Abstract.–Northern shrimp *Pandalus borealis* carapace length-frequency data collected from shrimp surveys and commercial catches between 1972 and 1986 were studied to estimate age, growth, and mortality in Pavlof Bay, Alaska. Dominant size modes representing 1971 and 1975 year-classes were separated from carapace length-frequency distributions by the use of a maximum-likelihood separation technique. The growth rate for the 1975 year-class was significantly greater than that of the 1971 year-class. Because the abundance of the 1975 year-class was lower than that of the 1971 year-class, an inverse relationship of growth to year-class strength was suggested. Age-at-sex transition appears to be related to year-class abundance or overall density as 1975 year-class shrimp completed transition at a younger age than that of 1971. Increases in natural mortality occurred after the 1971 year-class completed transformation to the female sex at age 6.4, and may indicate a combination of spawning stress and senescence or increasing abundance of the predator, Pacific cod *Gadus macrocephalus*. Dynamic pool yield-per-recruit analysis indicated maximum biomass of year-classes was achieved at or prior to full recruitment to the survey and commercial fishing gear. Because mortality rates are high, yield-per-recruit is optimized by harvesting more of the smaller male shrimp.

Age, Growth, and Mortality of the Northern Shrimp *Pandalus borealis* Kröyer in Pavlof Bay, Alaska

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The Alaska Peninsula region of the western Gulf of Alaska was the site of one of the world's major shrimp fisheries in the 1970s (Anderson and Gaffney 1977). A significant decline in shrimp abundance starting in 1978 lead to the closure of most areas to fishing in 1979, and to date the fishery has yet to reopen. The cause of this decline and the failure of stocks to recover to fishable levels are obscured by a lack of information on the population dynamics of pandalid shrimps in the western Gulf of Alaska. In an effort to fill this information gap, I have estimated the age, growth, and mortality of two year-classes from a stock of northern shrimp *Pandalus borealis* Kröyer, the major commercial species in the region.

The Pavlof Bay (Fig. 1) stock of *P. borealis* was chosen for this study because it has supported a major fishery and an extensive database was available. The Bay was a major producer accounting for over 13,000 metric tons (t) of pandalid shrimp landings in 1977 alone. *Pandalus borealis* made up 11–97% of landings, with variable quantities of *P. goniurus*, *P. hypsinotus*, and *Pandalopsis dispar* making up the remainder. Pavlof Bay shrimp have been surveyed annually by the National Marine Fisheries Service (NMFS) since 1972. Data collected from these surveys include weight, number, and carapace length-frequencies by sex for *P. borealis*. The Alaska Depart-

ment of Fish and Game (ADF&G) has collected species and size-composition data from commercial landings since the beginning of the fishery in 1968.*

Pandalus borealis in Pavlof Bay are managed as a discrete stock by the ADF&G. Analysis of data from commercial catches and shrimp surveys conducted by NMFS and ADF&G suggest that migration between adjacent bays along the Alaska Peninsula is minimal (Jackson et al. 1983). Vertical migrations in concert with ocean currents may act as dispersal mechanisms for pandalids (Barr 1970, Pearcy 1970, Gotshall 1972). In Pavlof Bay, effects of ocean currents probably are minimized by barrier islands and shallow entrances that favor confinement and limit immigration (Fig. 1).

Since there are no known anatomical structures for ageing *P. borealis*, researchers have used length-frequency analysis to estimate age and growth. For example, Rasmussen (1953) used dominant year-class modes to interpret growth and sex transformation of *P. borealis* in Norwegian stocks, and Skúladóttir (1981) used the positive deviations from long-term length-frequency distributions to identify average lengths-at-age for *P. borealis* from Icelandic fjords.

Figure 1

Pavlof Bay, Alaska, sampling area showing 55 m isobath (dotted/dashed line) and approximate location of the 20 m isobath (dotted).
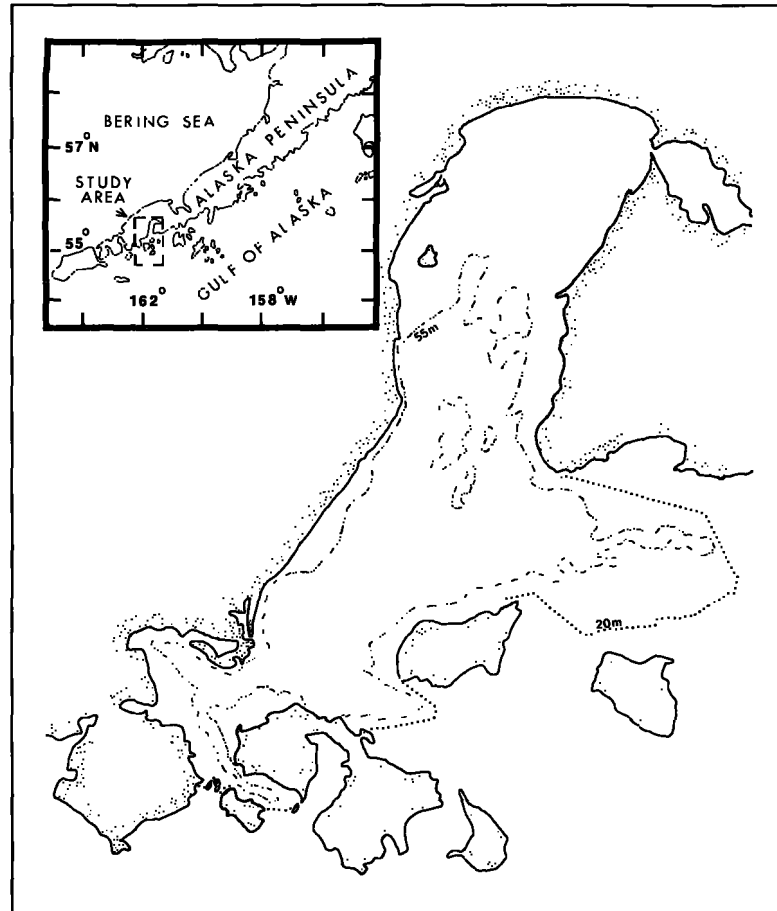
I have separated the dominant size modes representing year-classes from Pavlof Bay length-frequency distributions using the maximum-likelihood technique of Macdonald and Pitcher (1979). Annually, calculated mean lengths and numerical abundance of year-classes were then used to estimate growth and mortality using methods similar to those of Fréchette and LaBonté (1981) and Anderson (1981). The present study expands on previous work by using modal analysis of length-frequencies from commercial catches to estimate fishing and natural mortality rates. Results from these analyses were used to examine the yield-per-recruit function in relation to mortality and growth as well as year-class strength.

Materials and methods

Pavlof Bay was surveyed annually from 1972 to 1986 by trawling at randomly selected stations from August to mid-September (Table 1). During these months dense aggregations of *P. borealis* form in relatively deep water prior to mating and spawning. Earlier surveys had shown that shrimp concentrate in depths greater than 70 m (Ronholt 1963). Consequently, all survey tows were restricted to depths greater than 55 m (Fig. 1). Each year, except 1973, 10 to 13 randomly selected (with replacement) locations were chosen from a grid of the Bay's shrimp habitat divided into 22 stations ($\sim$13.7 km² each). Sampling was conducted with a 30-minute tow ($\sim$1.8 km) during daylight using a 32 mm mesh (32 mm mesh codend liner) high-opening shrimp trawl with an 18.6 m headrope and footrope (Wathne 1977). The mesh size and configuration of this trawl were similar to commercial fishing gear which allowed for direct comparison between survey and commercial data.

Carapace lengths (CL) were measured to the nearest 0.5 mm (eye socket to midposterior carapace edge) for approximately 300 specimens of *P. borealis* selected at random

Table 1

Biomass estimates and commercial landings (catch) of *Pandalus borealis* shrimp in Pavlof Bay, 1972-86 (metric tons with 80% confidence intervals for biomass; catches removed prior to next research survey).

Dates	No. tows	Biomass[1] (mt)		Catch[2] (mt)
7-10 Sep 1972	10	8,310	(6,999-9,616)	177
13 Sep 1973[3]	2	3,084	(3,062-3,107)	1,075
8-10 Sep 1974	13	11,476	(10,406-12,546)	150
19-21 Sep 1975	12	6,886	(5,597-8,174)	1,919
12-14 Sep 1976	12	10,796	(9,086-12,501)	5,670
25-27 Aug 1977	13	12,392	(9,462-15,318)	3,819
29-30 Aug 1978	13	3,602	(2,880-4,323)	826
4-7 Sep 1979	10	599	(367-830)	Closed
24-26 Aug 1980	12	549	(376-721)	Closed
10-11 Sep 1981	12	662	(485-839)	Closed
19-21 Aug 1982	13	749	(485-1,014)	Closed
11-12 Aug 1983	12	2,646	(2,094-3,197)	Closed
29-30 Aug 1984	13	308	(176-463)	Closed
12-15 Aug 1985	12	617	(397-838)	Closed
28 Aug-1 Sep 1986[4]	13	2,315	(1,631-3,020)	Closed

[1] Biomass estimates and confidence intervals were calculated by the "area swept" technique of Alverson and Pereyra (1969), using the equations developed by Smith and Bakkala (1982).
[2] Catches calculated from commercial samples and total pandalid catch (Albers and Anderson 1985).
[3] Survey curtailed due to severe weather.
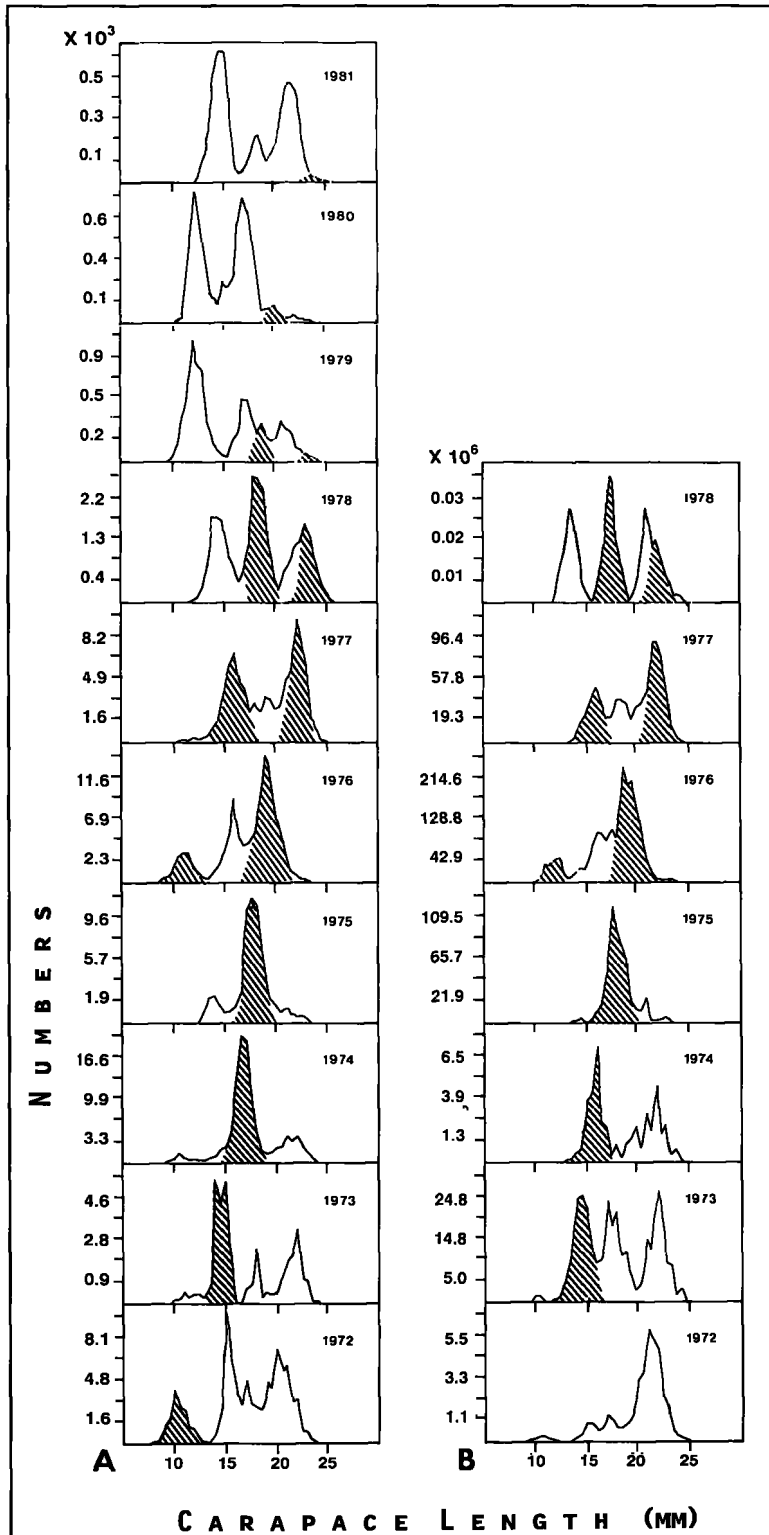[4] A 3.2 mm mesh liner was used during this survey.

Figure 2

Size-frequency distributions of *Pandalus borealis* from Pavlof Bay, Alaska, in catch per kilometer from (A) annual research surveys, 1972–81, and (B) total numbers in the commercial catch, 1972–78. Dominant 1971 and 1975 size modes are shaded.

from each survey tow. Endopodite structure of the first two pleopods (Allen 1959) was used to separate the sexes. Length-frequency data by sex from commercial catch samples were provided courtesy of the ADF&G (211 Mission Rd., Kodiak, AK 99615).

Estimating mean size and abundance of year-classes

The total number of *P. borealis* in a survey or commercial catch was estimated for each 0.5 mm CL group as

$$\hat{N}_{ij} = n_{ij} \frac{C_j}{w_j} \qquad (1)$$

where

$\hat{N}_{ij}$ = number of *P. borealis* in the i th size interval taken in the j th haul (i = 1....q; j = 1....r),

n_{ij} = number of *P. borealis* in the i th size interval sampled from the j th haul,

C_j = weight of *P. borealis* in the j th haul, and

w_j = sampled weight in the j th haul.

Estimates of abundance for each size group were summed for all tows annually to form length-frequency distributions (Fig. 2). The technique of Macdonald and Pitcher (1979) was then used to separate and quantify year-class modes. Length was assumed to be normally distributed for a given year-class. The computer algorithm (Macdonald 1980) requires starting values of parameters (mean, standard deviation, proportion) for each component (year-class). Starting values for parameters were visually determined and the program iteratively computed maximum-likelihood parameters.

The estimated number of shrimp of a given year-class ($\hat{N}_k$) was calculated as

$$\hat{N}_k = \hat{P}_k \, \hat{N}.. \quad \hat{B} / \sum_{j=1}^{r} C_j, \qquad (3)$$

letting

$\hat{P}_k$ = estimated proportion of the k th year-class in the sample population N..,

$\hat{N}..$ = estimated total number of shrimp captured in a survey period, and

$$\hat{B} = \frac{A}{r} \sum_{j=1}^{r} [C_j/a_j] \, q, \qquad (3)$$

where $\hat{B}$ = estimated biomass of *P. borealis*,

    A = total survey area (Pavlof Bay >55 m; 302 km^2),

    a_j = area covered in tow j, and

    q = catchability coefficient of the sampling gear.

In the absence of better information, the catchability coefficient (q) in this analysis was set at 1.0. Strictly speaking, this only applies to shrimp sizes that are fully recruited to the sampling area and gear. Equation (3) is modified from Alverson and Pereyra (1969). Biomass estimates are conservative because small (<18 mm CL) shrimp are not fully vulnerable to capture.

Finally, the number of *P. borealis* of a given year class ($\hat{R}_k$) caught by the fishery between research sampling surveys was estimated as

$$\hat{R}_k = \hat{P}_k \, N.. \, [L/W], \qquad (4)$$

where $\hat{P}_k$ is calculated similarly to survey catches above,

    N.. = total number of shrimp sampled from the commercial catch in a given year,

    L = total landed weight of *P. borealis* between surveys, and

    W = total sample weight from which N.. was calculated.

Determination of growth and mortality

Growth rates were estimated by following the 1971 and 1975 year-classes through a time series of length-frequency distributions (Fig. 2). The dominance of these year-classes minimizes the effect of overlap with adjacent modes. Nonlinear least-squares regression (Program BCG2, Abramson 1971) was used to fit von Bertalanffy growth curves to average size-at-age data.

Annual instantaneous total mortality rates (Z) for the dominant year-classes were calculated as

$$Z_k = -\ln (N_{k,t+1} / N_{k,t}) \qquad (5)$$

where t = one year and $N_{k,t}$ and $N_{k,t+1}$ represent the relative abundance of the kth year-class in two consecutive years.

Estimated fishing (F) mortality was derived from estimated total mortality using Ricker's (1975) formula

$$F_k = \hat{\mu} \, Z_k / (1 - e^{-Z_k}) \qquad (6)$$

where $\hat{\mu}$ = annual exploitation, the ratio of estimated catch in numbers (R_k from eq. 4) and estimated abundance (N_k from eq. 2) of the 1971 and 1975 year-classes.

Natural mortality (M) was calculated by subtraction:

$$M_k = Z_k - F_k. \qquad (7)$$

Results and discussion

Estimates of age, growth, and mortality rates in this study were made for two dominant year-classes that could be followed through most of their life span. Assumptions underlying the estimates were that size modes represented year-classes, and immigration and emigration of Pavlof Bay shrimp were minimal.

Identification of year-classes

The 1971 and 1975 year-class modes were identified and followed through 1981 in length-frequency plots (Fig. 2, Table 2). The size at which dominant modes are first identified is between 10 and 11 mm CL. *Pandalus borealis* of this size are approximately 1.4 years old if it is assumed that larvae hatch in April, and early growth is similar to that reported by other investigators (Butler 1964, Ivanov 1970, Fox 1972, Skúladóttir 1981). The plots indicate similar patterns between the two year-classes, as well as close agreement in location of dominant modes in both the survey and commercial data (Fig. 2 and Table 2). Close agreement in the modal structure of the two independent data sets supported the assumption that the survey and commercial catch data were drawn from the same population and made estimation of fishing mortality possible. Commercial gear used comparable mesh and had a similar fishing configuration to our survey gear, except for the codend liner. The presence of a codend liner in survey sampling gear may explain the better definition of 1.4 year-old modes in survey samples due to the smaller effective mesh size.

Problems in identifying the age of the smallest modal group have been noted by other researchers (Fréchette and Parsons 1983). Entering year-class modes from survey data were assigned the age of 1.4. A smaller mode (mean of 6.5–7.5 mm CL; numbers not large enough to be depicted in Fig. 2) was designated age 0.4 (~146 days assuming an April hatch). Nunes (1984) reported that laboratory-reared *P. borealis* postlarvae reached 3.6–3.9 mm CL by about 110 days after hatch-

Table 2
Mean carapace length (CL), standard deviation (SD), and estimated number in survey area or estimated number caught in millions (*N*) of domination year-class components separated by the Macdonald and Pitcher (1979) method from Pavlof Bay, Alaska, trawl survey and commercial catch length-frequency samples.

| | 1971 year-class | | | | | | 1975 year-class | | | | | |
| | Survey | | | Commercial catch | | | Survey | | | Commercial catch | | |
	CL	SD	$N \times 10^6$	CL	SD	$N \times 10^6$	CL	SD	$N \times 10^6$	CL	SD	$N \times 10^6$
1972	10.06	0.79	388.48	10.24	0.75	0.78						
1973	14.28	0.55	561.33	14.16	0.79	98.30						
1974	16.47	0.73	2337.62	15.54	0.70	21.93						
1975	17.44	0.71	1252.43	17.65	0.72	450.55						
1976	18.96	0.87	1738.33	19.10	0.91	642.08	10.66	0.81	413.90	11.01	0.49	53.33
1977	21.75	0.99	1007.98	21.67	0.85	184.36	15.68	0.93	225.03	14.74	0.68	26.70
1978	22.98	0.84	177.96	22.17	0.48	21.56	18.20	0.90	317.99	17.17	0.56	71.44
1979	23.61	0.67	3.93				19.23	0.79	23.63			
1980							21.45	0.60	9.83			
1981							23.01	1.17	3.48			

ing. Seasonal trawl sampling and larval surveys at Chiniak Bay, Alaska, showed juvenile young-of-the-year reaching an average size of 7 mm CL by September (~153 days after hatching) for three consecutive years (E. Munk, Kodiak Lab., Alaska Fish. Sci. Cent., pers. commun., 10 June 1987). Since no other modes were found between this juvenile group and the larger-age 1.4 mode in survey sampling, it was assumed the age designation of these groups was correct. Skúladóttir (1981) found difficulty in assigning ages to entering size modes (average size 10–12 mm CL), probably because the stretched mesh gradually increased from 32 to 38 mm over five years of sampling (Hallgrímsson and Skúladóttir 1981). Fréchette and LaBonté (1981) also noted a similar problem with a mesh size of 38 mm. The mesh size in this study was 32 mm with a 32 mm codend liner, which may have helped in the retention of young shrimp.

Abundance and variability of year-classes

The estimated biomass of *P. borealis* in Pavlof Bay peaked in 1977 and declined substantially in later years (Table 1). In response to reduced biomass, the fishery was closed by the ADF&G in 1979; the population subsequently stabilized at a lower level after 1978. The decline in abundance of the 1971 year-class (Table 2) reflected that of the total population (Table 1). The average number of *P. borealis* caught per survey tow declined steadily from approximately 199,000 in 1976 to 10,000 in 1981 (Table 3).

Dominant year-classes persisting in the population result from favorable conditions during their embryonic, larval, or juvenile stages. The relationship of

Table 3
Average number of *P. borealis* caught per survey tow 1972–86. Tow length standardized to one nautical mile (1.85 km).

Survey	Number	Survey	Number
1972	160,752	1980	11,521
1973	61,410	1981	10,370
1974	208,356	1982	2,780
1975	126,322	1983	11,679
1976	199,566	1984	1,209
1977	160,074	1985	3,524
1978	49,879	1986	11,488
1979	16,066		

shrimp landings to water temperatures prevailing during the spawning period 2 years earlier has been demonstrated in Gulf of Maine stocks (Dow 1966). Eggs incubated at 3 and 6°C resulted in larger newly hatched *P. borealis* larvae (1.41–1.49 mm CL) than those incubated at 9°C (1.09 mm CL) (Nunes 1984). If larger newly hatched larvae have a survival advantage, then colder incubation temperatures (6°C or lower) might enhance year-class strength. Warm temperatures may lead to lower survival of eggs and larvae of *P. borealis* due to increased egg parasitism and reduced food conversion efficiency (Paul and Nunes 1983). Minimum seawater temperatures in the study area normally range from 3 to 6°C (McLain et al 1979). Royer (1989) examined temperatures across the Gulf of Alaska and found very low-frequency fluctuations of ±2.0°C occur in the upper 250 m of the water column north of 55°N in the Gulf of Alaska (including Pavlof Bay). A cold temperature anomaly of more than 1.2°C was reported for the 1971–78 period in this region. These

anomalous low temperatures may have played a part in the formation of the strong 1971 and 1975 year-classes. Conversely, the relatively warm temperatures since 1980, perhaps peaking in 1984 (Royer 1989), may explain the lack of large year-classes in later years (Figs. 2, 3). It is possible that surveys of larval or juvenile abundance and related environmental parameters, mainly temperature, could be used to forecast future abundance trends.

Extreme variability in year-class strength can mean the success or failure of the commercial fishery. The 1971 year-class was dominant in commercial catches in Pavlof Bay during at least five fishing seasons (Fig. 2B). To calculate the contribution of dominant year-classes to the commercial catch, an average total weight, calculated from Pavlof Bay *P. borealis* length-weight data, $W = 0.00104 \ CL^{2.70160}$ (Anderson 1981) was multiplied by the estimated number caught in each year-class (Table 2). During the years 1974–78, the 1971 year-class contributed about 70% and the 1975 year-class about 3% of the 12,384 metric tons of *P. borealis* harvested from Pavlof Bay. Although the commercial fishery was closed in Pavlof Bay from 1979 to 1986, little or no improvement in stock condition occurred. In Pavlof Bay, it appears that the *P. borealis* fishery was largely supported by a single year-class.

Estimates of growth

Estimates of growth parameters in this study were generated only from the two dominant year-classes that could be followed through a time series (Fig. 2). Growth estimates depend heavily on the occurrence and definition of modes. *Pandalus borealis* have a synchronous and relatively abbreviated hatching period which gives rise to fairly well-defined size modes shortly after settlement of juveniles (Fréchette and Parsons 1983). Survey sampling was conducted in August–September, toward the end of the period of rapid summer growth. Studies that have continuously sampled throughout the spring and summer show growth slows in late summer, possibly as the result of spawning. Some instar growth is possible, however, even during mating and spawning, for the more frequently molting young males. I interpret the double-spike top of the 1971 year-class depicted in the 1973 survey data (Fig. 2A) as possibly representing year-class instar growth. As the shrimps age and transform to females, molting is reduced to perhaps two times a year, into and out of breeding dress (Allen 1959). Mode definition for year-classes after they become female is therefore not beset with an interpretation problem resulting from instar growth. The additional problem of overlap with adjacent but minor modes, especially with slower-
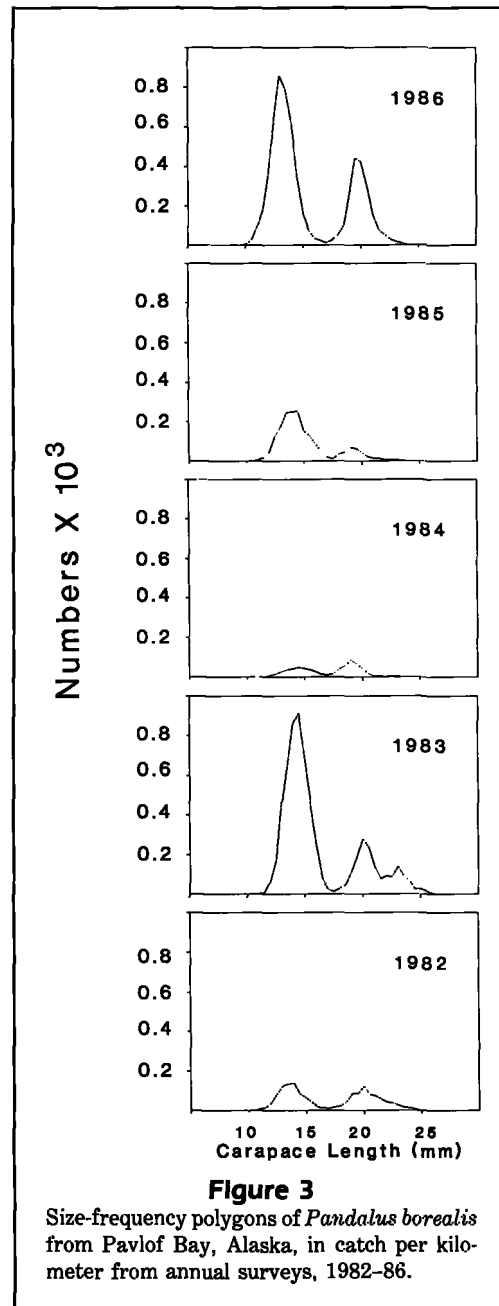

Figure 3
Size-frequency polygons of *Pandalus borealis* from Pavlof Bay, Alaska, in catch per kilometer from annual surveys, 1982–86.

growing females, is not so acute when using only dominant year-classes for growth estimates.

Separate von Bertalanffy growth curves were fit to average size-at-age data for the two dominant year-classes (Fig. 4). Parameters of the fitted relationship were $L_\infty = 29.64$, $K = 0.16$, and $t_0 = -1.30$ for the 1971 year-class, and $L_\infty = 26.31$, $K = 0.29$, and $t_0 = -0.47$ for the 1975 year-class. A Friedman two-way analysis of variance by ranks (Connover 1971) showed that members of the 1975 year-class were significantly ($P < 0.001$) larger for a given age, indi-
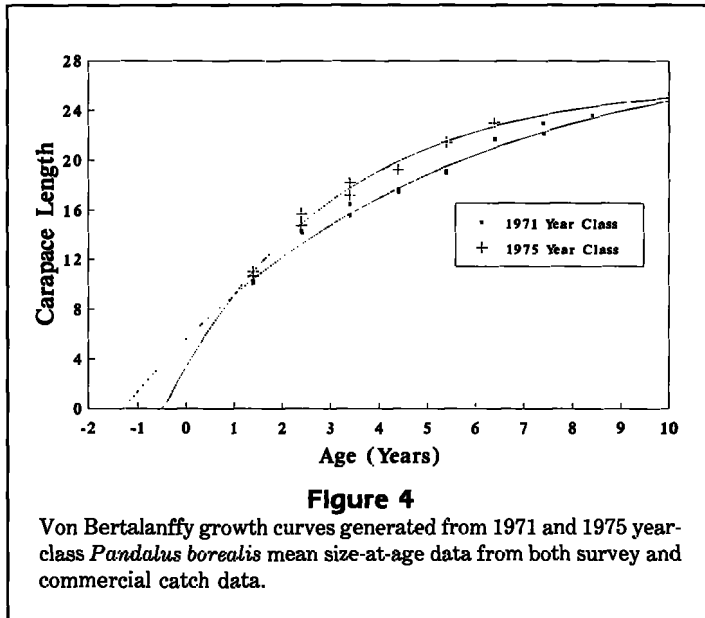
Figure 4
Von Bertalanffy growth curves generated from 1971 and 1975 year-class *Pandalus borealis* mean size-at-age data from both survey and commercial catch data.

Table 4
Mean size (CL) and standard deviation (SD) of 1.4 year-old *P. borealis* from 1972–86 survey samples in Pavlof Bay, Alaska.

Survey year	CL	SD
1972	10.06	0.79
1973	11.39	0.92
1974	10.62	0.92
1975	10.99	0.67
1976	11.84	1.98
1977	11.52	0.94
1978	11.72	0.70
1979	11.75	0.70
1980	13.21	0.83
1981	14.41	0.74
1982	13.70	1.12
1983	14.31	0.99
1984	13.97	1.24
1985	13.45	1.09
1986	13.24	1.04

cating a higher growth rate for this year-class. For example, the 1971 year-class attained average sizes of 16.47 and 21.75 mm CL at ages 3.4 and 6.4, respectively, whereas the 1975 year-class averaged 18.20 and 23.01 mm CL at these ages. Skúladóttir (1981) also detected large differences in growth rates between year-classes. In her study, one slow-growing year-class had a K = 0.15 and L_∞ = 28 which is similar to the parameters calculated for the 1971 year-class in this study. On the other hand, parameters calculated for the average of five fast-growing year-classes in her study indicated a K = 0.23 which is lower than the K (0.29) calculated for the 1975 year-class in the present study.

While growth of *P. borealis* is probably not related to overall population density, there is evidence of an inverse relationship relative to within year-class strength. Both the 1971 and 1975 year-classes hatched during periods of high overall population levels (Table 1), but the faster early growth of the 1975 year-class may be explained by its relatively lower abundance (Table 2) and, presumably, reduced competition for food during the juvenile phase. *Pandalus borealis* is an aggregating species exhibiting differential distribution by size, sex, age, and season (Shumway et al. 1985). Although most larvae are captured between 20 and 30 m in the water column (Haynes 1983), Wolotira et al. (1984) report a downward shift in vertical distribution with progressive stages of larval development. They theorized distribution differences reflect either a change in diet or distribution of food items. Berkeley (1930) also describes the apparent segregation of juveniles from the adult population. The effect of ecological

separation of life-history stages could, therefore, explain differing growth rates among year-classes even though overall population density was high.

Since 1979, the occurrence of small shrimp (<12 mm CL) in survey samples has been much less than in previous years (Figs. 2A, 3). Three possible explanations for the virtual disappearance of this size-class are (1) small shrimp may only be retained when overall catch rates are as high as they were in 1972–77, (2) juvenile shrimp may not normally be found within the same area as larger adult shrimp except when high population levels force them into the less-preferred adult habitat, and (3) faster growth of juvenile shrimp may have led to entering year-classes growing beyond 10 mm CL to 13–15 mm CL since 1979. I believe the most plausible explanation for the disappearance of small shrimp from survey samples is faster growth of juveniles. Results of this study suggest growth is inversely related to year-class strength. The overall population decline of *P. borealis* in Pavlof Bay (Table 1) is attributed to the dying out of the relatively strong 1971 and 1975 year-classes and a series of relatively weak entering year-classes since 1979 (Figs. 2, 3). The 1.4 year-old group is now between 13.2 and 14.4 mm CL rather than the 10–11.8 mm CL that was observed for 1972–79 survey samples (Table 4). The possibility of missing size modes in this recent data series is low because sample sizes remained large (about 5000 shrimp per survey). Independent sampling of shrimp length frequency from cod stomachs captured in 1980 and 1981 trawl surveys showed cod consume smaller shrimp, probably the 0.4 year-olds (6.5 mm CL), than were found in trawl samples (Albers and Anderson 1985). Beyond 10 mm

CL, length frequencies were similar for both cod and trawl data, suggesting that the age designation of this larger 1.4 mode is correct.

Variability in growth rates of year-classes also causes variability in the age of full recruitment in survey sampling, owing to the size selectivity of our 32mm mesh trawl. Recruitment was complete at ages 5.4 and 3.4 (18.96 and 18.20mm CL) for the 1971 and 1975 year-classes, respectively. Likewise, selectivity experiments by Blott et al. (1983) showed complete vulnerability of 19mm CL *P. borealis* in a 32mm stretch mesh trawl. Fox (1972) reported full recruitment at age 3 (≈18.0mm CL) in stocks of *P. borealis* from Kodiak Island, Alaska, in which sampling was accomplished with trawls having a mesh size similar to those in the present study.

Mortality estimates

Total mortality estimates were based on year-class abundance after full recruitment to survey sampling (eq. 5; Table 5). The age of full recruitment to survey sampling was identified as 5.4 for the 1971 year-class and 3.4 for the 1975 year-class based on the visual inspection of the catch curve (Fig. 5). Since the commercial fishery was closed before the 1979 survey, total mortality rates estimated for the 1975 year-class beyond age 4.4 are equivalent to natural mortality. Table 5 also presents annual exploitation and fishing mortality rates estimated for both year-classes (from eq. 6). The 1971 year-class showed increasing natural mortality between ages 5.4 and 8.4, while fishing mortality remained relatively stable during this period.

Increasing total mortality with age for the 1971 year-class is attributed to increasing natural mortality since fishing mortality was constant. Apparent increases in natural mortality could also be caused by emigration of older individuals from the Pavlof Bay population, but this seems unlikely since it has been demonstrated that larger (older) shrimp are less active in diel vertical migration (Barr 1970) and would tend to be retained by the shallow entrance of Pavlof Bay. The observed higher natural mortality in this study may be the result of spawning stress or senescence since the 1971 year-class may have approached their maximum longevity. Predation by Pacific cod *Gadus macrocephalus* may have also contributed to the high mortality observed from ages 6.4 to 8.4 when cod catches increased from 10 to about 500kg per nautical mile towed (Albers and Anderson 1985).
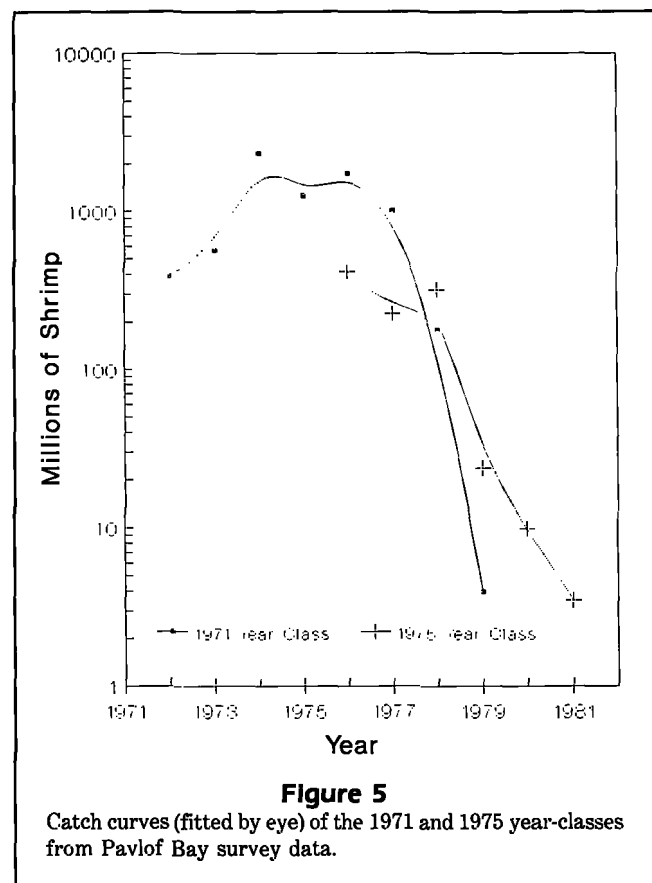
Table 5

Annual exploitation (μ), total (Z), fishing (F), and natural (M) mortality rates for the 1971 and 1975 year-classes.

	1971 year-class				1975 year-class[2]			
Age[1]	μ	Z	F	M	μ	Z	F	M
3.4/4.4					0.225	2.600	0.632	1.968
4.4/5.4					0.000	0.877	0.000	0.877
5.4/6.4	0.369	0.545	0.478	0.067	0.000	1.038	0.000	1.038
6.4/7.4	0.183	1.734	0.385	1.349				
7.4/8.4	0.121	3.813	0.472	3.341				

[1] Ages of year-classes correspond with years 1974–79 for 1971 and 1978–81 for 1975 (see Table 2).
[2] Fishery closed in 1979; thus, μ and F are both zero.

Figure 5
Catch curves (fitted by eye) of the 1971 and 1975 year-classes from Pavlof Bay survey data.

The 1975 year-class showed its highest calculated natural mortality between ages 3.4 and 4.4 (Table 5); however, these rates were subsequently lower. After closure of the fishery, the total mortality rates for the 1975 year-class beyond age 4.4 are equivalent to natural mortality. Albers and Anderson (1985) reported the significance of Pacific cod predation on *P. borealis* in Pavlof Bay. Pacific cod abundance peaked in 1979

and declined to about one-sixth of its former abundance by 1981. Lower observed natural mortality for the 1975 year-class beyond age 4.4 could be explained by decreasing cod predation.

Mortality estimates rely not only on the suitable definition of the year-class modes but also on the accuracy of biomass estimates (see eq. 2). Accuracy of biomass estimation is a function of the vulnerability, gear selectivity, and accessibility of shrimp in Pavlof Bay to the annual surveys. Knowledge of the life history of *P. borealis* were used to address these sources of variability in survey sampling. The late summer-fall period was chosen for sampling because *P. borealis* may be more vulnerable to capture due to the formation of mating and spawning aggregations. Small males and the larger females are not segregated, and even juvenile shrimp ≈6mm CL can be found in these aggregations. Sampling was restricted to daylight hours to minimize the effect of diel vertical migration; thus, shrimp were more susceptible to capture by bottom trawling. Shrimp smaller than 18mm CL are known to be less vulnerable to capture with the 32mm mesh survey sampling gear. Sampling with smaller mesh (3.2mm) in 1986 did indicate that more small shrimp could be captured, but small mesh sampling of the entire population was not deemed feasible due to increased sorting time.

Biomass estimates are considered conservative due to the lesser vulnerability of small shrimp. Likewise, larger/older shrimp may be able to escape capture by swimming out of the water column sampled by the survey trawl, leading to an overestimate of mortality. The high opening shrimp trawl used in this study (Wathne 1977) was designed to sample a substantial portion (3.8–4.4m off bottom) of the water column. Biomass trends tend to refute avoidance of larger shrimp as a source of error.

Biomass estimates, while they may not be an absolute estimate of the population size, can represent an index. Sources of variability that could affect the validity of biomass estimates being used as an index were controlled. Survey timing, gear, methods, and even vessel type were the same throughout the survey series. Survey sampling methodology, while minimizing, may not always eliminate possible changes caused by availability of shrimp. *Pandalus borealis* may be more vulnerable to capture during mating and spawning because dense aggregations are probably beneficial for mating success. The exact timing of this event may vary from year to year. As an example, the 1972 and 1974 surveys both took place during the second week in September (Table 1). In 1972, about 60% of females were carrying eggs externally while only head roe (egg mass clearly visible

Table 6

Percent female of the 1971 and 1975 year-classes at age (years) from Pavlof Bay, Alaska, survey sample analysis.

Year-class	Age							
	1.4	2.4	3.4	4.4	5.4	6.4	7.4	8.4
1971	0	0	0	2	38	100	100	100
1975	0	0	0	100	100	100	—	—

under carapace) females were found in 1974. Changes in availability probably explain the dip in the catch curve for the 1971 year-class at age 4.4 and at 2.4 for the 1975 year-class (Fig. 5). These apparent changes in availability perhaps associated with some life-history stage or abiotic factor should be studied in order to improve both biomass and mortality estimates.
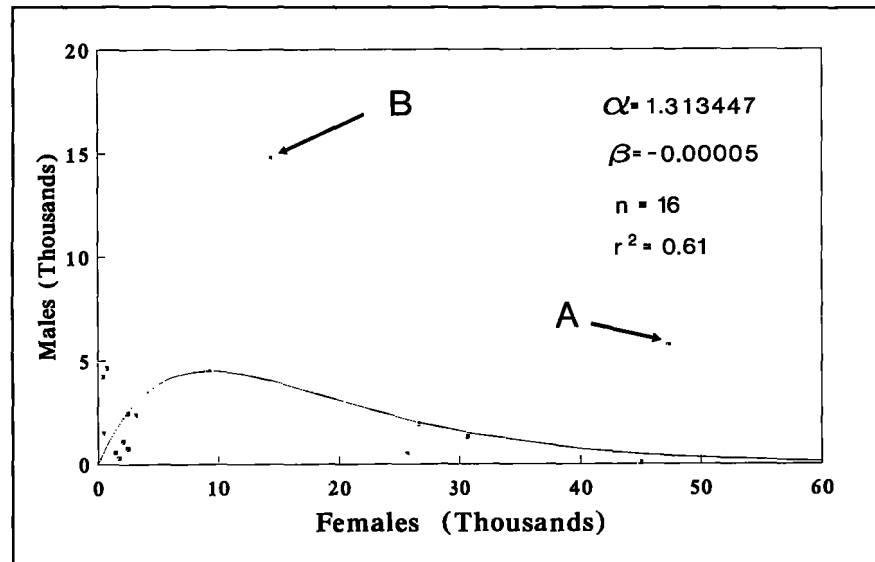
Sex transformation

The rate of transformation from male to female was considerably different for the two dominant year-classes studied (Table 6). Some members of the 1971 year class initiated sex transformation during their fourth year; however, others transformed during either their fifth or sixth year. In contrast, all members of the 1975 year-class initiated and completed transformation during their fourth year. The age at and rate of sex change for a year-class also appear to be closely related to year-class size or overall population density. Charnov (1979, 1981) proposed a model in which high mortality rates lead to a shorter male phase. Charnov et al. (1978) also considered how natural selection might act to alter the sex ratio of Pandalid shrimp in response to environmental influences. I feel that accelerated sex transition observed for the 1975 year-class in this study was influenced by short-term phenomena and is evidence of the labile timing in sex change of this species. The occurrence in 1980 and again in 1984–86 of the smallest ovigerous females ever sampled (13.0mm CL) is further evidence that accelerated sex reversal may be a possible mechanism by which northern shrimp attempt to increase reproductive capacity in the face of decreasing density (Table 1). Charnov and Anderson (1989) reported on an analysis of Pavlof Bay *P. borealis* that demonstrated the size of shrimp at the time of sex-transformation changes through time in relation to changes in the breeding size distribution.

Stock/recruit relationship and yield

While a compensatory relationship between lower population levels or density and the occurrence of early
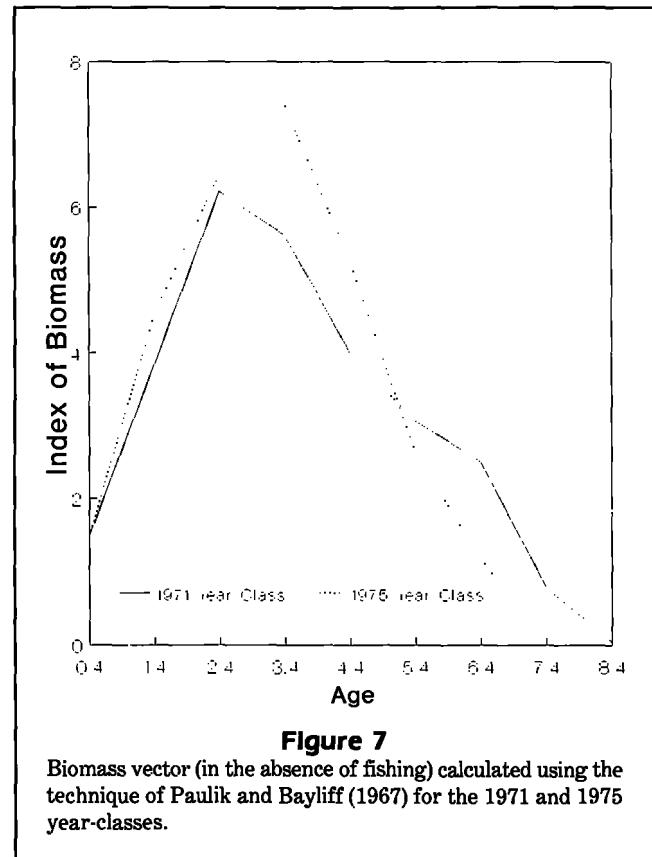
Figure 6

Spawner/recruit curve fit on female *Pandalus borealis* caught per kilometer as index of spawning biomass, and 1.4 year-olds (lagged one year) as recruit index, captured in Pavlof Bay shrimp surveys 1972–86. Points labeled A and B show effect of strong 1.4-age male year-classes of 1973 and 1975, respectively.

transformation of shrimp has been suggested in this study, the relationship between stock and recruitment appears to elude suitable definition. Using the average catch of females per tow as an index of spawning population and the catch rate of 1.4 year-old males as an index of recruits (lagged one year), a Ricker (1975) stock-to-recruit relationship was constructed (Fig. 6). While other combinations representing spawning and recruit biomass were tried, this combination gave the best fit to the recruitment function. Possible reasons for this combination rendering the best fit are that females are almost fully vulnerable to trawl capture and remain near the bottom during the fall survey period. On the other hand, while the 1.4 year-old males are not fully vulnerable to trawl capture, they do seem to represent a good relative index of incoming year-class strength. When dominant year-classes could be identified and followed through time, they were first identified as being relatively strong as 1.4 year-olds (Fig. 2). Since the 1.4 year-old mode is usually well separated from the remaining frequency distribution, weak as well as strong incoming year-classes could be quantified with the mode-separation technique.

Extreme fluctuations in the abundance of young year-classes make it difficult to devise management strategies. In some years, a relatively small spawning stock may give rise to a large year-class. The fit to the stock recruitment curve (Fig. 6) shows that the majority of the data points mostly conform to the fitted relationship. Outlying points labeled as A and B (A, 1973 year-class males (age 1.4) vs. brood females of 1972; and B, 1975 year-class males (age 1.4) vs. brood females of 1974) illustrate how relatively dominant 1.4 year-old male year-classes can push data points well outside the bounds of the curve (Fig. 6). The relative abundance of 1.4 year-old shrimp is probably a function of the variable survival of larvae and juveniles in response to environmental conditions rather than spawning biomass. The inadequacy of the fitted stock to recruit function to describe these important contributions to stock biomass means that other methods

Figure 7

Biomass vector (in the absence of fishing) calculated using the technique of Paulik and Bayliff (1967) for the 1971 and 1975 year-classes.

for defining management are needed. Therefore, strategies based on yield-per-recruit of dominant year-classes were examined.

Incorporating the growth and mortality estimates from this study into a Ricker yield model (Paulik and Bayliff 1967) indicated that maximum biomass, in the

absence of harvest, would be achieved at a relatively early age (Fig. 7) and small size. The maxima of biomass vectors were attained between age 2.4 (14.3 mm CL) and 3.4 (16.5 mm CL) for the 1971 year-class, and at age 3.4 (18.2 mm CL) for the 1975 year-class (Fig. 7). A management strategy based on maximizing the yield-per-recruit for the 1971 year-class would have resulted in the harvest of mostly male shrimp prior to their transformation to females. A similar finding was also reached by Abramson and Tomlinson (1972) in yield studies of *Pandalus jordani*. Harvesting more young shrimp may also lead to a possible lower economic return due to market resistance to small meats. Optimum management of Pandalid shrimp fisheries probably involves a trade-off between size-related economic return and larger yields from the harvest of young shrimp.

Conclusions

1 The bathymetric features of the Pavlof Bay region make it an ideal area for studying populations of *P. borealis*. The confining sills probably allow little immigration or emigration of shrimp. Thus dominant size modes, representing year-classes, could be followed through time in both the research survey and commercial data sets. It is necessary to rely on following dominant size modes to gain insight into population parameters owing to the problem of overlap with less dominant year-classes in the size-modal structure.

2 The Pavlof Bay population of *P. borealis* showed significant differences in year-class strength, with the 1971 year-class predominating during the study. Dominant year-classes are first detected when they are young (1.4 years old). Biotic or abiotic factors that control year-class strength have their greatest effect during the larval and juvenile stages.

3 There is evidence that growth may be inversely related to year-class strength. Since 1979, 1.4 year-old shrimp have averaged 13–15 mm CL rather than the 10–11 mm CL observed prior to 1979.

4 Age at sex transition was highly variable for the two dominant year-classes studied. The 1971 year-class showed transition over three years, while the 1975 year-class completed transformation in one year.

5 Total mortality rates of Pavlof Bay *P. borealis* are some of the highest reported for the species (Fréchette and Parsons 1983, Teigsmark 1983, Hopkins and Nilssen 1990) and are mostly a reflection of the high natural mortality rates. High natural mortality rates

for the 1971 year-class are attributed to intense predation by Pacific cod (Albers and Anderson 1985). After the cod population subsided within the Bay, natural mortality, along with total mortality, declined.

6 Yield could have been maximized by harvesting more young (male) shrimp, since mortality rates were high for the year-classes studied.

Worldwide, other *P. borealis* fisheries have experienced similar cycles of high and low abundance (Balsiger 1981) that characterized the rise and fall of western Gulf of Alaska fisheries in the 1970s. The decline of shrimp in Pavlof Bay was probably inevitable, regardless of the presence of a fishery, since many adjacent areas lightly or seldom fished experienced similar population declines (Anderson and Gaffney 1977). These declines may be directly attributable to the demise of a single or series of strong year-classes. Little is known about the parameters controlling shrimp natality and its relationship to subsequent recruitment. This problem deserves study, along with the effects of predation (Albers and Anderson 1985) and ecological and environmental parameters (Nunes 1984). Continuing shrimp research surveys in Pavlof Bay may lead to understanding the dynamics and perhaps the mechanisms driving the cycle of low and high shrimp abundance in the western Gulf of Alaska.

Acknowledgments

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