalis*. Veliger *17(1)*, 47–55 (1974)

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