

# FACTORS AFFECTING THE DISTRIBUTION, ABUNDANCE, AND SURVIVAL OF *PANDALUS JORDANI* (DECAPODA, PANDALIDAE) LARVAE OFF THE OREGON COAST

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## ABSTRACT

Abundance, distribution, and survival of larval pink shrimp, *Pandalus jordani*, differed between 1971 and 1972. Consistent southwest winds in the February-March spawning season of 1972 kept surface flow onshore and larvae closer to the coast than did the mixed winds of 1971. The early season of 1972 was warmer than that of 1971, and development was faster: Zoea V were prevalent at the end of April 1972, compared with median advancement to Zoea III by early May in 1971. Corresponding to the lesser dispersal and faster development of 1972, survival was substantially better than in 1971.

Overall larval survival at settlement time appears from analysis of long-term fishery data and upwelling indices to have some dependence upon the strength of June to August upwelling. Extrapolation from laboratory studies suggests that is because survival is enhanced by the temperatures consistently 12°C and below maintained by strong upwelling. Timing of spawning and development interacts with timing of the flow regime. Summer upwelling generally keeps the habitat suitably cold for optimal development and survival and returns larvae to seaward for settlement roughly at the beds from which they were spawned.

Hjort (1914, 1926) was the first to suggest the importance of larval mortality in establishing year class strength of marine fish. This concept has been useful generally, and, in particular, larval mortality most fully explains fluctuations of stocks in species both short-lived and fecund. However, larval mortality per se is only one component of total mortality. Factors affecting parental stock size, fecundity, spawning and hatching rates, larval dispersal, metamorphosis, and postlarval and prerecruitment mortality will also generate year-to-year variation in population size. In many marine animals these life history phases are in totally different habitats and have very different durations.

Given the complexity of the life cycle and the variety of habitat features which can therefore act importantly, it is not surprising that sound explanations of year class variations have begun to emerge only now. Long time series of catch data and well-developed understanding of oceanographic processes are both required. Interesting recent examples include Southward et al. (1975), Boudreault et al. (1977), Driver (1978), and Dow (1978). Creation of indices of coastal upwelling strength (Bakun 1973) has given us an important variable for study of factors influencing

year class strength in marine populations. Upwelling acts in several ecologically significant ways, affecting temperature, salinity, nutrient concentrations, and current patterns. Enhancement of productivity in nearshore regions is well documented (Steemann Nielsen and Jensen 1957; Ryther and Menzel 1965; Ryther 1969). However, not only enhancement of productivity, but the specific changes in flow caused by upwelling can have important effects. Success of life stages is likely to be related to the time of onset of seasonal upwelling, intensity and duration of upwelling, and even to details of its intermittency. Effects can be negative. Lasker (1978) found that upwelling dispersed the food of larval northern anchovy, *Engraulis mordax*, reducing food availability below levels established in the laboratory (Lasker 1975) as minimal. Coe (1956), Winnor (1966), Lough (1976), and Nelson et al. (1976) have all shown that upwelling can both improve and reduce survival by transport of larvae toward or away from favorable habitat.

We report here an attempt to evaluate the importance of larval survival to the year class strength of the pink shrimp, *Pandalus jordani*, and to determine which aspects of ocean dynamics affect larval survival. First, larval distribution and abundance of *P. jordani* were ascertained by field sampling. Second, apparent survival in several spawning seasons was compared with laboratory studies of the effects of habitat factors (Rothlisberg 1979) and with the hydrographic regime during sampling to estimate the degree to which environmental factors determined

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larval survival in the field. Finally, an attempt was made to examine the contribution of year-to-year variation in ocean conditions during the postspawning season to variation in year class strength. Ocean conditions were primarily characterized by Bakun's upwelling indices.

## MATERIALS AND METHODS

Sampling for *Pandalus jordani* larvae was carried out during 32 cruises from January 1971 to August 1972 along a transect extending 60 nmi from the coast off Newport, Oreg., U.S.A. (Newport Hydro-line; stations designated NH-1, etc. according to distance from coast; Fig. 1). Sampling was at approximately fortnightly intervals (Fig. 2). On all but one cruise the 24.4 m RV *Cayuse* was used. In March and April 1972 a more extensive grid sampling was conducted on two cruises along a series of seven transects from Tillamook Head (I, Fig. 1) south almost to the Siuslaw River (VII). These transects extended 30 mi from the coast.

Temperature and a salinity sample were taken at the surface at each station, and temperatures at lower depths were obtained by bathythermograph (BT) cast to the bottom or a maximum of 150 m. Bottom salinity was obtained from a bottle sample collected at the greatest extent of the BT cast. On 9 of the 11 cruises in 1972 (C7205D and C7207E excluded), drift bottles were released. Plankton was collected by stepped oblique tows to near the bottom or to a maximum of 150 m with a 0.7 m diameter bongo net (cylinder-cone nets 5.1 m long of 0.571 mm Nitex<sup>3</sup> with effective filtering area to mouth area ratio of 8:1). The tows with three to five steps lasted 10 to 25 min, depending on depth. At towing speeds of 2 to 3 kn the nets filtered 600 to 1,000 m<sup>3</sup>; specific amounts were determined from TSK flowmeters in the mouth of each net. Depths were maintained by a 40 kg kite-otter depressor (Colton 1959) and recorded by time-depth recorder. Samples were preserved at sea with formaldehyde. Only the port side sample was analyzed from each pair, a total of 367 from the two years. Because of their relatively low density, the entire sample was sorted for shrimp larvae.

The National Weather Service gathers hourly wind data at a recording anemometer located at the base of the south jetty at Newport, Oreg. We used this data in their stored form (north-south and east-west vector components; m/s) to generate progressive vector diagrams.

<sup>3</sup>Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

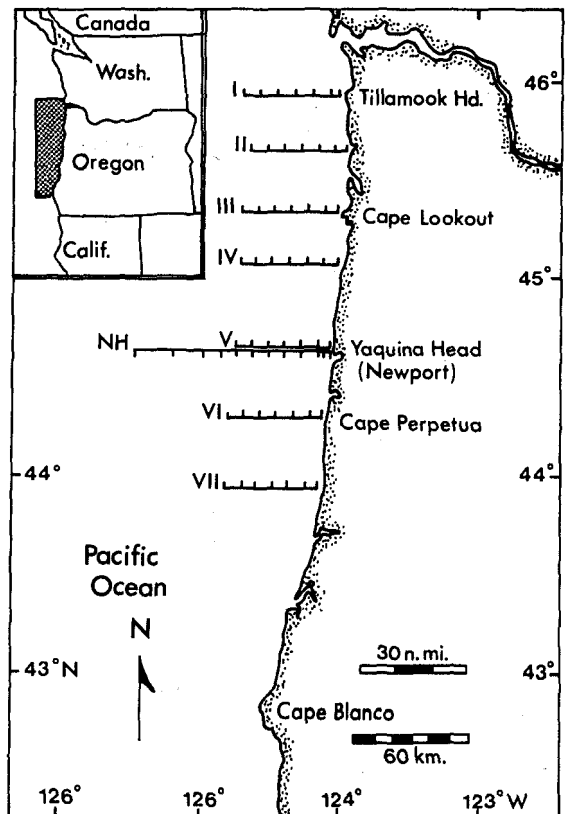


FIGURE 1.—Sampling transects off the Oregon coast. Newport Hydro (NH) line with stations: 1, 3, 5, 10, 15, 20, 25, 30, 35, 40, 50, and 60 nmi from the coast. Transects I-VII with stations 1, 5, 10, 15, 20, 25, and 30 nmi from coast. Transect V and NH line overlap.

## RESULTS

### Seasonal Wind, Current, and Temperature Regimes, 1971 and 1972

Progressive vector diagrams for wind from January through July in 1971 and 1972 (Fig. 3) show that the two years differed in several respects. In February 1971 winds were mixed, while in 1972 the southwest winds typical of winter were consistent. Southwest winds dominated in March 1971, except for a spell of northwest wind from the 15th to the 21st. March winds in 1972 were mostly from the southwest, but less intense. There were a few 1-d reversals to northwest wind. April in both years was transitional, and a short spell of northwest wind initiated the upwelling season. Winds of the upwelling season, May through August, were stronger in 1972 than in 1971.

Comparison of upwelling indices for 1971 and 1972 with the 25-yr average for 1946-71 puts them in long-

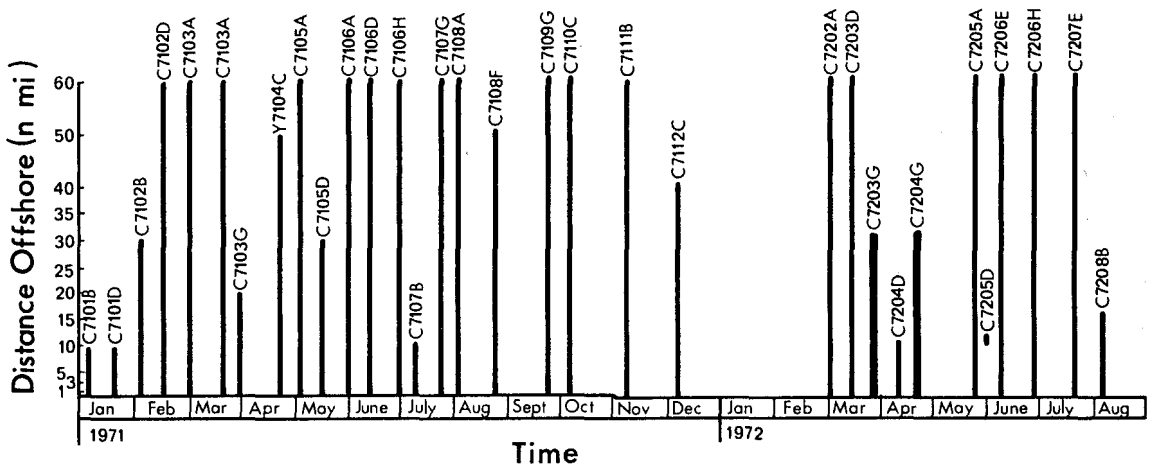


FIGURE 2.—Date and offshore extent of 32 cruises sampling larval *Pandalus jordani* from January 1971 to August 1972.

term perspective. These monthly indices (Bakun 1973, footnote 4) estimate the magnitude of the offshore component of Ekman transport (mtons/s per 100 m coast) from mean monthly sea surface, geostrophic winds based on pressure fields. Deviations from the long-term mean (Table 1) imply that surface flow onshore in the first quarter of 1971 was below average, while that of 1972 was near normal. Upwelling in 1971 was less than normal, while that of 1972 was close to the long-term mean.

The northward Davidson Current was well demonstrated by the drift of bottles released in March and early April. There was also an onshore component which produced high return rates in those months (mean for March and early April = 47%; Fig. 4). By late April currents acquired a large southward component, and an offshore component reduced return rates (19.8% for late April through August; Fig. 4). Surprisingly, a considerable northward component remained in all months in the zone very close to the coast, as implied by returns from the 1 to 5 nmi stations in all periods except late May and early August.

In February through April 1971, temperatures varied between 8° and 10°C inside 20 nmi (Fig. 5). From late April through July they increased to between 14° and 15°C due to increased sunshine and lack of strong upwelling. The sharp, temporary decrease of early June corresponded to a pulse of upwelling in late May 1971 (Fig. 3). Nearshore temperatures in 1972 were more constant and warmer in

TABLE 1.—Upwelling indices by year and quarter for 1971 and 1972 along with the anomalies from a 25-yr average (from Bakun 1973, see text footnote 4).

	1973		1972	
	Index	Anomaly	Index	Anomaly
Entire year	1	10	-2	7
First quarter (Jan.-Mar.)	-33	20	-49	3
Second quarter (Apr.-June)	26	-5	29	-2
Third quarter (July-Sept.)	33	-15	42	-5

the early part of the larval season than in 1971, ranging between 10° and 12°C. We attribute that to the strong onshore flow of late winter in that year. Temperatures rose slightly in spring but were held below the highs reached in late June of 1971 by the stronger upwelling conditions of 1972.

### Larval Distribution and Abundance of *Pandalus jordani* in 1971

Zoeae I, II, and III were found first on 16 February. They were widely distributed but most abundant at 5, 10, and 15 nmi (Fig. 6). In early March all larvae were within 20 nmi with highest density at 5 nmi; most were recently hatched, but there were some Zoeae II's, III's, and IV's. The cruise of 20 March appeared to coincide with the peak of larval hatching, Zoa I predominating and most abundant within 20 nmi of shore. The late March cruise was abbreviated because of bad weather. However, all larvae found at the 3 and 5 nmi stations were Zoa I. By 22 April the *P. jordani* were dispersed as far as 50 nmi offshore, but the peak of abundance was still at 5 nmi and consisted mostly of Zoeae II's and III's. A few

\*A. Bakun, Pacific Environmental Group, Southwest Fisheries Center, NMFS, NOAA, c/o Fleet Numerical Oceanography Center, Monterey, Calif., pers. commun. February 1982.

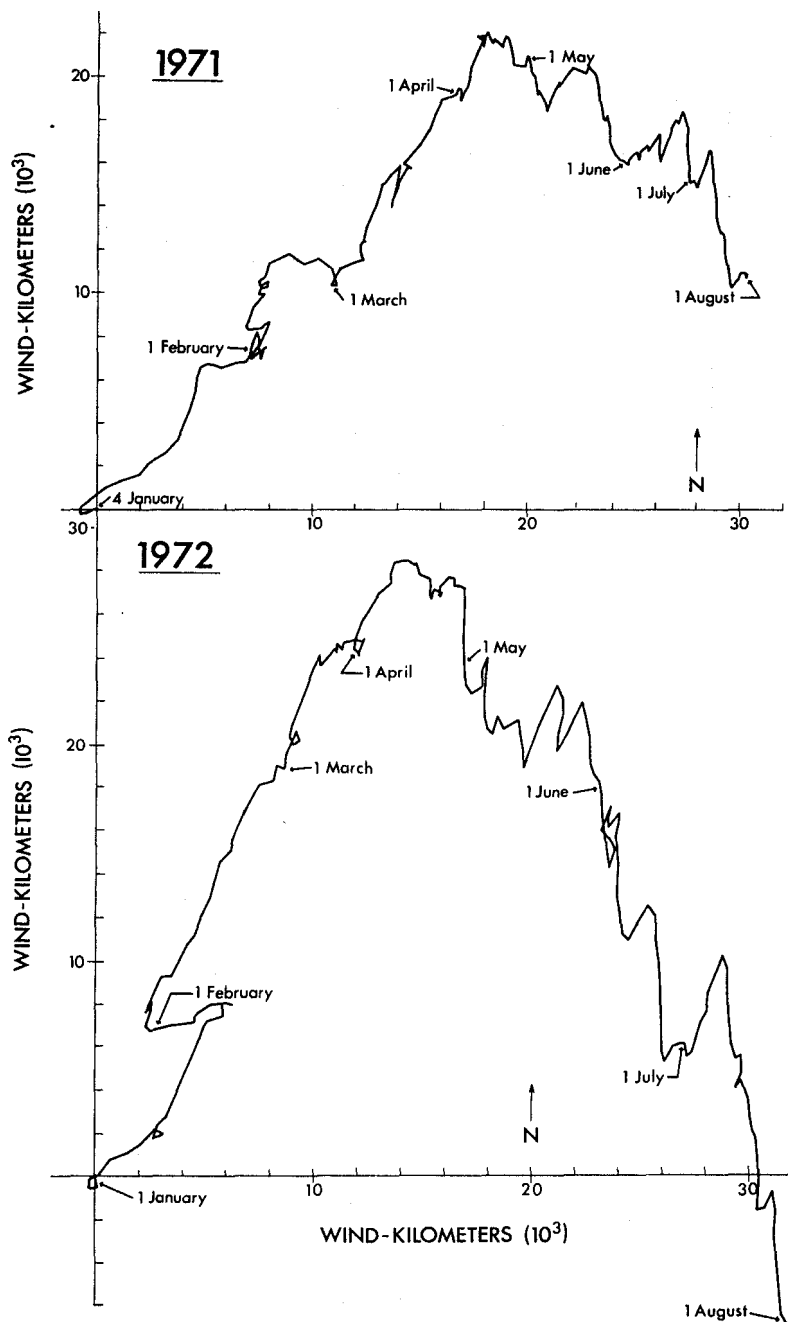


FIGURE 3.—Progressive vector diagrams for wind at Newport, Oreg., 1 January-1 August 1971 and 1972.

Zoeae VI's and VII's were caught at the 15 nmi station. On the early May cruise there were two centers at 5 and 50 nmi with young stages predominant at both. Samples collected 14 May contained a few intermediate and later larvae between 5 and 30 nmi. On 1 June, larvae were widely distributed between 10 and 60 nmi and were Zoeae VI to XIII. Larval abundance, though greater than in mid-May, was still low.

Even greater dispersion was seen on 12 June (3 to 60 nmi), but there was a peak at 25 nmi. The cruise of 28 June produced the only two juveniles of the season at 5 and 15 nmi. Other larvae in late zoeal stages (X to XIII) were found between 10 and 40 nmi. No larvae or juveniles were found on 6 or 21 July.

To simplify the depiction of distribution of specific larval stages, abundances (no./1,000 m<sup>3</sup>) were

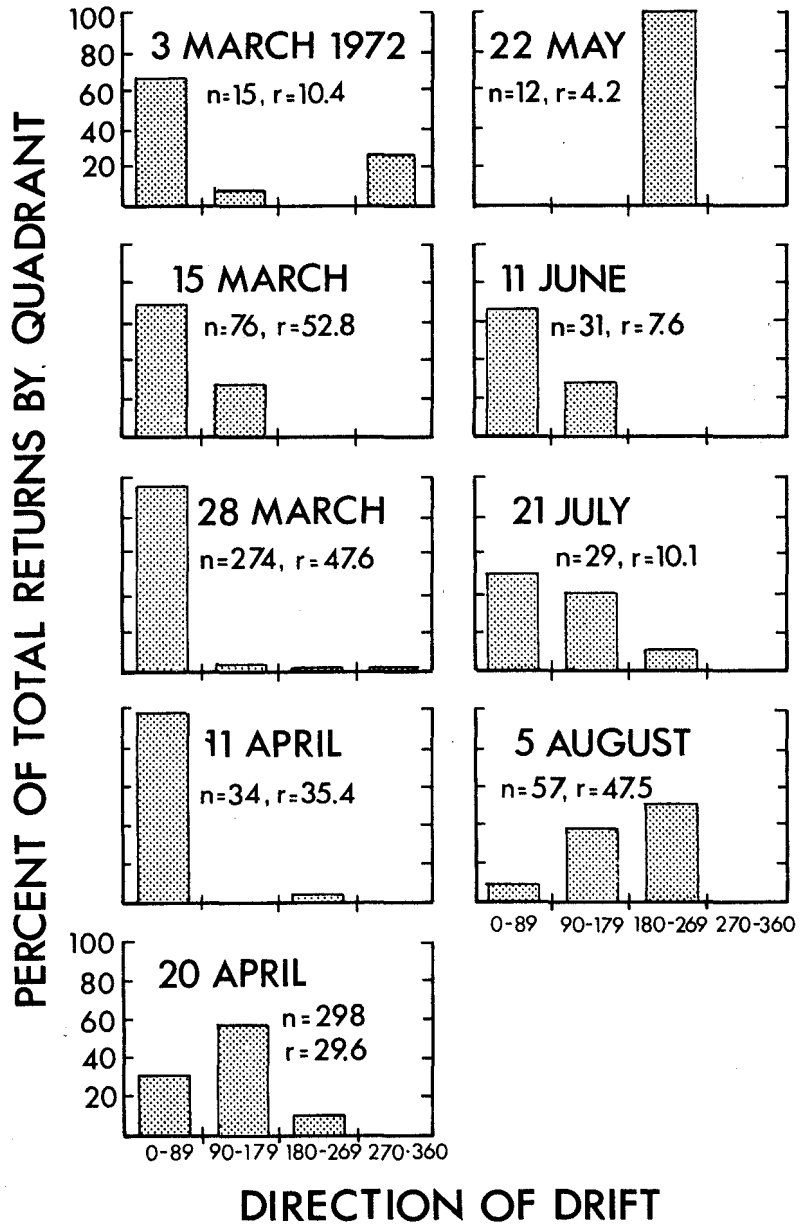


FIGURE 4.—Drift bottle-returns, 1972. Number, rate of return, and direction of drift summarized by quarterly components (from data supplied by M. J. Hosie, Fish Commission of Oregon, and W. Gilbert, Oregon State University School of Oceanography).

summed for each station over all cruises (Fig. 7). In 1971, Zoea I, though most abundant inshore, was spread over the entire 60 nmi of the transect. This trend continued to Zoea V, but increasing numbers appeared in the two seaward stations for II through V. By Zoea VI numbers were much diminished and most larvae were outside 15 nmi. This trend persisted through Zoea XIII. Small captures of late larvae and juveniles make generalizations for them difficult.

### Larval Distribution and Abundance of *Pandalus jordani* in 1972

No cruises were made in 1972 until 4 March, when small numbers of young larvae (I and II) were found between 3 and 15 nmi (Fig. 6). On 16 March there were many Zoea I at 3 and 5 nmi and lower numbers farther out. Small numbers of Zoaes II and III were also present. A 30-mi transect in late March showed the center of abundance was at 10 nmi; mostly they

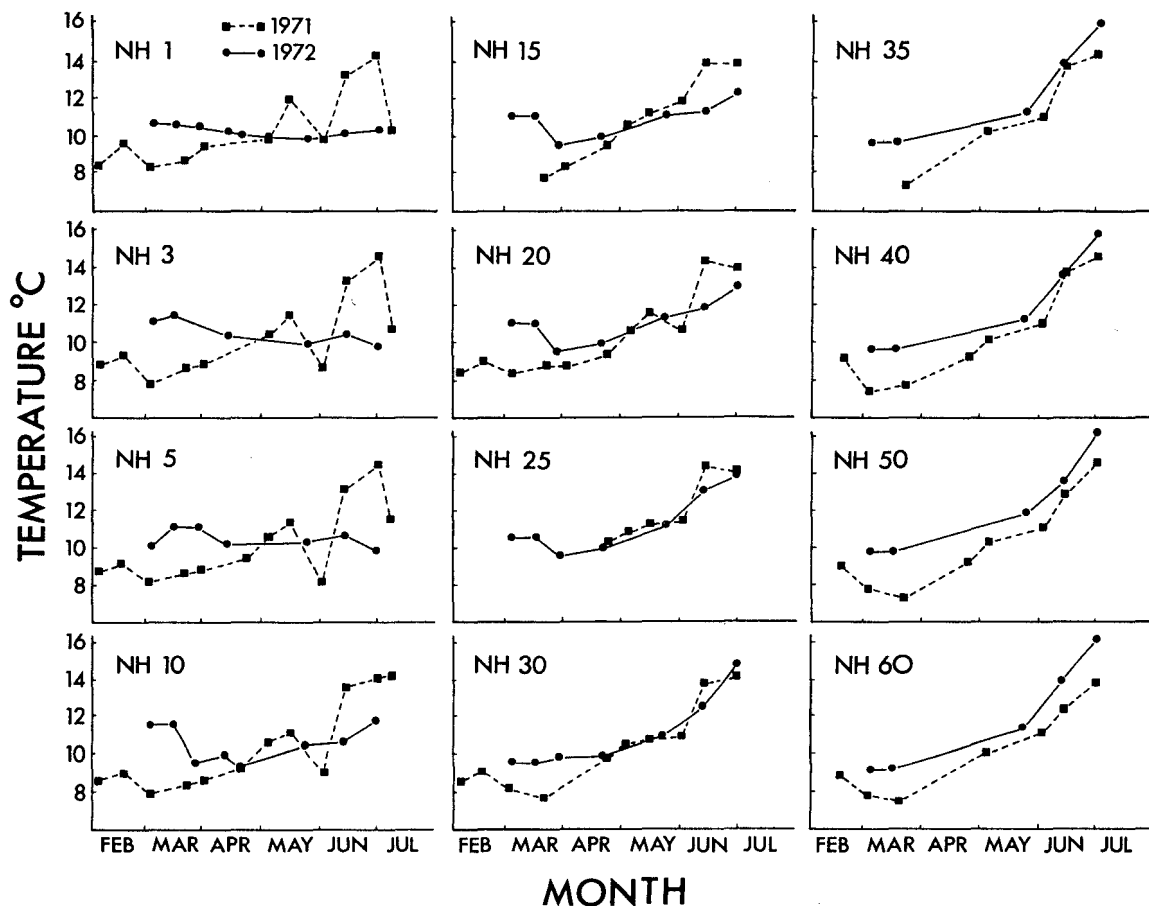


FIGURE 5.—Surface seawater temperatures at 12 sampling stations (NH-1 to NH-60) for February-July 1971 and 1972.

were Zoea III. The peak of larval hatching had apparently passed by that date. Larvae were present at the 1 nmi station for the first time and were present at all stations to 20 nmi. This contrasts to 1971, when *P. jordani* larvae were never found so close to shore. The 11 April cruise was curtailed for rough seas at 10 nmi. The most abundant stages were III's and IV's, but all stages from I to VIII were present. On 20 April stages I to XI were scattered between 5 and 30 nmi with VI to VIII most common. The distribution on 22 May was displaced offshore and spread between 10 and 45 nmi. Development was well advanced, and the first juveniles of the season were found at 25 and 30 nmi. Zoeae X to XII were dominant. Larvae on 11 June were advanced, older than XI, and distributed from 5 to 60 nmi with a peak between 10 and 20 nmi. Many juveniles were caught in a night tow at 15 nmi.

Figure 7 shows that early stages were generally less dispersed seaward in 1972 than in 1971. Zoeae I to

IV were found only inside 15 nmi. Older larvae were found farther offshore, but rarely extended beyond 40 nmi. Late larvae (XIII) and early juveniles, though present in small numbers, were more abundant than in 1971 and were most abundant between 15 and 30 nmi.

### Coastal Distribution and Abundance

All seven 30-nmi transects from Tillamook Head to the Siuslaw River were completed in late March 1972, but, due to bad weather, only the northern six were sampled in late April. As on the Newport line (Transect V), early larvae were most numerous inside 15 nmi, extending in to the 1 nmi stations in March (Fig. 8) over the whole grid. Larvae were most numerous at the 1 and 5 nmi stations, significantly more so than elsewhere as indicated by analysis of concordance of rank order of the stations according to larval density ( $W = 0.62$ ;  $df = 7,7$ ;  $P < 0.01$ ; see

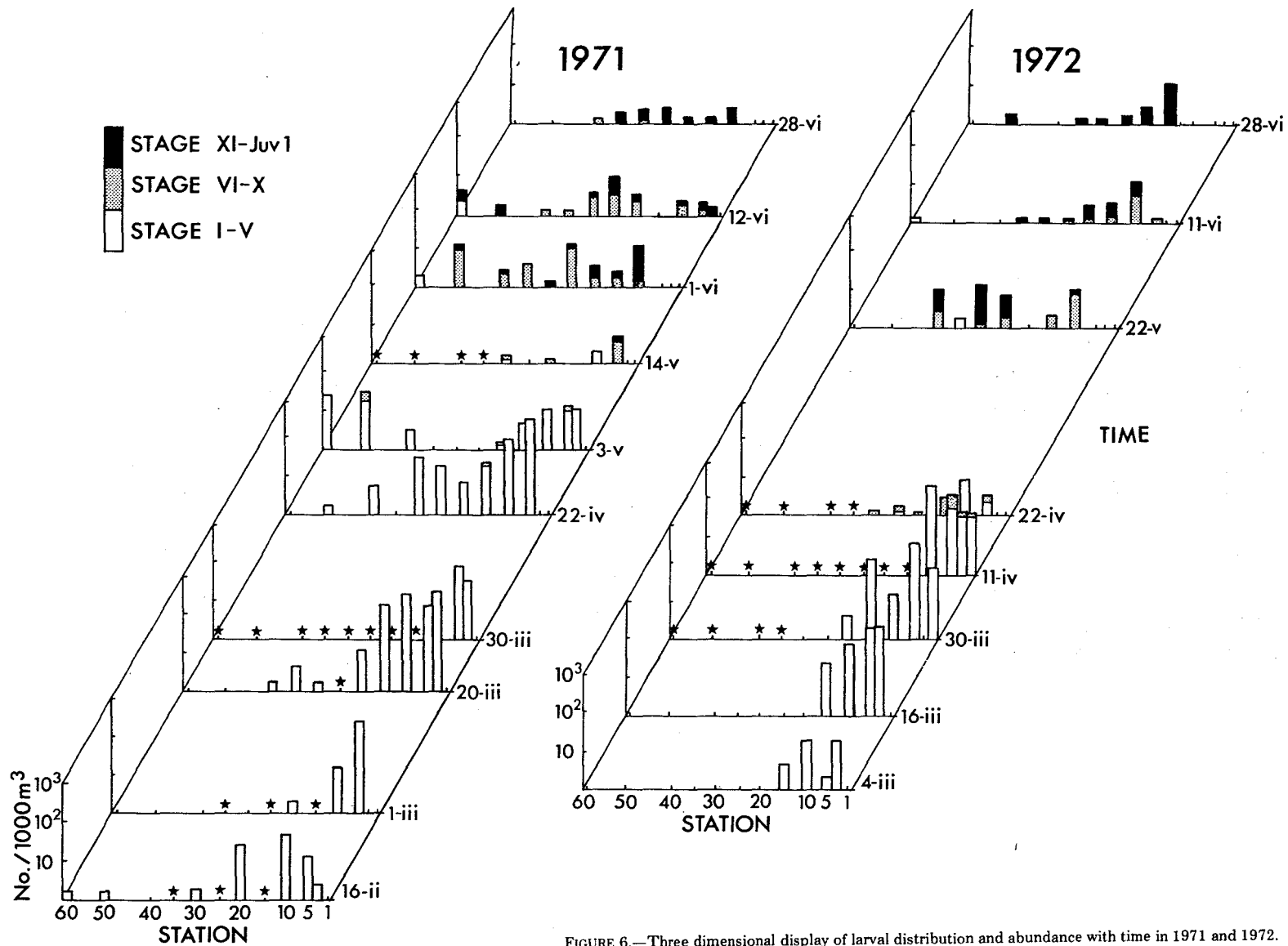


FIGURE 6.—Three dimensional display of larval distribution and abundance with time in 1971 and 1972.

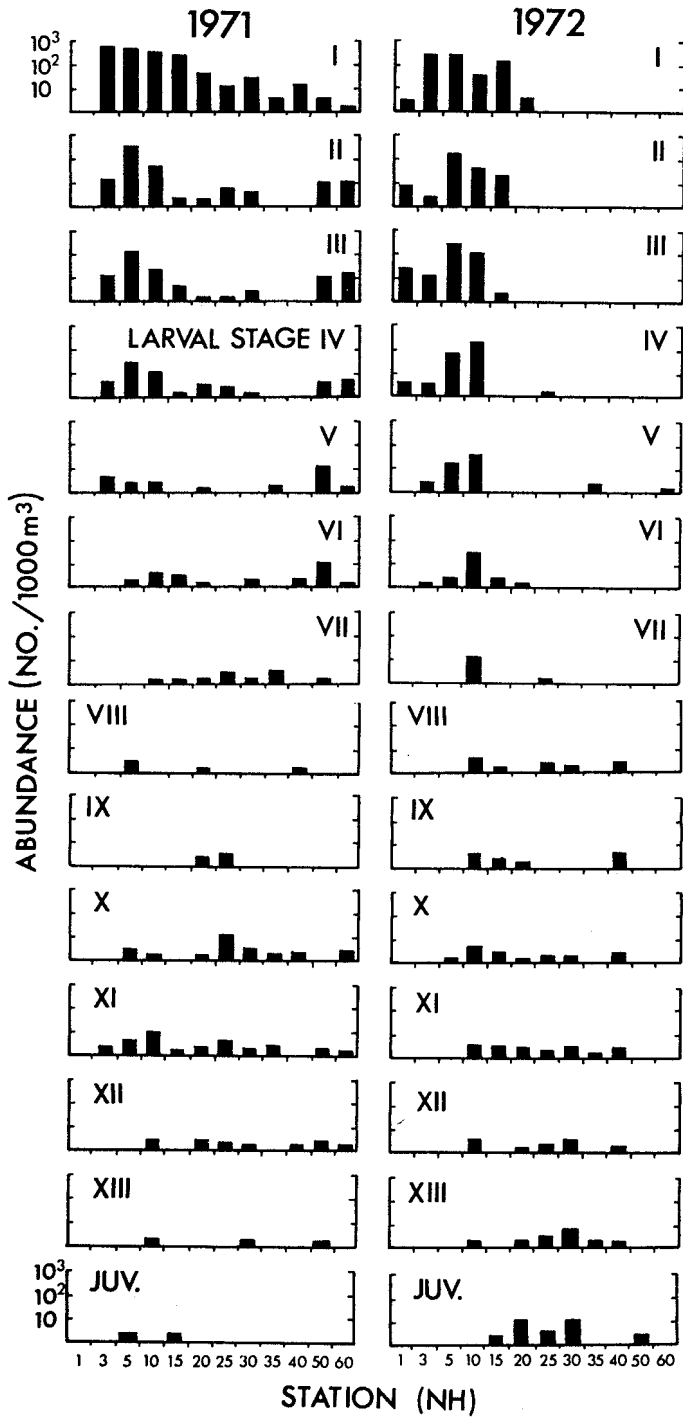


FIGURE 7.—Stage-specific larval distribution and abundance over all cruises in 1971 and 1972.



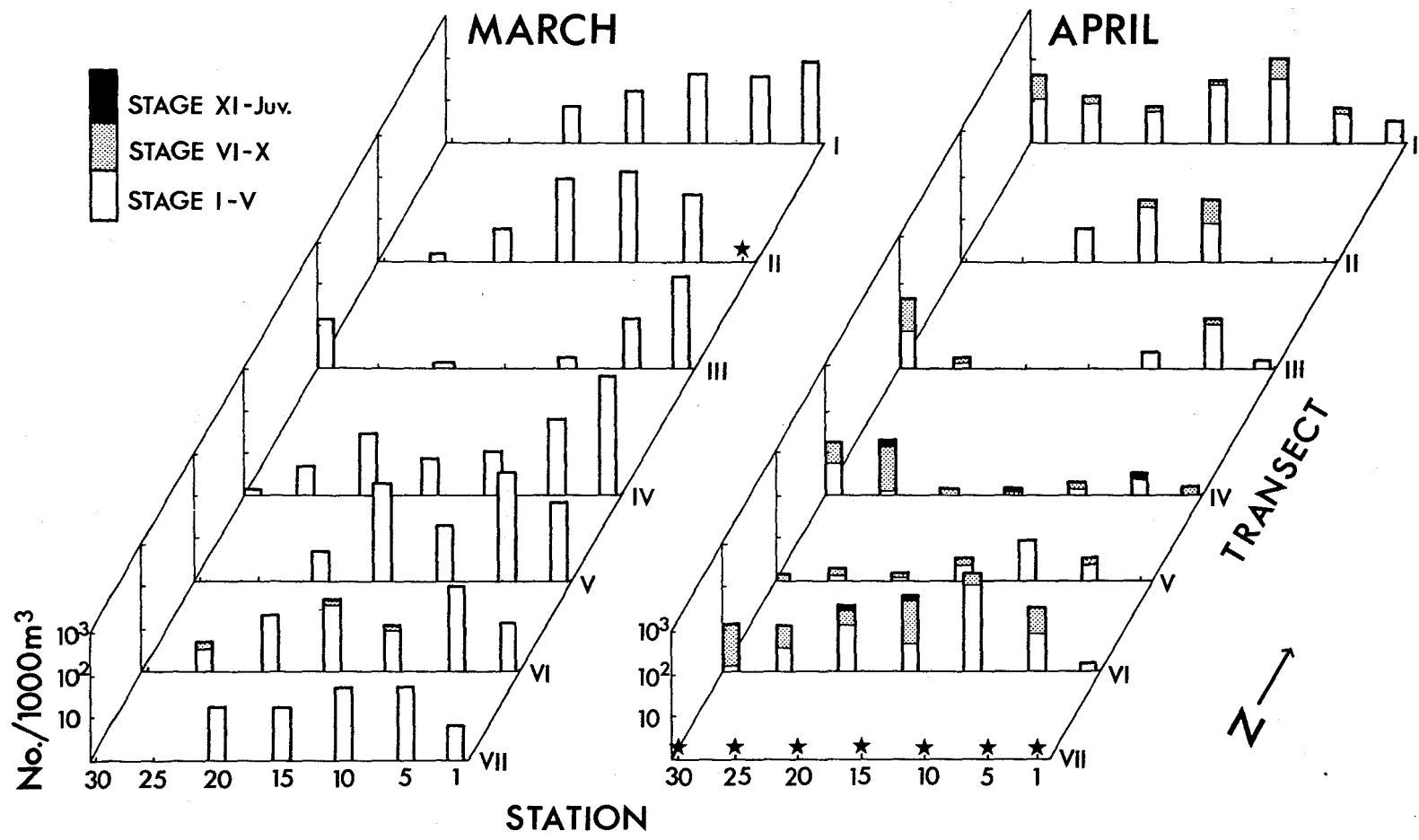


FIGURE 8.—Alongshore and offshore larval distribution and abundance in March and April 1972.

Tate and Clelland 1957). Overall larval abundance also varied between transects, IV and V having higher total numbers of larvae than the rest (1,093 and 718/1,000 m<sup>3</sup> compared with ca. 250). Offshore displacement and dispersion of larvae had occurred by late April. Larvae were most numerous at the 10 nmi station, and many were collected out to 30 nmi. Concordance among transects with respect to rank order of stations was less than in March but still significant ( $W = 0.43$ ;  $df = 7,6$ ;  $P < 0.01$ ). Larval numbers were reduced from March. Transects VI and I had the most larvae (418 and 232/1,000 m<sup>3</sup> compared with <100 in the others).

The gradient of larval age along the coast was evaluated by summing abundance of each stage within transects (Fig. 9). March showed no consistent gradient, but there were considerable differences in median stage among transects. Medians for transects V and VI were 3.28 and 3.43, respectively. Others averaged 2.0. By April transects were more uniform in this respect. Median stage was 4.9 with a low of 4.2 and high of 5.8. The median increased 2.4 stages

from March to April. While transects were more uniform, there was a wider range of stages in April with a slight increase in occurrence of older larvae in more southerly transects (IV to VI).

Onshore-offshore distribution was characterized by summing stage abundance at equivalent stations between transects for each cruise (Fig. 10). Zoeae I to IV predominated in March and were most abundant within 15 to 20 nmi. By April older larvae were dispersed outside 5 nmi.

### Field Estimates of Larval Growth Rates

The two years differed in the rate of change of developmental stage frequency. Development can be followed roughly by successive estimates of the median stage in the pooled samples for each cruise (arrows in Fig. 11). In early cruises of 1971 larvae already were widely dispersed and subject to temperatures below 9°C in the whole region (Fig. 5). Cold persisted until late April, and median stage only in-

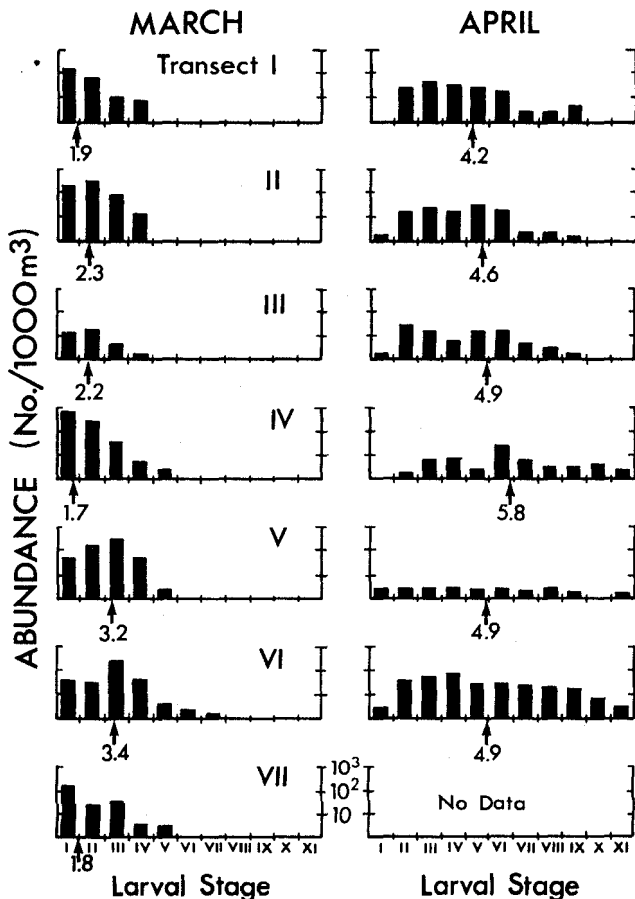


FIGURE 9.—Stage-specific larval distributions and abundance in March and April 1972. Larval abundance summed by stage within transects.

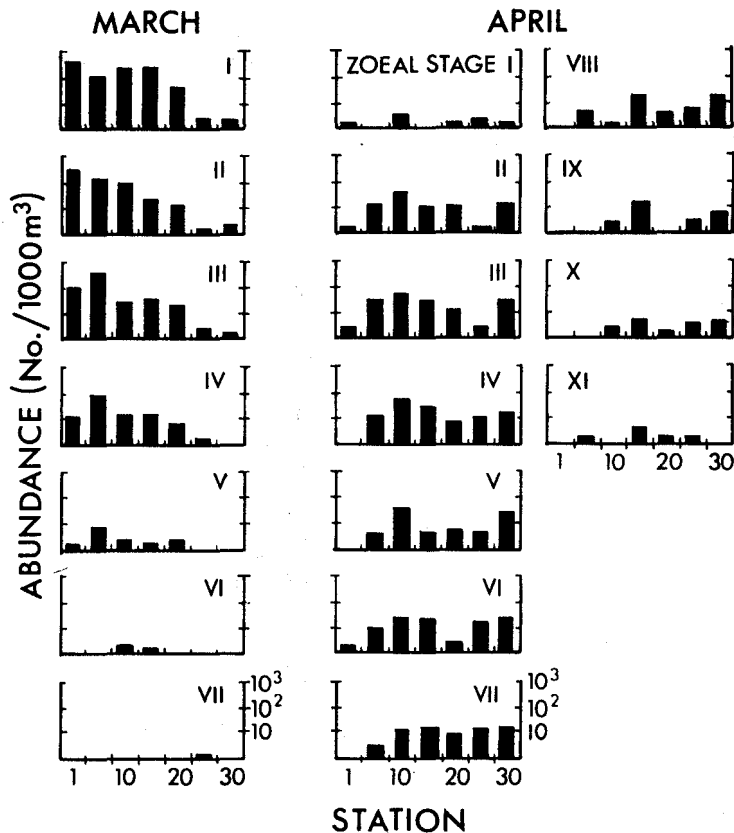


FIGURE 10.—Stage-specific larval distribution in March and April 1972. Larval abundance summed by stage over all transects.

creased to III by 4 May. There was rapid increase in median stage between 22 April and 1 June 1971, coinciding with rapid increase in surface temperature through May. In early cruises of 1972, larvae were confined to stations inshore of 20 nmi. Temperatures at those stations were about 2°C warmer than in 1971, and development was greater through 22 April, when median stage was V. Individuals up to Zoea XI were already present, which did not occur in 1971 until after the May spurt in development. Faster development in 1972 corresponded to water temperatures consistently higher than in 1971 from mid-March until June. By May of both years larvae were mostly dispersed between 10 and 50 nmi. Over that range temperatures were about the same and increasing from early May through June. Despite this, the increase in median stage slowed through June in both years. The median stage on 29 June was nearly XII in 1971 and XIII in 1972. The difference is not significant, and Zoea X through juvenile stages were present on that date in both years.

### Larval Survival—Estimates from Field Sampling, 1971 and 1972

To assess larval survival in the field, total abundance was calculated for each larval stage over all cruises and stations ( $\text{no./1,000 m}^3 \times \text{sampled depth} = \text{no./1,000 m}^3$ ). In each year the total number of Zoea I was taken to be 100% of the larval hatch, and the number of each successive stage was expressed as a percent of that hatch (Fig. 12). Sampling effort was very similar between the two years in respect to timing and total number of cubic meters of water filtered (72,246 m<sup>3</sup> in 1971; 67,979 m<sup>3</sup> in 1972), so that the difference in survival probably was not an artifact.

We caught 1,653 Zoea I in 1971 and 530 in 1972. There is a reversal in this estimate from the order of the years in respect to hatch as estimated from egg counts in the commercial catch. Table 2 shows that the latter estimate was quite close in the two years:  $1.75 \times 10^{12}$  and  $2.20 \times 10^{12}$  in 1971 and 1972, respec-

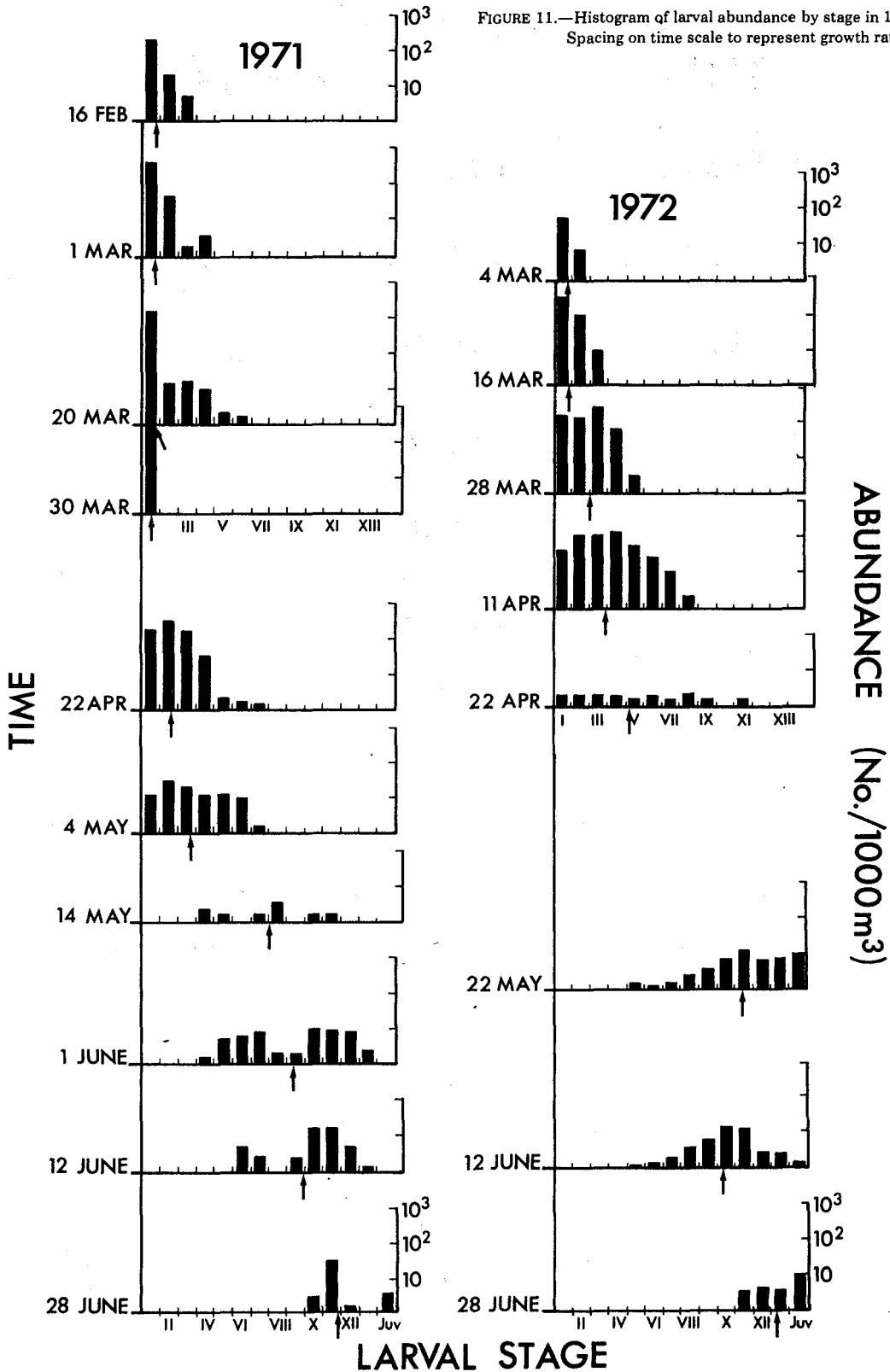


FIGURE 11.—Histogram of larval abundance by stage in 1971 and 1972. Spacing on time scale to represent growth rate.

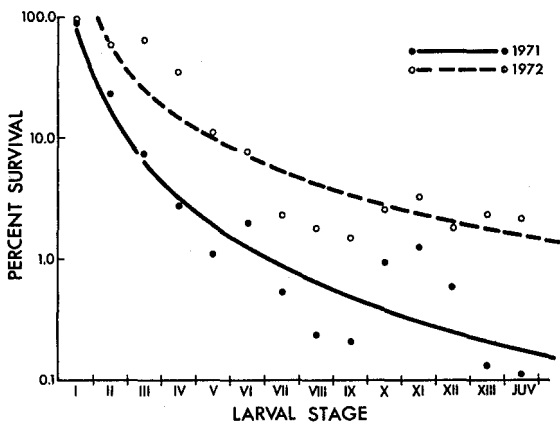


FIGURE 12.—Larval survival (percent) based on total numbers at each stage caught in the plankton sampling along NH line.

tively. Compared with the long-term variation in the commercial estimate of egg number, 1971 and 1972 were both close to average (mean 1961-80 = 1.93). In 1971, only 26.9% survived to Zoea II and <1% survived past Zoea VII. Only two Stage I juveniles (Rothlisberg 1980) were found in 1971, representing 0.17% of the hatch. In 1972 over 64% survived

through Zoea III, with numbers and percentages decreasing gradually with age. Five Stage I juveniles were caught, 1.06% of the hatch. Percent surviving to the juvenile phase in 1972 was an order of magnitude higher than in 1971. This is not, of course, simply a comparison of two versus five survivors. There was a consistent difference between the years throughout the developmental sequence. Some survival estimates from the decreasing abundance at successive stages are shown at the bottom of Table 2. Such estimates depend on the assumption that reproduction is relatively synchronous (Mullin and Brooks 1970; Fager 1973). In both years the main pulse of hatching of *P. jordani* occurred within a relatively limited period, essentially synchronously.

Some of the variability of percent survival at individual stages (Fig. 12) can be due to the relationship between sampling frequency and molting frequency (mean intercruise period was 14.5 d, while mean intermolt period is 6.8 d, a ratio of 2.1:1). Stages can effectively be passed by the bulk of the population between two samplings. A simulation model of survival through stages of development and time was developed to illustrate this effect. The model imposed an intermolt period of 6 d over the entire

TABLE 2.—Estimates of larval survival ( $e^{-it}$ ) from fishery data supplied by Fish Commission of Oregon (J. Robinson, see text footnote 5) and from field estimates of larval abundance  $i = \ln(N_t/N_0)/t$  where  $t = 1.5$  yr, the interval from hatching to recruitment to the commercial gear,  $i_{juv}$  = calculation for first year instantaneous mortality after recruitment to the bottom, from stomach analysis of hake, *Merluccius productus*, by Gotshall (1969, 1972);  $i_{larval}$  = instantaneous larval mortality as a proportion of the total instantaneous mortality ( $i$ ) with instantaneous juvenile mortality ( $i_{juv}$ ) held constant, see text.  $t = 1.274$  yr (100 d), estimated time of larval period in plankton;  $t = 0.364$ , period between calculations of  $N_0$  and  $N_t$  in 1971;  $t = 0.263$ , period between calculation of  $N_0$  and  $N_t$  in 1972.

Year	$N_0 \times 10^{12}$	$N_t \times 10^9$	$N_t/N_0 \times 10^4$	$-\ln N_t/N_0$	$i$	$i_{juv}$	$i_{larval}$	$e^{-it} \times 10^4$
1961	2.45	0.50	2.04	8.50	5.66	1.50	24.30	12.8
1962	1.25	1.10	8.80	7.04	4.69	1.50	18.96	55.4
1963	2.30	0.33	1.43	8.85	5.90	1.50	25.58	9.0
1964	4.20	2.60	6.19	7.39	4.93	1.50	20.26	38.8
1965	0.75	0.75	10.00	6.91	4.61	1.50	18.51	62.7
1966	2.95	1.20	4.07	7.81	5.20	1.50	21.78	25.6
1967	0.80	1.25	15.62	6.46	4.31	1.50	16.87	98.3
1968	2.25	1.30	5.78	7.46	4.97	1.50	20.50	36.3
1969	1.00	0.75	7.50	7.20	4.80	1.50	19.55	47.2
1970	2.15	3.00	13.95	6.58	4.38	1.50	17.28	87.8
1971	1.75	0.25	1.43	8.85	5.90	1.50	25.60	9.0
1972	2.20	1.95	8.86	7.03	4.69	1.50	18.94	55.7
1973	1.85	1.66	8.97	7.02	4.68	1.50	18.89	56.5
1974	3.14	2.70	8.60	7.06	4.71	1.50	19.05	54.1
1975	3.24	1.98	6.11	7.40	4.93	1.50	20.30	38.4
1976	1.51	0.88	5.83	7.45	4.96	1.50	20.47	36.7
1977	1.50	0.64	4.27	7.76	5.17	1.50	21.61	26.8
1978	2.28	0.22	0.96	9.25	6.16	1.50	27.03	6.1
1979	0.72	0.30	4.17	7.78	5.19	1.50	21.69	26.2
1980	0.47	0.50	10.64	6.85	4.56	1.50	18.27	66.9
Mean								42.52
Estimation of larval survival, from larval abundance (no./1000 m <sup>2</sup> )								
1971	140,040	236	18.85	6.38	—	—	17.51	8.25
1972	40,148	475	118.32	4.44	—	—	16.88	98.02

length of the development and an instantaneous daily mortality rate ( $i$ ) of 0.0788, the mean observed, overall rate of the two sampling years. This mortality was constant over all stages and constant within the molt cycle. The mortality rate was incorporated in a simple exponential decay formula to estimate survival rate over time ( $N_t = N_0 e^{-it}$ ). Two hatching-time distributions were used: 1) A standard Normal distribution with  $10^6$  individuals released over 20 d, and 2) a severely peaked distribution with 850,000 of the  $10^6$  released over 5 d around median hatch time. We feel the latter distribution most accurately reflects hatching of *P. jordani* in the field.

The population was sampled in the model at various intervals, and the sequence of abundance of successive stages was determined by summing the abundance of each over all samples, just as we have done with the field estimates. These model stage abundances were presented in Figure 13. As would be expected, sampling more than once within an intermolt period (every 4 d) tends to overestimate survival to each larval stage. Sampling every 9 d (1.5 times the intermolt period) consistently underestimated larval numbers and survival. The severely peaked distribution of larval hatching times resulted in an oscillating estimate of larval survival. Magnitude of the oscillation was related to the degree of phase agreement between the sampling and molting. In all cases, however, whether the number of larvae was over- or underestimated at any particular stage, the survival rate based on sums of estimates of abundance paralleled the "actual" rate.

Table 3 summarizes the time between cruises, the estimated surface temperatures for each intercruise

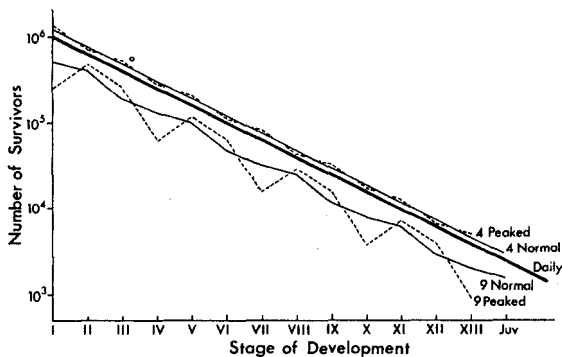


FIGURE 13.—The effect of sampling interval and larval hatching distribution on estimates of larval abundance and survival rate. Heavy line indicates "actual" survival rate; 4-normal, sampling standard normal distribution of larval hatch every 4 d; 9-normal, sampling every 9 d; 4-peaked, sampling peaked distribution of larval hatch every 4 d; 9-peaked, sampling peaked distribution every 9 d (see text for further explanation).

period (taken from Fig. 5), and an estimated intermolt period based on larval rearing experiments (Rothlisberg 1979). The shortest period between two cruises over the 2-yr sampling period was 8 d (22-30 May 1972), while the average was 14.5 d. Surface temperature for the larval period was rarely below  $8^{\circ}\text{C}$  (expected intermolt period = 8,08 d) and was  $10^{\circ}$  between 22 and 30 May 1972 (expectation = 7.0 d). The mean ratio of interval between cruises to intermolt period was 2.1, indicating that the survival estimates of this study would be low to an extent. Larvae could progress more than two stages between some cruises.

TABLE 3.—Period between cruises (days), estimated temperature for the period (from Fig.5), intermolt period at the temperature (from Rothlisberg 1979), and the ratio between intercruise (IC) period and intermolt (IM) period.

Sampling date	Intercruise period (days)	Temperature ( $^{\circ}\text{C}$ )	Intermolt period (days)	Ratio IC/IM
1971				
16 Feb.	13	9	7.3	1.8
1 Mar.	19	9	7.3	2.6
20 Mar.	10	8	8.1	1.2
30 Mar.	23	9	7.3	3.2
22 Apr.	12	10	7.0	1.7
4 May	10	11	6.6	1.5
14 May	16	11	6.6	2.4
1 June	11	12	6.4	1.7
12 June	16	14	6.3	2.5
28 June				
Mean				2.1
1972				
4 Mar.	12	11	6.6	1.8
16 Mar.	12	11	6.6	1.8
28 Mar.	14	10	7.0	2.0
11 Apr.	11	10	7.0	1.6
22 Apr.	30	10	7.0	4.3
22 May	8	10	7.0	1.1
30 May	13	10	7.0	1.9
12 June	16	10	7.0	2.3
28 June				
Mean				2.1
Overall Mean				2.1

## Estimates of Larval Survival from Commercial Landings

Long-range trends in larval survival of *P. jordani* were sought from Oregon fishery statistics to put the apparent differences in larval survival between 1971 and 1972 into perspective. Data on number of ova and of age 1 shrimp were provided by J. Robinson<sup>2</sup>. He estimated ova from adjusted estimates of numbers of females in samples of the April commercial landings and an empirical length to fecundity relationship (Robinson 1971). Numbers of age 1

<sup>2</sup>J. Robinson, Oregon Department of Fisheries and Wildlife, Marine Science Drive, Newport, OR 97365, pers. commun. February 1982.

shrimp were estimated from commercial landings 1.5 yr later (November) when they were fully recruited to the fishing gear. Figure 14 shows the fluctuations in these data from 1961 to 1980. Instantaneous rate of total mortality,  $i$ , was calculated from the data according to formulae of Ricker (1958). Results are shown in Table 2.

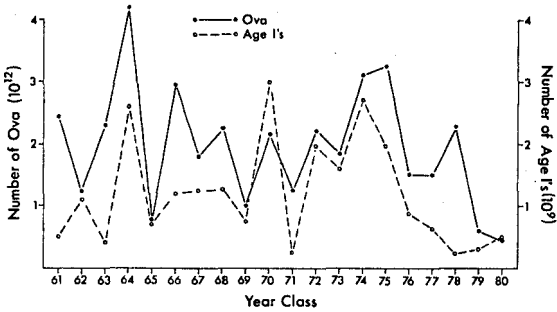


FIGURE 14.—Number of ova and number of age I shrimp recruited to the commercial fishery 1.5 yr later, by year class (Robinson unpubl. data).

Separation of the planktonic larval mortality from total mortality required an estimate of juvenile mortality. Gotshall (1969,1972), using an analysis of stomach contents of Pacific hake, *Merluccius productus*, which has been shown to prey on *P. jordani* without respect to age, has calculated that juvenile mortality rate,  $i_{juv}$ , is 1.50/yr. Proportioning total instantaneous mortality within the 18 mo from hatchling to first harvest was done according to:

$$i = \frac{0.274 (i_{larval}) + 1.226 (i_{juv})}{1.5}$$

where  $i = \ln(N_t/N_0)/t$ , with  $t = 1.5$  yr

$$i_{juv} = 1.50 \text{ (Gotshall 1969, 1972)}$$

$i_{larval}$  = instantaneous rate of larval mortality.

$$\text{Solving } i_{larval} = \frac{1.5(i) - 1.226(i_{juv})}{0.274}$$

Computed values of  $i_{larval}$ , along with overall larval survival ( $e^{-i}$ ), from commercial catch sample estimates for 1961 to 1980 are shown in Table 2 and compared with our results for 1971 and 1972. Both sets of estimates indicated that 1971 was a very poor year for larval survival, while 1972 was slightly above average.

## Factors Affecting Larval Survival

Comparison of onshore-offshore distribution patterns and wind patterns between 1971 and 1972 suggested that Bakun's upwelling index (1973, footnote 4) might be a useful indicator of habitat quality for survival of larval *P. jordani*. A study of possible correlations was originally made with data from 1961 to 1973. Fortnightly, monthly, and quarterly indices were calculated and regressed against the apparent overall larval-juvenile survival ( $e^{-i} \times 10^4$ ). The July index was the most highly correlated for a single month ( $R = 0.599$ ), while the average for the June through August period gave the highest correlation found ( $R = 0.749$ ). For those months the equation

$$\text{Larval survival} = e^{-i} \times 10^4 = 0.73 \text{ (upwelling index)} - 8.31$$

accounted for 56.2% of variability in larval survival. A new equation based on data from 1961 through 1980,

$$\text{Larval survival} = e^{-i} \times 10^4 = 0.889 \text{ (upwelling index)} - 9.652,$$

accounts for 54.9% of the 20 yr variability in larval survival. The slope is significantly different from zero ( $t_{18} = 4.81, P < 0.001$ ). The point for 1967 contributes strongly to the strength of the relationship, but the regression is significant without it ( $t_{17} = 3.35, P < 0.01$ ). The relationship between larval survival and upwelling index is shown in Figure 15.

This relationship of survival to upwelling strength

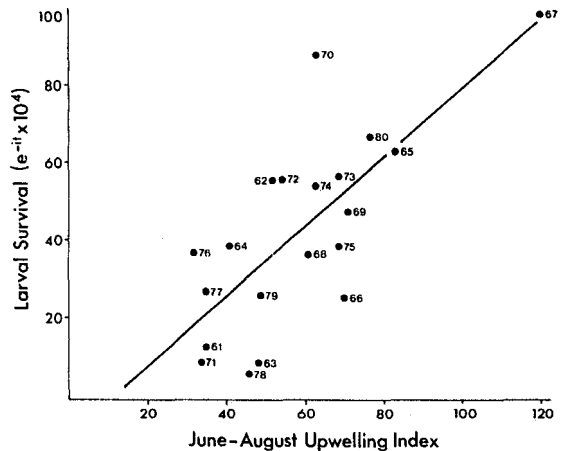


FIGURE 15.—Relationship between average upwelling in June through August 1961 to 1980 and estimated larval survival ( $e^{-i} \times 10^4$ ) 1961 to 1980, with fitted regression line.

gives some insight into what factors may limit survival, and thus year class strength, in the *P. jordani* fishery. Surface seawater temperatures in 1971 and 1972 (Fig. 5) were different in several respects. The regression analysis draws attention to months from June through August. In these late months of larval development, temperatures were several degrees higher at nearshore stations in 1971 than in 1972. Evaluation of laboratory rearing experiments showed that survival was highest at 11° to 12°C, and it decreased rapidly above that range (Rothlisberg 1979).

## DISCUSSION

Movements of adult *Pandalus jordani* associated with reproductive events have not been well defined. In contrast to other pandalids, e.g., *P. borealis* (Haynes and Wigley 1969; Horsted and Smidt 1956) and *P. montagui* (Lebour 1939, 1947; Mistakidis 1957; Allen 1963), there is no evidence of an inshore migration of female *P. jordani* prior to hatching of eggs they bear. Dahlstrom (1970) found that *P. jordani* at Morro Bay, Calif., moved 2 to 3 nmi farther offshore to spawn in the winter. Lukas and Hosie (1973) reported that female *P. jordani* left their study area 10 to 20 nmi off Tillamook Head, Oreg., in the fall. Numbers in March were greater at the south end of their grid than to the north, but there was no evidence of inshore or offshore movement associated with hatching. During the present study off Newport, Oreg., we found highest concentrations of adult *P. jordani* between 20 and 25 nmi offshore. While trawling was casual, and results are not reported here, there was no evidence of shoreward movement of ovigerous females during the period of hatching.

Prevailing wind and resultant currents could have transported larvae to the nearshore zone during the present study. Differences in wind and current between 1971 and 1972 are reflected in larval distributions for the two years. Furthermore, extended alongshore sampling in 1972 showed that shifts in distribution along the Newport line were representative of shifts along the whole coast. Shifts were not restricted to areas of high adult abundance.

Widespread distribution of early zoea in early and mid-March 1971 can probably be attributed to the mixed winds of February and to the spell of northwest wind in mid-March. More dramatic offshore displacement was seen in early May 1971, when larvae were found in abundance at 50 and 60 nmi. Numbers decreased markedly after May, probably through continued offshore displacement beyond the sampling area. More limited offshore dis-

placement of early larvae in 1972 coincides with stronger, more consistent southwest winds in February and March of that year. Older larvae were generally closer to shore in 1972 than in 1971. Offshore displacement by upwelling probably was reduced in 1972 by the advanced larval development at the initiation of upwelling compared with 1971. Since older larvae live deeper in the water column (Rothlisberg and Percy 1977), late onset of upwelling with respect to the development sequence will produce less offshore displacement.

Year-to-year fluctuations in seasonal winds, upwelling, and surface advection in the northwest Pacific have been repeatedly described (e.g., Wickett 1967; Hubbard and Percy 1971; Peterson and Miller 1975). However, until the upwelling index was developed by Bakun (1973), it was difficult to correlate strength of upwelling in a long sequence of years with variations in productivity at any level. This now can be done, although specific processes involved may remain obscure. Several of the features of upwelling may act to change production of a given life stage or species. The correlation we found between upwelling index and larval survival is something of a surprise. Earlier studies (Winnor 1966; Wickett 1967; Hubbard and Percy 1971) stressed the advective nature of upwelling. Thus we expected greater larval "wastage" to seaward for years with early onset and greater strength of upwelling. The colder temperatures also might be supposed detrimental to *P. jordani* because they should slow development. The unexpected, high, positive correlation of larval survival and June to August upwelling can be explained by other knowledge of larval physiology in *P. jordani*. Laboratory rearing experiments have shown optimal larval survival at 11° to 12°C (Rothlisberg 1979). Upwelling maintains these relatively low temperatures through the summer months, whereas weaker upwelling allows summer warming (Patullo et al. 1969). Temperatures above 14°C in June 1971 would have been harmful and may have contributed directly to low larval survival in that year.

The reproductive strategy of *P. jordani* appears to rely on the complex advection of late winter and spring. Many demersal species of the Pacific northwest spawn in winter and spring, apparently to maximize onshore drift of larvae and retention in coastal nursery grounds (Parrish et al. 1981). *Pandalus jordani* larvae, on the other hand, hatch in late winter and have a planktonic phase extending through the transition from northward-onshore to southward-offshore currents. They should usually encounter 1) onshore retention in early stages and 2) offshore displacement of later stages during subse-



quent upwelling, reaching deeper water over habitat suitable to settling.

Application to all years uniformly of Gotshall's (1969, 1972) instantaneous mortality for juvenile *P. jordani* on the bottom ignores the certain variation in that mortality. Despite this limitation, the estimate of larval survival derived from the analysis was similar to estimates from our 2 yr of intensive plankton sampling. We are aware of the dangers of a comparison based on only two spawning seasons, but the comparison is in the correct direction, and it is all we have. Although there are limitations, comparison of egg numbers with numbers of first fishery recruits shows promise for identifying conditions critical in establishing year class strength. Higher resolution could be obtained if annual estimates of early benthic mortality were made, perhaps using the Pacific hake, *Merluccius productus*, as a biological sampler.

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