

# GROWTH, RECRUITMENT, AND DISTRIBUTION OF THE LITTLENECK CLAM, *PROTOTHACA STAMINEA*, IN GALENA BAY, PRINCE WILLIAM SOUND, ALASKA

A. J. PAUL AND HOWARD M. FEDER<sup>1</sup>

## ABSTRACT

Specimens of the littleneck clam, *Protothaca staminea*, were collected in Galena Bay, Prince William Sound, Alaska, during the summer months of 1971 for a study of recruitment, growth, and distribution.

The average size of *P. staminea* in Galena Bay at the end of the first growing season is approximately 2 mm in length. At any given age, littleneck clams from Galena Bay are smaller than those from British Columbia. In Galena Bay 8 yr are needed for *P. staminea* to reach a length of 30 mm as compared with 3 yr for individuals from British Columbia.

In Galena Bay the intertidal distribution of *P. staminea* generally follows a bell-shaped curve with upper and lower extremes occurring between the tidal heights of +0.73 and -0.76 m. The young-of-the-year are essentially epifaunal, and the majority of the specimens of all age classes are found within 4 cm of the sediment surface.

The number of individuals surviving annual recruitment into the populations studied was variable.

*Protothaca staminea* (Conrad), commonly called the littleneck clam, is frequently encountered on beaches in Prince William Sound, Alaska. It is a clam of commercial importance in the State of Washington, and was harvested in southeastern Alaska until 1946 when the presence of toxic clams in Alaska resulted in regulatory action halting commercial production (M. Hayes in Felsing, 1965). Feder and Paul (1973) and R. Nickerson (Alaska Department of Fish and Game, pers. comm.) suggested that a small clam fishery is feasible in Prince William Sound since paralytic shellfish poison (P.S.P.) does not seem to be a problem there, and many beaches with sizable populations of *P. staminea* from beaches near Victoria, British Columbia, occur in the area.

Considering the extensive distribution of the littleneck clam along the Pacific coast of North America, few papers on the basic biology of the species are available. The most extensive paper is that of Fraser and Smith (1928) which

provides information on size at age, sex ratios, size at maturity, and time of spawning for *P. staminea* from beaches near Victoria, British Columbia. Smith (1928) compared the different types of normally available food and the effects of these food types on growth rates of *P. staminea*. The only paper providing detailed information on reproduction of *P. staminea* is that of Quayle (1943) for clams of Ladysmith Harbour, British Columbia. General, but brief reviews of the species are included in Marriage (1954) for Oregon, Fitch (1953) primarily for California, and Amos (1966) for the entire range of the species. Toxicity of *P. staminea* from P.S.P. is considered by Felsing (1965) and Quayle (1967, 1969). No intensive work on littleneck clams from Alaskan waters is available.

The major purpose of this investigation was to study age and growth of *P. staminea* in Galena Bay, Prince William Sound, Alaska. The material collected also provided information on recruitment, distribution, and abundance of *P. staminea*. This project was conducted with funds provided by the University of Alaska's Sea Grant Program for a study of

<sup>1</sup> Institute of Marine Science and College of Biological Sciences, University of Alaska, Fairbanks, AK 99701.

shellfishes in Prince William Sound, Alaska (Grant No. 1-36109).

## METHODS

Field work was accomplished from June 1971 through October 1971 in Galena Bay, a small embayment in the northeastern portion of Prince William Sound (lat.  $60^{\circ}58'N$ , long.  $146^{\circ}44'W$ ), 20 miles from the town of Valdez. Two gravel beaches and one mud flat were sampled on the north side of Galena Bay (Figure 1); all were completely covered by water at the highest spring tides. The major features of the study sites are summarized in Table 1 and Figure 2.

The weather conditions in the study area were, in general, typical of south-central Alaska with overcast skies and considerable precipitation. Summer air temperatures were generally

on the order of  $7.5^{\circ}$  to  $10^{\circ}C$  (also see Searby, 1969). Longshore surface-water temperatures in Galena Bay ranged from  $8^{\circ}$  to  $18.2^{\circ}C$  during the study period. No extended winter water temperatures are available for Galena Bay; however, we observed the freezing of shallow tidal pools in Galena Bay in January 1973 (Feder and Paul, unpubl. data). The National Ocean Survey (1970) recorded mean surface-water temperatures in the Cordova region (approximately 60 miles from Galena Bay) as a minimum of  $2^{\circ}C$  in February and a maximum of  $11^{\circ}C$  in August. Beach-surface temperatures during the study period ranged from  $9^{\circ}C$  in October to  $32^{\circ}C$  in July with the latter value  $15^{\circ}C$  higher than longshore seawater temperatures measured at the same time.

Sampling was accomplished by transecting; the actual positions of the transects on the beaches were arbitrarily selected. Collections

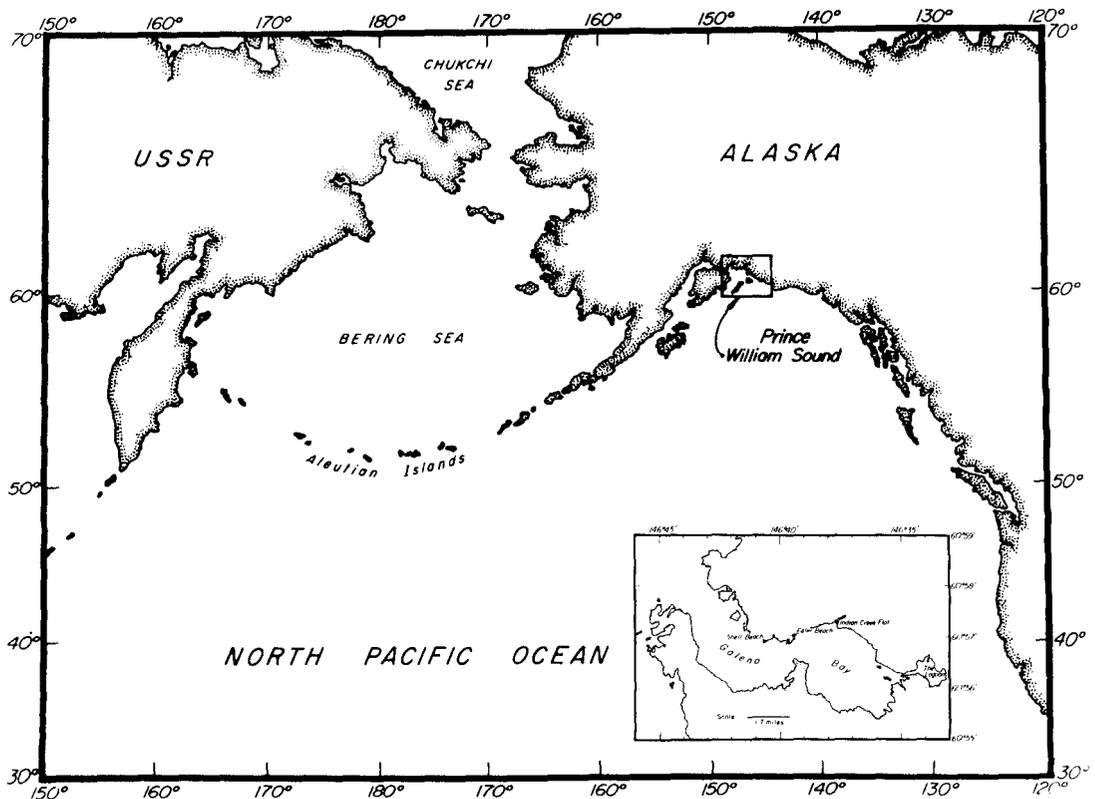


FIGURE 1.—Galena Bay, Prince William Sound, Alaska. The study area for the investigation.

TABLE 1.—A description of the three study areas in Galena Bay, Prince William Sound. Description of the beach and its biota refers to appearance at low water.

Item	Shell Beach	Eater Beach	Indian Creek Flat
Wave and wind exposure	Most exposed	Well protected	Protected but exposed to occasional rain squalls
Longshore currents	Obvious	Not obvious	Not obvious
Study area: Size (feet) (m)	190 × 70 57.6 × 21.2	220 × 100 66.7 × 30.3	900 × 900 272.7 × 272.7
Slope	6°47'	6°3'	0°21'
Substratum	Fine gravel for first few centimeters overlying fine sediment	Fine gravel intermingled with large rocks scattered over beach; fine sediment closer to surface than on Shell Beach	Mixture of gravel and fine sediment
Freshwater drainage	Minimal	Typically minimal; strong outwash after persistent rains dissects center of beach	Located at mouth of permanent stream; flat; dissected by numerous tributaries
Flora and fauna	No <i>Fucus</i> ; no <i>Mytilus edulis</i> ; <i>Balanus</i> spp. very sparse	Light cover of <i>Fucus</i> ; moderate cover of <i>M. edulis</i> ; <i>Balanus</i> cover over entire beach	Light cover of <i>Fucus</i> at upper edge; moderate cover of <i>M. edulis</i> ; moderate cover of <i>Balanus</i> .

from each transect were made from a series of stations, with each station defined by a 0.25-m<sup>2</sup> (115 × 22 cm) frame. The sediment within each station was sampled to a depth of 15 cm. The first collection made along a transect (Station 1) was positioned 1 m up the beach from the location of the first *P. staminea* encountered in a preliminary trench dug directly adjacent to the proposed sampling transect. The number of stations on a transect was dependent on the width and slope of the beach and the tidal range at the time of collection. On the two gravel beaches all stations sampled were contiguous; however, on the mud flat, a much larger area was involved, and collections here were made at 5.75-m intervals.

Utilizing reference points from a standard tide table (U.S. Coast and Geodetic Survey, 1970), a hand level, and a stadia rod, the tidal heights were determined for the midpoint of each station.

Prior to sampling, distribution of *P. staminea* was determined by removing sediment in 2-cm layers to a depth of 8 cm from selected plots (36 × 15 cm) along each transect. Samples collected were examined in the laboratory under a 2× lens for the presence of *P. staminea*, and sediments from these samples were then used for sieve analysis of grain-size distribution (Morgans, 1956).

Vertical distribution studies indicated that most of the smaller *P. staminea* (1.5 to 20 mm in length) were restricted to the upper 2 cm of sediment; thus, sampling was accomplished in two steps at each transect station. The young clams were collected with the upper 2 cm of sediment; the larger clams were collected with the remaining sediment.

Each surface sample was washed through a series of screens, the smallest mesh being 1.5- × 1.5-mm window screening. Screens of 3.5- and 6.5-mm<sup>2</sup> mesh were used for washing deep samples. Seawater used for the washing process was furnished by a portable Homelite Pump (Model XL5).<sup>2</sup> The sediment trapped in the finest screen was returned to the laboratory and examined for small individuals with a 2× lens.

Standard measurements taken on all clams were greatest length and height (width) (see Fraser and Smith, 1928 for details on measurement technique). In an older *P. staminea* an increase in shell height is often apparent when the increase in shell length is so small that it is difficult to measure. Therefore, shell height is the most sensitive measurement for describing

<sup>2</sup> Reference to trade names does not imply endorsement by the National Marine Fisheries Service.

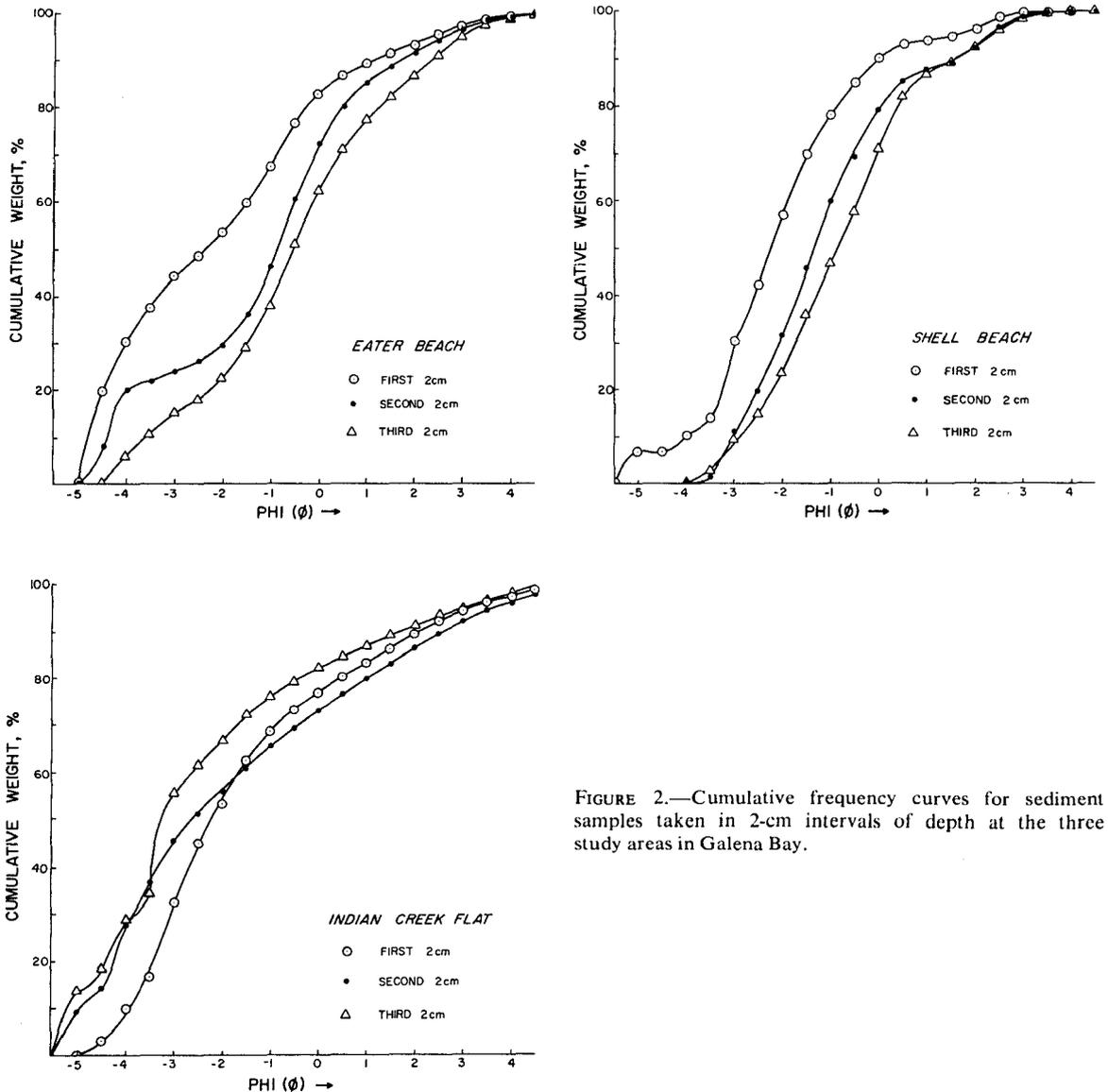


FIGURE 2.—Cumulative frequency curves for sediment samples taken in 2-cm intervals of depth at the three study areas in Galena Bay.

the growth of these clams. In this paper length data is included for comparative purposes.

Age was estimated for all clams less than 20 mm in length utilizing the annular method (Weymouth, 1923). All the larger clams from Shell Beach, one station on Eater Beach, and one station on Indian Creek Flat were also aged. In the aging procedure the distance between annuli<sup>3</sup> was measured along the radial sculpture line that originated at the approxi-

mate center of the umbonal region and roughly bisected the ventral margin of the shell (Figure 3).

BIOMED programs BMD01D, BMD05D, and BMD01V were adapted for this investigation (Dixon, 1965), and data were processed

<sup>3</sup> Annulus-A series of closely spaced concentric growth rings; the result of slow growth at low winter temperatures.

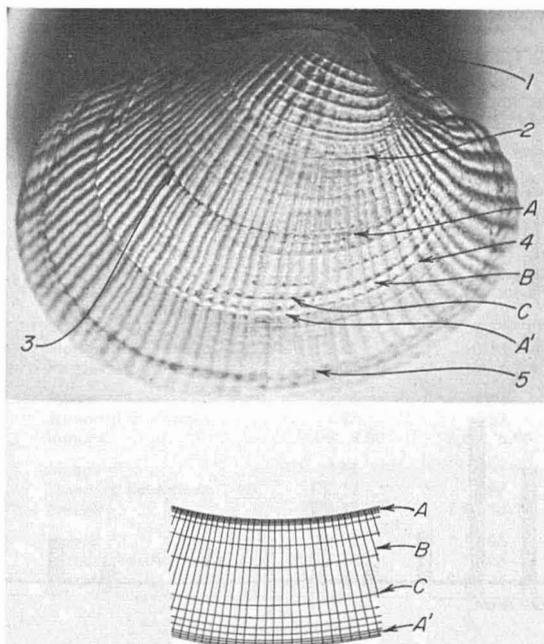


FIGURE 3.—The use of shell sculpture as a means of aging *Protothaca staminea*. Above: Photograph of a 5-yr-old *P. staminea* illustrating shell sculpture. Below: Graphic illustration of the shell sculpture between two annuli. A = annulus (winter growth). B = radial sculpture line. C = concentric growth line. A' = annulus. A to C = increasing distances between concentric growth lines C to A' = decreasing distances between concentric growth lines during late summer and fall growth. 1, 2, 3, 4, and 5 = successive annuli. Clam length = 11 mm.

with an IBM 360 Computer. Several additional programs were designed to arrange and plot the data. A one-way analysis of variance was used to test the accuracy of the annular aging technique.

## RESULTS

### Aging

Annuli on valves less than 20 mm in length were quite distinct. False checks<sup>4</sup> which super-

<sup>4</sup> False checks are series of concentric growth rings, resembling annuli, formed in spring and summer when growth is normally most active. These checks are also termed disturbance checks.

ficially resemble annuli (see first section under Discussion for comments), although present, could be readily distinguished from true annuli. Although false checks and shell abrasion made aging more difficult for clams greater than 20 mm in length, specimens from all three study sites were aged. The oldest clam collected in Galena Bay was 15 yr old with a length of 47.6 mm.

The validity of the annular aging method was examined with a standard one-way analysis of variance, utilizing the individual shell heights within each age class from Shell Beach as a basis for comparison (Snedecor, 1956). The calculated  $F$  ratio indicates that, in general, age classes, as defined by shell heights, are statistically distinguishable ( $P = 0.01$ ;  $N = 368$ ). Similar data plotted for Eater Beach further indicate the integrity of the aging method used (Figure 4). In addition, annuli for 3 yr of growth have been validated by the recovery and subsequent examination of over 100 marked *P. staminea* from Galena Bay (Feder and Paul, unpubl. data).

Histograms plotting size and age indicate that age classes form fairly distinct but overlapping groups (Figure 5).

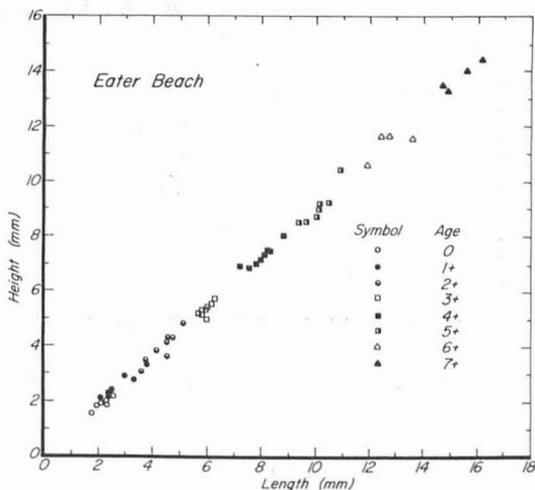


FIGURE 4.—Average length and height plotted as a function of age for specimens collected on the Eater Beach transect, Galena Bay. Each point represents a mean value for specimens of a given age group collected at a single station.

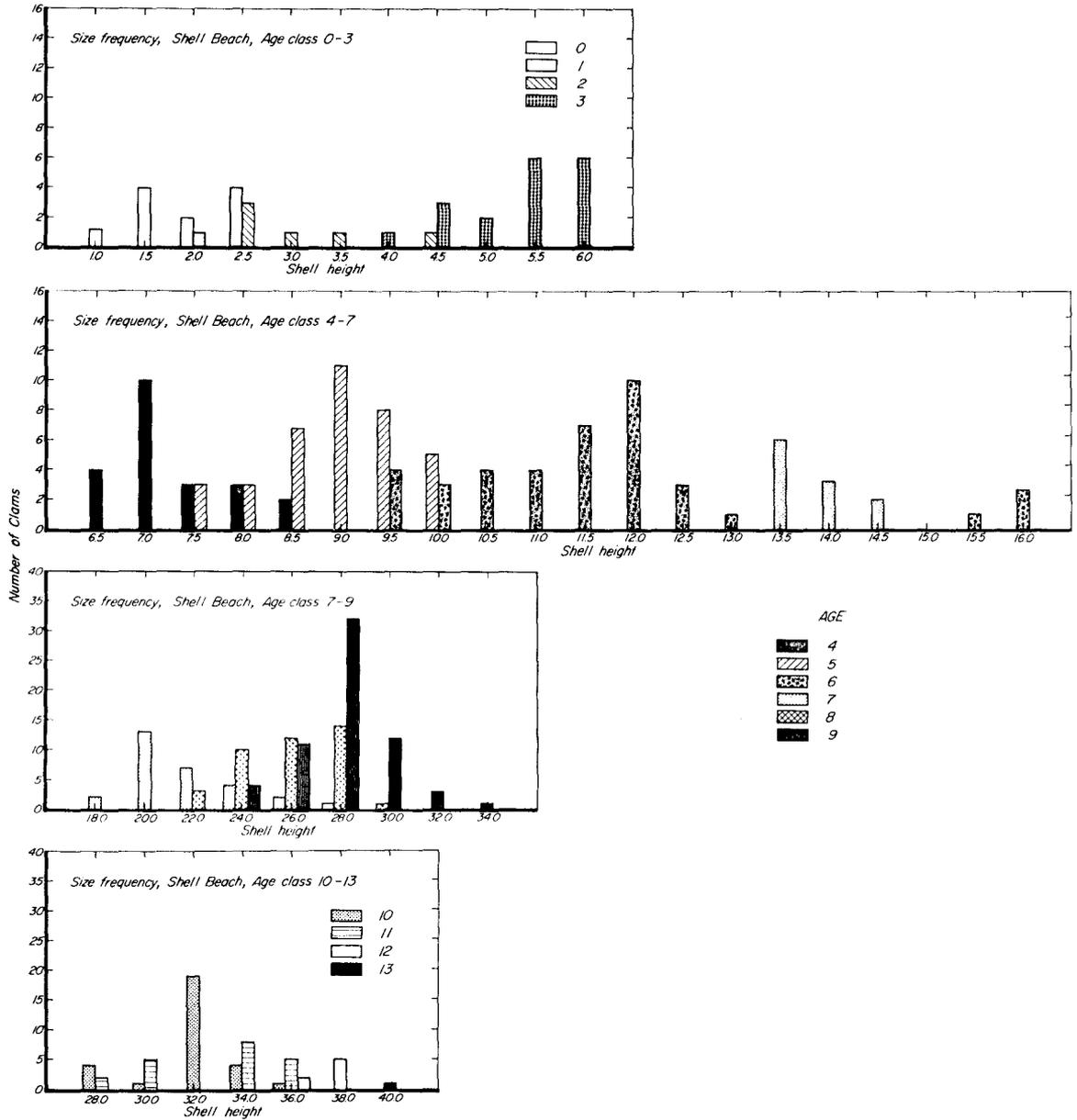


FIGURE 5.—Size distribution of annular age classes of *Protothaca staminea* from Shell Beach, Galena Bay.

### Growth

The littleneck clams in Galena Bay (Table 2) at a given age are smaller than those collected by Fraser and Smith (1928) in British Columbia (Table 3). The annual increase in shell length

for the various size classes in Galena Bay is typically 2 to 5 mm. As a result, 8 to 9 yr are needed for *P. staminea* to reach a length of 30 mm, the minimum size generally harvested in the sport fishery in Prince William Sound (J. Van Hyning, Wildlife Department, Univer-

TABLE 2.—Average size at age of littleneck clams from Shell Beach ( $N = 368$ ).

Age (yr)	Item	Length (mm)	Height (mm)	Age (yr)	Item	Length (mm)	Height (mm)
0	Means	2.06	1.84	7	Means	21.56	18.63
	Standard deviations	0.37	0.28		Standard deviations	5.04	3.99
	Ranges	1.60- 2.60	1.50- 2.30		Ranges	14.50-37.20	12.50-32.60
1	Means	2.88	2.68	8	Means	28.84	25.70
	Standard deviations	0.40	0.33		Standard deviations	4.52	4.07
	Ranges	2.20- 3.20	2.10- 2.90		Ranges	15.00-36.00	12.90-30.90
2	Means	3.78	3.35	9	Means	32.68	29.06
	Standard deviations	0.90	0.70		Standard deviations	1.99	1.96
	Ranges	2.90- 5.10	2.70- 4.60		Ranges	27.80-38.50	24.50-34.30
3	Means	6.53	5.63	10	Means	36.44	32.59
	Standard deviations	1.59	0.73		Standard deviations	1.89	1.83
	Ranges	4.40- 7.30	4.10- 6.50		Ranges	32.00-39.70	28.90-37.90
4	Means	8.10	7.54	11	Means	37.19	34.74
	Standard deviations	1.97	0.63		Standard deviations	8.09	2.25
	Ranges	7.00- 9.80	6.60- 8.90		Ranges	33.00-46.00	29.30-37.30
5	Means	10.95	9.71	12	Means	42.08	37.68
	Standard deviations	2.13	1.87		Standard deviations	2.52	1.69
	Ranges	9.00-18.90	7.60-16.30		Ranges	37.80-45.50	34.50-39.90
6	Means	14.70	12.86				
	Standard deviations	3.74	3.26				
	Ranges	19.90-29.30	9.60-26.00				

TABLE 3.—Length in millimeters at end of each year for clams collected in Victoria, British Columbia (based on Fraser and Smith, 1928).

		Year									
	1	2	3	4	5	6	7	8	9	10	
12.6	25.4	35.3	43.1	48.2	52.7	54.6	55.9				
12.9	23.2	33.4	39.9	44.3	46.3	49.4	52.3	53.8			
13.0	25.7	37.0	44.0	48.0							
13.9	25.7	27.5	43.6	48.7	54.1						
13.9	28.2	38.6	48.3								
—	—	—	—	—	—	—	—	—	—	—	
15.7	27.4	37.2	44.2	49.0	52.8	55.8					
13.2	24.8	35.3	42.9								
11.8	30.0										
13.5	25.8	34.9	41.4	46.3	50.0	52.6	55.8	58.9			
12.6	23.6	30.6	36.2	40.9	44.2	47.4	48.7	49.9			
12.2	22.9	33.5	41.7	47.7	51.8	55.7	57.8	59.1			
13.4	25.9	35.7	42.9	48.5	52.5						
14.0	24.5	33.6	38.7	43.2	45.9	48.0	49.5	51.3	53.8		
25.4	34.2	39.3	43.2	47.1							
13.4	25.2	32.5	38.8	43.6	46.1	50.3	52.6				
12.2	24.5	35.1	42.8	48.9	54.1	57.8	60.7				
13.1	26.3	37.0	45.6	50.6	54.6	57.7	60.3	62.2	63.4		
12.4	23.0	31.6	38.3	42.9	46.4	49.0	50.1	53.6			
11.2	25.4	35.4	44.4	51.1	54.3						
11.3	22.1	31.3	37.3	42.1	45.8	48.8					
11.2	22.0	31.3	38.6	43.6	46.8	49.9	51.1				
12.7	27.4	36.0	42.4	47.2	50.0	52.0					
14.8	28.4	36.6	42.9	47.8	52.0	54.5					
13.3	26.9	37.2	44.1	47.5	49.7						
13.1	29.5	40.2	47.3	52.0	57.3	59.5					
13.4	24.7	33.7	40.0	44.7	48.4						
11.1	26.5	36.0	43.4	49.4	52.9	55.7					
13.6	28.4	38.6	45.8	50.9	54.2	57.3	58.7				
14.6	30.8	41.5	48.8	54.1	57.0	59.9					
17.0	32.7	44.4	50.6	54.9							
12.5	22.9	32.6	40.0	45.2	49.3	57.0					

sity of Alaska, pers. comm.; Feder and Paul, 1973).

A comparison of growth rates in the three study areas indicates that differences in length at age are less than 2 mm by the end of the sixth year (Figure 6). In older clams the difference in growth rates between individuals from the three study sites is more pronounced. The annual increase in size for individuals 6 to 12 yr of age was generally greatest on Shell Beach, and by age 12 specimens from this beach were, on the average, 12 mm longer than those from Eater Beach and 9.5 mm longer than specimens from the Indian Creek Mudflat.

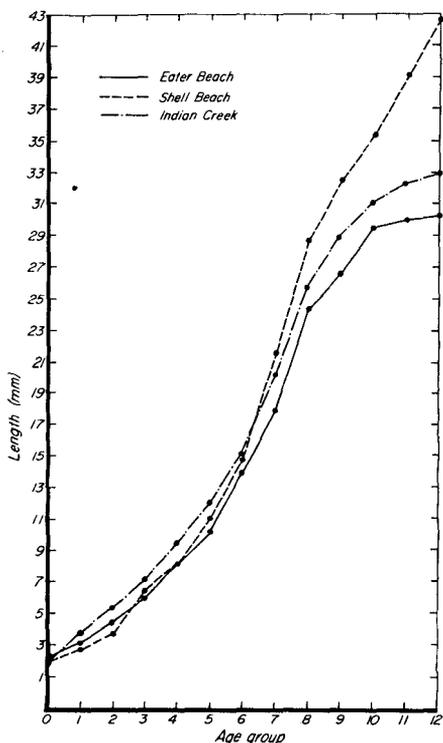


FIGURE 6.—Cumulative growth in shell length for clams from Shell ( $N = 368$ ) and Eater Beaches ( $N = 554$ ) and Indian Creek Flat ( $N = 642$ ). Plotted points represent mean values.

### Recruitment and Distribution

The number of recruits surviving in a littleneck clam population varies considerably from year to year. This is indicated in Figures 7

and 8 where the number of clams surviving as a function of year of settlement are plotted. On the beaches examined, individuals of the 1966, 1967, and 1968 year classes are more abundant than those of the 1970 or 1971 year classes, even after surviving 3 to 5 yr of natural mortality. It is also evident that the 1964 year class, which represented the newest recruits to the sport fishery in 1971, was not very abundant.

The total number of young littleneck clams found on the Eater Beach transect (352 clams on a 12-station transect) as compared with the number found on the Indian Creek transect (528 clams on a 10-station transect) indicates

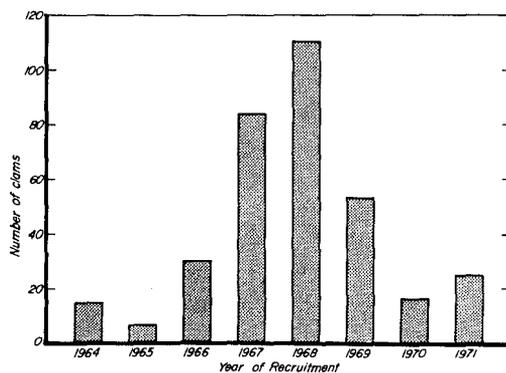


FIGURE 7.—Abundance of clams 0 to 7 yr of age on a 12-station transect from Eater Beach, Galena Bay.

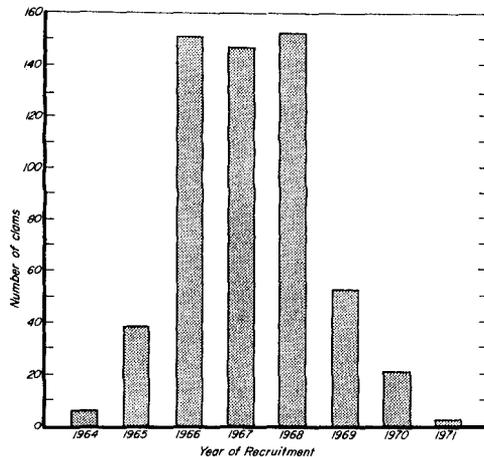


FIGURE 8.—Abundance of clams 0 to 7 yr of age on a 10-station transect from Indian Creek Flat, Galena Bay.

a greater density of young littleneck clams per unit area on the latter site. On the other hand, a comparison of the average number of older *P. staminea* per 0.25-m<sup>2</sup> station along these same transects reveals 55 littleneck clams per station on Eater Beach and 25 per station on the mud flat.

The intertidal distribution of *P. staminea* is influenced by tidal height; Figure 9 provides a general picture of the intertidal distribution of two size groups of *P. staminea* in Galena Bay. The distribution and frequency of age classes 0<sup>5</sup> through 6 for different tidal heights along one transect on Eater Beach are shown in Figure 10.

The intertidal distribution of *P. staminea* in Galena Bay in 1971 was similar to that reported for pre-earthquake Kodiak Island (Nybakken, 1969) and pre-earthquake Olsen

<sup>5</sup> The term 0 age group refers to those individuals of the settling year class that have undergone only one growing season (5 to 6 mo) before forming their first winter annulus. Thus, individuals referred to as 1 yr of age are actually 17 or 18 mo old and have lived through two growing seasons.

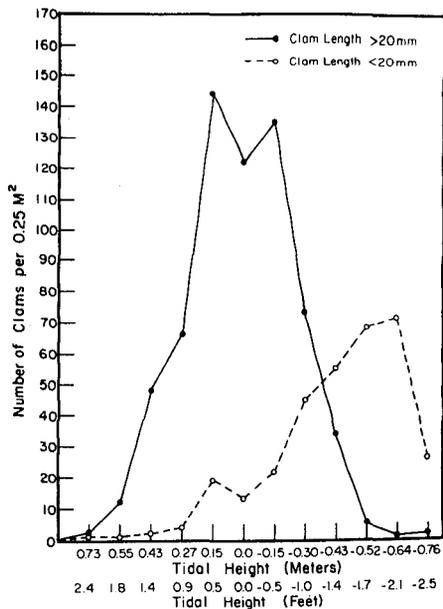


FIGURE 9.—An example of the typical intertidal distribution of *Protothaca staminea* as observed in Galena Bay. Data plotted here is from Eater Beach. Clams less than 20 mm in length are primarily ages 0-7; those larger than 20 mm in length are mainly ages 8-12.

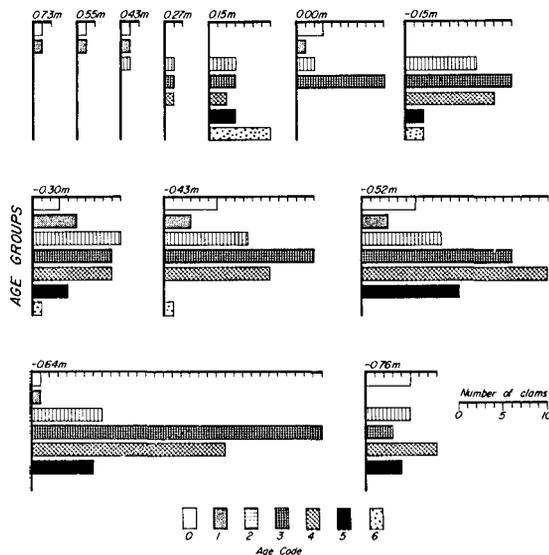


FIGURE 10.—The horizontal distribution of *Protothaca staminea*, age groups 0-6, grouped according to tidal height. Specimens were collected on Eater Beach, Galena Bay. Numbers above each plot refer to tidal height.

Bay (Hubbard, 1971), with the upper and lower extremes of this distribution occurring between the tidal heights of + 0.73 and -0.76 m, respectively. On the three study beaches the maximum density for clams larger than 20 mm in length, primarily individuals 8 to 12 yr of age, occurred between the tidal heights of +0.43 and -0.43 m, while the greatest density for smaller individuals occurred between -0.43 and -0.64 m (Figure 9).

The maximum depth in the sediment at which *P. staminea* was observed in Galena Bay was 8 cm. Clams of ages 0 through 7 consistently occurred in the upper 2 cm with most individuals of all age groups within 4 cm of the surface. Clams as large as 10 mm in length were often clearly visible between or just under small rocks. There was no apparent difference in vertical distribution of *P. staminea* on the gravel beaches or the mud flat.

## DISCUSSION

### Aging

Aging by the annular method is a time-consuming process best accomplished with a

dissection microscope. The patterns created by the radial sculpture and the concentric growth lines of the valves are invaluable aids for aging *P. staminea* by the annular method (Figure 3).

During the winter increase in shell size is negligible, and growth at the shell margin consists of a series of closely spaced concentric lines which form a winter annulus. Spring growth results in a progressively increasing distance between these lines; as summer progresses the distance between these lines gradually decreases until a new annulus is formed the following winter. True annuli extend from near the umbo anteriorly and merge with the hinge structure posteriorly. False checks may also appear as an aggregation of fine concentric lines; however, such checks generally fail to merge dorsally, and do not fit within the pattern of gradually increasing and decreasing distances between the concentric growth lines mentioned above.

Size-frequency distribution histograms cannot be used to accurately age *P. staminea* from Galena Bay (Figure 5). The individual differences in yearly growth within age groups, even when taken from a single 0.25-m<sup>2</sup> plot, result in a considerable overlap in size distribution. As a result, an aging error of 1 or 2 yr may occur if a clam were assigned an age based on size alone. Fraser and Smith (1928) found a similar disparity in the range of sizes within annular age groups for *P. staminea* from British Columbia, and Quayle (1952) reports that length-frequency distributions could not be used to determine age groups for *Venerupis pullastra* in Scotland.

### Growth

Our study indicates that *P. staminea* grows much more slowly in Galena Bay, Prince William Sound, than in British Columbia (Fraser and Smith, 1928). The average length for *P. staminea* at the end of its first year in Galena Bay is approximately 2 mm (Table 2, Figure 6) while in British Columbia it is approximately 12 mm (Table 3). Slow growth in Alaskan waters is probably the result of severe winter conditions which reduces clam-feeding

activities at this time. The adverse effect of low-water temperatures on growth rate has been reported for a number of bivalve molluscs including *Pinctada martensii* (Kobayashi and Watabe, 1959), *Crassostrea virginica* (Loosanoff, 1958), *Mytilus edulis* and *Mercenaria mercenaria* (Pratt and Campbell, 1956).

Both Fraser and Smith (1928) and Smith (1928), working in Canadian waters, observed that the most favorable growth occurred on beaches near strong tidal currents while poor growth took place on beaches at the heads of quiet bays. An examination of older specimens of *P. staminea* from Galena Bay supports this observation (Feder, unpubl. data). The cumulative growth curve (shell length) for littleneck clams from Shell Beach is nearly a linear expression (Figure 6). This beach, the most exposed study site, is subject to strong tidal currents (Table 1). On the other hand, cumulative growth plots for Eater Beach and Indian Creek Flat, protected locations with little current or wave action, provide more standard growth curves which become asymptotic at about age 10 (Figure 6).

### Recruitment and Distribution

The differences in year-class strength of *P. staminea* noted in Galena Bay (Figures 7, 8) have also been observed for other bivalve species, e.g., *Saxidomus giganteus* (Fraser and Smith, 1928), *Cardium edule* (Hancock, 1970), and *Venerupis pullastra* (Quayle, 1952). There are a number of interrelated factors affecting larval production in bivalve molluscs, but in general the most important ones appear to be the number and physical condition of mature females and the temperature requirements necessary for the liberation of the larvae (Hancock, 1970). Survival of larvae in the plankton and successful settlement are also affected by several environmental conditions, especially temperature, adequate food supply, predation, and favorable conditions for settlement (Thorson, 1966, 1971; Christensen, 1970; Hancock, 1970). Data on most of these conditions are not available for *P. staminea* in Prince William Sound.

Hancock (1970) working in England noted

that the number of 0-age group cockles (*C. edule*) appeared to be poorly correlated with abundance of spawning stock. He also observed that poor to moderate settlements followed years of good to exceptional recruitment. If larval production and settlement of *P. staminea* is affected by year-class densities in a similar manner, it is possible that the strong year classes of 1966, 1967, and 1968 are responsible for the moderate to poor recruitment observed in Galena Bay during the following years (Figures 7, 8).

*P. staminea* does not move horizontally (Feder and Paul, unpubl. data); therefore, the only source of recruitment of this species to an area is the annual settlement of veligers. Thus, the large number of clams 20 mm in length and longer that are found between the tidal heights of +0.43 and -0.43 m must be the result of relatively good survival of these larvae (Figure 9).

Very few littleneck clams were located above the tidal height of +0.43 m (Figure 9); the number of clams observed is probably the result of environmental stresses which act on young clams at the upper, more frequently exposed portions of a beach. The 2-foot uplift of land in Galena Bay following the Alaska Earthquake in March 1964 (National Research Council, 1971) may have affected settlement and/or survival of clams at the upper limits of their intertidal distribution during that year (Figures 7, 8). The time of the year for settlement of *P. staminea* veligers in Prince William Sound is not known.

Strong tidal currents may affect the numbers of settling veligers in the intertidal zone (Fraser and Smith, 1928). On Shell Beach, the study site with the strongest currents (Table 1), the number of clams under 5 yr of age (seven clams per 0.25 m<sup>2</sup>) was consistently lower than that found on the Indian Creek Mudflat (23 clams per 0.25 m<sup>2</sup>) where the shore was relatively undisturbed by wave action and currents.

On most beaches and flats of Prince William Sound, there are many temporary and permanent streams fed by rain, melting snow, and glacial ice. *P. staminea* is rarely encountered in areas where permanent freshwater streams flow over or percolate through beach sediments

at low tide (Feder and Paul, unpubl. data). Mortality resulting from rainfall on exposed beaches is negligible; however, heavy rainfall affects distribution of *P. staminea* by altering beach topography. Freshwater runoff after a period of prolonged rainfall is often responsible for the active transport of beach sediments; in such areas clams are washed away with these sediments (Feder and Paul, unpubl. data).

Throughout its range *P. staminea* is found within 15 cm of the sediment surface and occasionally at the surface (Amos, 1966). In areas of Prince William Sound examined by us, clams 0 through 4 yr of age are essentially epifaunal in their distribution while older individuals are subsurface dwellers. Siphon length is almost certainly the limiting factor in determining the depth at which various sizes of clams occur. Sieve analysis of sediment from Eater and Shell Beaches shows that coarse gravel at the beach surface covers medium gravel and finer sediment (Figure 2). The geology of such gravel beaches affords young *P. staminea* protection from predation, exposure, and ice scouring by providing spaces between the gravels in which the clams can lodge themselves. These spaces, filled with water at high tide, provide a haven for young clams. Here they can remain and feed below the level of the beach surface at a depth greater than their siphon length. On the Indian Creek Flat, sediment fills the intergravel spaces (Figure 2), thereby forcing young *P. staminea* to remain closer to the surface for longer periods of time than if they had settled on a gravel beach. Clams on mud flats such as Indian Creek are then more vulnerable when young, and this may, in part, explain better survival of clams on gravel beaches.

In Galena Bay few individuals that settle between the tidal heights of -0.43 and -0.76 m survive beyond their fourth year, despite the fact that it is here that the heaviest concentrations of young clams occur (Figure 10). This distribution may be the result of selective settlement by veliger larvae (Thorson, 1957, 1966), hydrographic concentrations of larvae in the plankton at time of settlement (see Ryther, 1968 for discussion), or some form of selective mortality such as predation (see

Newcombe, 1935; Paine, 1969, 1971; Feder, 1970; Birkeland and Chia, 1971 for discussion).

## SUMMARY AND GENERAL COMMENTS

The results of this paper provide information on growth rates of *P. staminea* in northeastern Prince William Sound, Alaska. Growth rates for this species in Galena Bay are considerably less than those reported for British Columbia (Fraser and Smith, 1928). *P. staminea* in Galena Bay reach a harvestable size (length = 30 mm) in 8 to 9 yr.

Examination of recruitment and distribution on three beaches studied suggests that the number of recruits entering and/or surviving recruitment on an annual basis in Prince William Sound is extremely variable. On each of the beaches examined, recruitment was at its maximum between the tidal heights of -0.43 and -0.64 m while survival was best between the tidal heights of +0.43 and -0.43 m. The majority of *P. staminea* were found within 4 cm of the sediment surface.

Based on the large number of beaches in Prince William Sound having populations of littleneck clams, this species undoubtedly represents a potential, although probably limited fishery resource in Prince William Sound (R. Nickerson, pers. comm.; Feder and Paul, 1973). Since the variable recruitment and slow growth rates observed for Galena Bay appear to apply throughout Prince William Sound (Feder and Paul, unpubl. data), such a fishery would probably require that beaches be harvested on an 8- to 10-yr rotational basis.

The large port facility proposed for Valdez to receive crude oil from Prudhoe Bay, Alaska will undoubtedly result in some degree of oil contamination as a result of accidental spillages, ballast treatment, and shipboard operations (Arthur, 1968; Dudley, 1968; Nelson-Smith, 1970; Blumer, 1971; U.S. Department of the Interior, 1972:64). Therefore, beyond its potential as a commercially harvestable species, *P. staminea* may have additional value as an indicator of environmental change since this clam is the only intertidal invertebrate whose natural history has been examined in detail

in Prince William Sound.

## ACKNOWLEDGMENTS

We would like to thank R. T. Cooney (University of Alaska) for valuable advice; Rosemary Hobson (Institute of Marine Science, University of Alaska) for invaluable advice on computer programming techniques; Shirley Wilson (Institute of Marine Science, University of Alaska) for drafting all the figures; Richard B. Nickerson (Alaska Department of Fish and Game) for discussions and for use of an Alaska Department of Fish and Game boat; Carol Anderson, George Perkins, David Roseneau, and Frederick Smith for technical assistance.

## LITERATURE CITED

- AMOS, M. H.  
1966. Commercial clams of the North American Pacific Coast. U.S. Fish Wildl. Serv. Circ. 237, 18 p.
- ARTHUR, D. R.  
1968. The biological problems of littoral pollution by oil and emulsifiers—a summing up. In J. D. Carthy and D. R. Arthur (Editors), Biological effects of oil pollution on littoral communities, p. 159-164. (Proc. Symp. held at Orieltor Field Center, Pembroke, Wales, 17-19 February 1968.) Field Studies Council, Lond.
- BIRKELAND, C., AND F. S. CHIA.  
1971. Recruitment risk, growth, age and predation in two populations of sand dollars, *Dendraster excentricus* (Escholtz). J. Exp. Mar. Biol. Ecol. 6:265-278.
- BLUMER, M.  
1971. Scientific aspects of the oil spill problem. Environ. Aff. 1:54-73.
- CHRISTENSEN, A. M.  
1970. Feeding biology of the sea star *Astropecten irregularis* Pennant. Ophelia 8:1-134.
- DIXON, W. J. (editor).  
1964. BMD biomedical computer programs. Health Sciences Computing Facility, Dep. Preventive Medicine and Public Health School of Medicine, Univ. Calif., Los Ang., 585 p.
- DUDLEY, C. G.  
1968. The problem of oil pollution in a major oil port. In J. D. Carthy and D. R. Arthur (editors), Biological effects of oil pollution on littoral communities, p. 21-29. (Proc. Symp. held at Orieltor Field Center, Pembroke, Wales, 17-19 February 1968.) Field Studies Council, Lond.
- FEDER, H. M.  
1970. Growth and predation by the ochre sea star,

PAUL and FEDER: LITTLENECK CLAM IN GALENA BAY

- Pisaster ochraceus* (Brandt), in Monterey Bay, California. *Ophelia* 8:161-185.
- FEDER, H. M., AND A. J. PAUL.  
1973. The littleneck clam, *Protothaca staminea*, a potential fishery resource in Prince William Sound, Alaska. 23d Alaska Sci. Conf., p. 46.
- FELSING, W. A., JR.  
1965. Proceedings of joint sanitation seminar on North Pacific clams. Alaska Dep. Health and Welfare; U.S. Public Health Serv., 34 p.
- FITCH, J. E.  
1953. Common marine bivalves of California. Calif. Dep. Fish Game, Fish Bull. 90, 102 p.
- FRASER, C. M., AND G. M. SMITH.  
1928. Notes on the ecology of littleneck clam, *Paphia staminea* Conrad. Trans. R. Soc. Can., Ser. 3, 22, Sect. V:249-269.
- HANCOCK, D. A.  
1970. The relationship between stock and recruitment in exploited invertebrates. Int. Counc. Explor. Sea. C. M. 1970 Symposium on "Stock and Recruitment" 34, 28 p.
- HUBBARD, J. D.  
1971. Distribution and abundance of intertidal invertebrates at Olsen Bay in Prince William Sound, Alaska, one year after the 1964 earthquake. In *The great Alaska earthquake of 1964. Biology*, p. 137-157. Natl. Acad. Sci., Wash., D.C.
- KOBAYASHI, S., AND N. WATABE  
1959. *The Study of Pearls*. Gihodo Press, Tokyo, 280 p.
- LOOSANOFF, V. L.  
1958. Some aspects of behavior of oysters at different temperatures. Biol. Bull. (Woods Hole) 114:57-70.
- MARRIAGE, L. D.  
1954. The bay clams of Oregon, their economic importance, relative abundance, and general distribution. Fish Comm. Oreg., Contrib. 20, 47 p.
- MORGANS, J. F. C.  
1956. Notes on the analysis of shallow-water soft substrata. J. Anim. Ecol. 25:367-387.
- NATIONAL OCEAN SURVEY.  
1970. Surface water temperature and density. Pacific coast, North and South America & Pacific Ocean islands. NOS Publ. 31-3. 3d ed., 88 p.
- NATIONAL RESEARCH COUNCIL.  
1971. The great Alaska earthquake of 1964. Biology. Natl. Acad. Sci., Wash., D.C., 287 p.
- NELSON-SMITH, A.  
1970. The problem of oil pollution of the sea. Adv. Mar. Biol. 8:215-306.
- NEWCOMBE, C. L.  
1935. A study of the community relationships of the sea mussel. Ecology 16:234-243.
- NYBAKKEN, J. W.  
1969. Pre-earthquake intertidal ecology of Three Saints Bay, Kodiak Island, Alaska. Biol. Pap. Univ. Alaska 9, 115 p.
- PAINE, R. T.  
1969. The *Pisaster-Tegula* interaction: prey patches, predator food preference, and intertidal community structure. Ecology 50:950-961.
1971. A short-term experimental investigation of resource partitioning in a New Zealand rocky intertidal habitat. Ecology 52:1096-1106.
- PRATT, D. M., AND D. A. CAMPBELL.  
1956. Environmental factors affecting growth in *Venus mercenaria*. Limnol. Oceanogr. 1:2-17.
- QUAYLE, D. B.  
1943. Sex, gonad development and seasonal gonad changes in *Paphia staminea* Conrad. J. Fish. Res. Board Can. 6:140-151.
1952. The rate of growth of *Venerupis pullastra* (Montagu) at Millport, Scotland. Proc. R. Soc. Edinb. Sect. B Biol. 64:384-406.
1967. Paralytic shellfish poisoning—safe shellfish. Fish. Res. Board Can., Biol. Stn., Nanaimo, B.C., Can., Gen. Ser. Circ. 75, 9 p. (1966).
1969. Paralytic shellfish poisoning in British Columbia. Fish. Res. Board Can. Bull. 168, 68 p.
- RYTHER, J. H.  
1968. The status and potential of aquaculture. Volume I: Particularly invertebrate and algae culture, p. 104. Natl. Tech. Inf. Serv., U.S. Dep. Commer.
- SEARBY, H. W.  
1969. Coastal weather and marine data summary for Gulf of Alaska, Cape Spencer westward to Kodiak Island. ESSA (Environ. Sci. Serv. Adm.) Tech. Memo. EDSTM 8, 30 p.
- SMITH, G. M.  
1928. Food as a factor in growth rate of some Pacific clams. Trans. R. Soc. Can., Ser. 3(22), Sect. V:287-291.
- SNEDECOR, G. W.  
1956. *Statistical methods applied to experiments in agriculture and biology*. 5th ed. Iowa State Coll. Press, Ames, 534 p.
- THORSON, G.  
1957. Bottom communities (sublittoral or shallow shelf). In J. W. Hedgpeth (editor), *Treatise on marine ecology and paleoecology*, Vol. 1:461-534. Geol. Soc. Am., Mem. 67.
1966. Some factors influencing the recruitment and establishment of marine benthic communities. Neth. J. Sea Res. 3:267-293.
1971. *Life in the sea*. World University Library. McGraw-Hill, N.Y., 256 p.
- U.S. COAST AND GEODETIC SURVEY.  
1970. Tidal current tables 1971. Pacific coast of North America and Asia. 254 p.
- U.S. DEPARTMENT OF THE INTERIOR.  
1972. Final environmental impact statement proposed trans-Alaska pipeline. Vol. 1, 322 p.
- WEYMOUTH, FRANK W.  
1923. The life-history and growth of the Pismo clam (*Tivela stultorum* (Mawe)). Calif. Fish Game Comm., Fish Bull. 7, 120 p.