AN ABSTRACT OF THE THESIS OF

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       (Name)   (Degree)

in <u>   ZOOLOGY   </u> presented on <u>   March 12, 1975   </u>
    (Major Department)   (Date)

Title: LARVAL ECOLOGY OF <u>PANDALUS JORDANI</u> RATHBUN

Abstract approved: <u> Redacted for Privacy   </u>
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In this study the distribution and abundance of larval <u>Pandalus jordani</u> have been characterized for the Oregon area for the first time by an intensive plankton survey. Seasonal wind regimes and surface currents were shown to affect larval distribution. Upon hatching in March, larvae were concentrated nearshore by the onshore component of the currents generated by the predominant southwest winds that occurred from February through April. As the wind shifted to the northwest in late April, larvae were moved offshore. Differences in the distribution of <u>P. jordani</u> larvae between 1971 and 1972 corresponded with the strength, duration and direction of the predominating wind.

Growth rates of larval shrimp were observed to be slower in 1971 than in 1972. This corresponded with the generally lower temperatures in the early larval season of 1971. Larval survival, as estimated in the plankton survey, was lower in 1971 than in 1972.

Stratified plankton tows and the use of an epibenthic sampler demonstrated that P. jordani larvae occupied the entire water column. There was an age gradient with depth, with older larvae found deeper. Vertical migratory habits were demonstrated in the last larval and first juvenile instars. Late larvae were not recruited to the bottom until after the molt to the first juvenile instar.

Response surface techniques were used to determine the combined effects of temperature and salinity on survival of larval P. jordani reared in the laboratory. In early larvae, the optimal temperature range was 9 to 11°C. This was observed over the entire range of salinities (26-34‰)tested. In older larvae the temperature optimum increased to 11-12°C, and low salinities (~26‰) reduced survival. Increased temperatures had a direct effect on larval growth rate. Molting frequency was increased and intermolt period shortened at higher temperatures. An inverse relationship between temperature and maximum larval size was not observed. Larvae reared at 8, 11 and 14°C all attained similar sizes which were larger than those reared at 5 and 17°C. Larval growth increments were measured in laboratory reared and field sampled larvae. There was no apparent relationship between temperature or stage of development and the growth increment in laboratory reared animals. Growth increment measured in field larvae decreased with increasing stage of development.

Extrapolations from commercial shrimp landing data were used to assess long term trends in larval survival from 1960-1973 in order to compare these levels with the levels of larval survival observed in this study. By this method larval survival in 1971, estimated from the plankton survey, appeared to be below average, while in 1972 larval survival was slightly above average. Regression analysis indicated that the variation in hydrographic conditions in June, July and August, explained a significant amount of the year-to-year variation in larval survival based on estimates from commercial landings (1960-1973). This analysis, and knowledge gained in the laboratory rearing experiments, indicates that the colder temperatures or other conditions that accompany strong upwelling enhance larval survival, while the elevated temperatures that characterize weak upwelling have an adverse effect on larval survival.

Larval Ecology of Pandalus jordani Rathbun

by

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A THESIS

submitted to

Oregon State University

in partial fulfillment of
the requirements for the
degree of

Doctor of Philosophy

Completed March 1975

Commencement June 1975

APPROVED:

Redacted for Privacy

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Date thesis is presented _____ March 12, 1975 _____

Typed by Mary Jo Stratton for __Peter Charles Rothlisberg__

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ACKNOWLEDGMENTS

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LARVAL ECOLOGY OF PANDALUS JORDANI RATHBUN

INTRODUCTION

Shrimps of the family Pandalidae support important fisheries throughout the world, but those of major importance are concentrated in cool temperate and boreal waters (Scrivner and Butler, 1971). Pandalus jordani Rathbun ranges from Unalaska (53°45'N, 166°40'W) to San Diego, California (32°30'N, 117°20'W) at depths of 64-326 m (Rathbun, 1904). The population appears to have its maximum density off the central Oregon coast, but the species is also abundant in waters from northern California to at least Cape Beale, Vancouver Island (Dahlstrom, 1970). The highest catch rates occur off the Oregon and Washington coasts at depths of 110-183 m (Ronholt, 1963). Pandalus jordani is the predominant species of pandalid shrimp off Washington, Oregon and California and is largely replaced by P. borealis Kroyer in waters off British Columbia and Alaska. Fluctuations in landings associated with varying year-class strengths have been observed in this fishery during the past 17 years (Lall, 1970; McCrary, 1973).

Hjort (1914, 1926) emphasized the importance of considering the success of larval forms in determining the size of incoming year classes. Gulland (1965) reviewed efforts to correlate incoming year-class strength and environmental conditions during early development.

These efforts were largely unsuccessful because correlations between year-class strength (based on landings) and environmental parameters have been inadequate to assess larval mortality (Gulland, 1965). Gulland believed that the only adequate way to measure larval mortality, and the factors affecting it, was by intensive egg and larval surveys.

An intensive effort to assess the abundance, geographic distribution and seasonal occurrence of larvae of fish, shellfish and associated zooplankton was undertaken by the Oregon State University Sea Grant Early Life History Project from 1970 through 1972.

The present study represents one facet of the Early Life History Project, the larval ecology of P. jordani. The purpose of this study was to determine the temporal and spatial distribution and abundance of the larvae and to relate the year-to-year changes in larval distribution, abundance and survival to environmental factors. Larvae were cultured in the laboratory, under conditions of temperature and salinity that encompassed those occurring in the field during the period of larval development, to assess the effect of these factors on growth and survival of the larvae. It was expected that a study of this nature would lead to greater understanding of the factors affecting fluctuations in the P. jordani fishery off Oregon.

MATERIALS AND METHODS

Field Sampling

All sampling, except on cruises C7203G, C7204G and C7205D, was restricted to the stations on the Newport Hydro-line (Figure 1, Table I). Cruises C7203G and C7204G were grids in which a series of seven transects from Tillamook Head (I) south to near the Siuslaw River (VII) were run from 1-30 nautical miles (1.85 to 55.5 km) off the coast (Figure 2, Table II). Cruise C7205D was a 24 hour sampling period at grid station IV-10. With one exception, Y7104C, all sampling was done from the 24.4 m R/V CAYUSE. Figure 3 summarizes the dates and extent of the 34 Early Life History cruises in 1971-1972, on which samples were taken to determine the distribution and abundance of P. jordani larvae.

Hydrographic data were gathered at each station. At the surface, a temperature and a salinity sample were taken. Temperatures at lower depths were obtained by means of a bathythermograph (BT) cast to the bottom or 150 m, and a salinity sample was taken from the lowest extent of the BT. Salinity samples were analyzed with a CSIRO inductively coupled salinometer. On cruise Y7104C, data were read from an electronic salinity-temperature-depth meter.

On seven cruises drift bottles were released in cooperation with M. J. Hosie, Fish Commission of Oregon (Table III). Data on
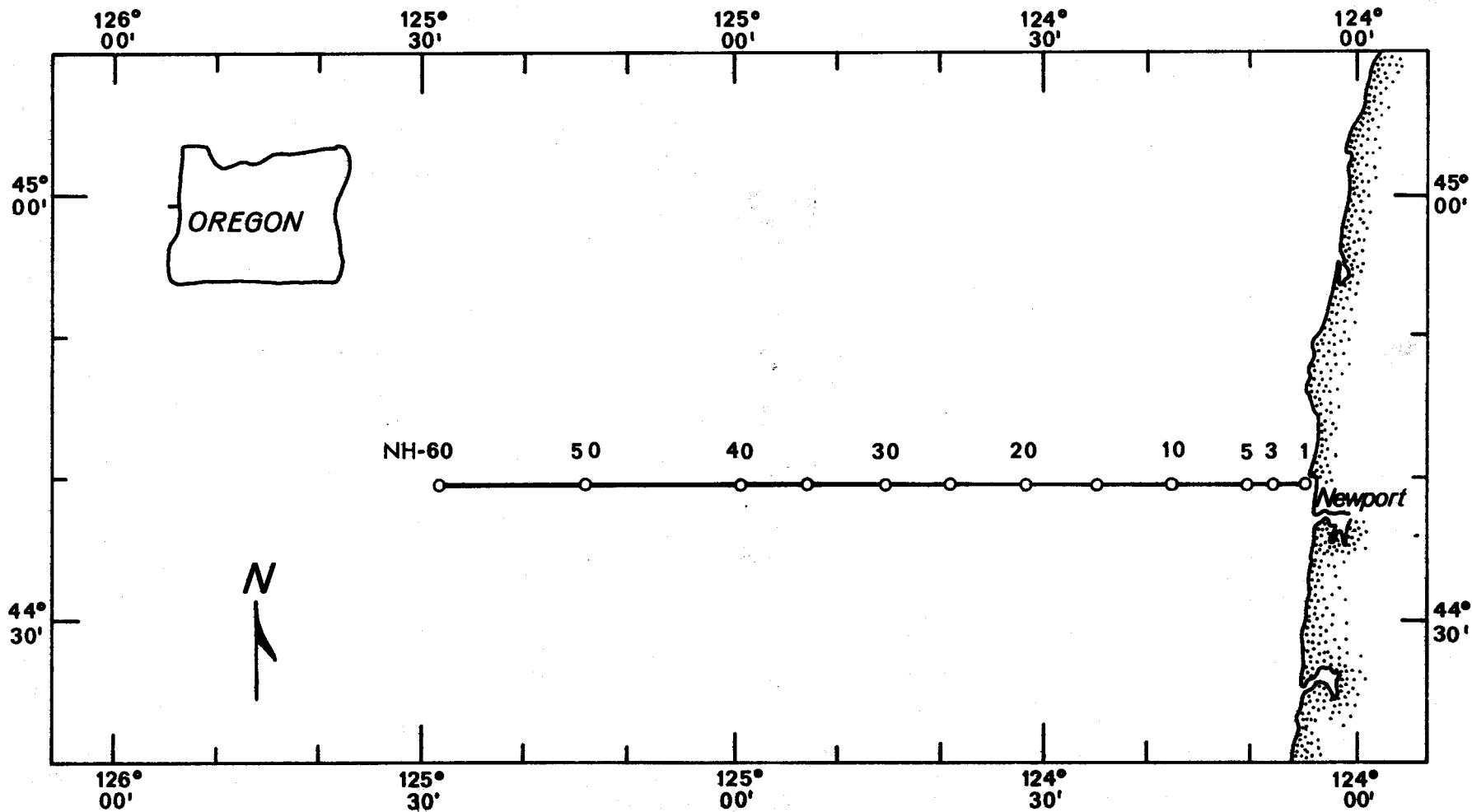
Figure 1. Newport hydro-line with the 12 stations used routinely for the Early Life History sampling.

Table I. Location and depth of sampling stations on the Newport hydro-line. (Latitude $44°39.1'N$)

Station	Distance from shore (km)	Longitude	Depth (m)
NH 01	1.85	$124°05.4'W$	20
NH 03	5.56	$124°08.6'W$	46
NH 05	9.26	$124°10.7'W$	59
NH 10	18.52	$124°17.7'W$	85
NH 15	27.75	$124°24.7'W$	95
NH 20	37.04	$124°31.7'W$	142
NH 25	46.30	$124°38.7'W$	330
NH 30	55.56	$124°45.7'W$	220
NH 35	64.82	$124°52.7'W$	340
NH 40	74.08	$124°59.7'W$	1,060
NH 50	92.60	$125°13.7'W$	1,300
NH 60	111.12	$125°27.7'W$	2,850
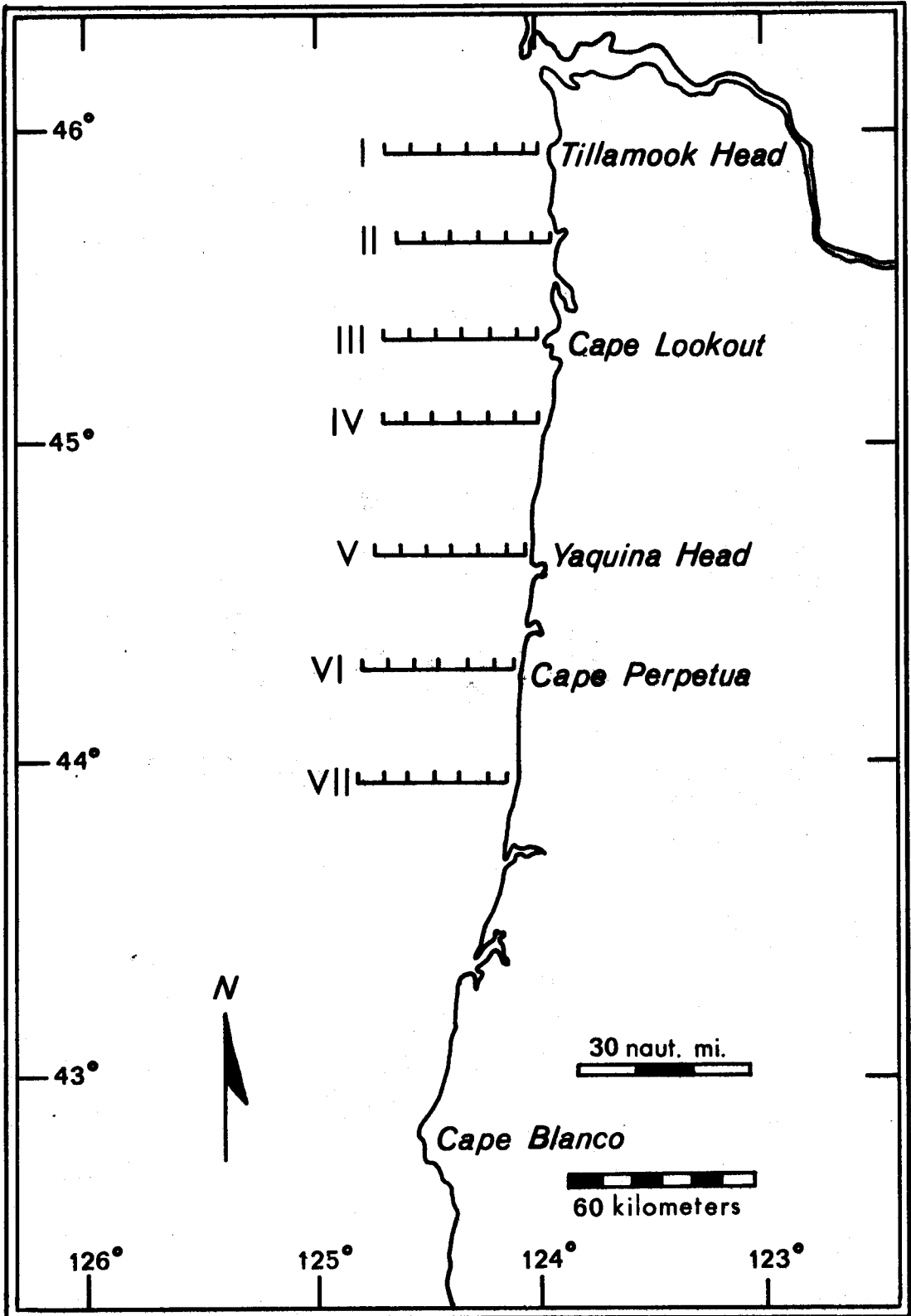
Figure 2. Grid transects and stations used on cruises C7203G and C7204G.

Table II. Location and depth of sampling stations on the seven Grid transects.

Station	Latitude	Longitude	Depth (m)	Station	Latitude	Longitude	Depth (m)
I-1	45°56.1'N	124°02.2'W	55	V-1	44°39.1'N	124°05.5'W	20
I-5		124°06.5'W	80	V-5		124°10.5'W	58
I-10		124°13.8'W	109	V-10		124°17.6'W	80
I-15		124°20.9'W	137	V-15		124°24.5'W	90
I-20		124°28.0'W	155	V-20		124°31.6'W	146
I-25		124°35.2'W	161	V-25		124°38.6'W	285
I-30		124°42.2'W	226	V-30		124°45.6'W	205
II-1	45°39.5'N	123°57.8'W	24	VI-1	44°17.3'N	124°08.4'W	33
II-5		124°03.5'W	78	VI-5		124°13.8'W	55
II-10		124°10.5'W	105	VI-10		124°20.7'W	80
II-15		124°17.7'W	145	VI-15		124°27.8'W	95
II-20		124°24.9'W	175	VI-20		124°34.8'W	95
II-25		124°32.0'W	219	VI-25		124°41.6'W	87
II-30		124°39.0'W	350	VI-30		124°48.6'W	146
III-1	45°20.0'N	124°02.2'W	55	VII-1	43°56.0'N	124°10.8'W	20
III-5		124°07.4'W	110	VII-5		124°15.6'W	87
III-10		124°14.6'W	168	VII-10		124°22.5'W	117
III-15		124°21.6'W	219	VII-15		124°29.2'W	130
III-20		124°28.8'W	402	VII-20		124°36.2'W	180
III-25		124°35.8'W	410	VII-25		124°42.8'W	167
III-30		124°42.9'W	500	VII-30		124°49.8'W	140
IV-1	45°04.0'N	124°02.3'W	30				
IV-5		124°08.0'W	95				
IV-10		124°15.1'W	168				
IV-15		124°22.3'W	245				
IV-20		124°29.3'W	366				
IV-25		124°36.5'W	440				
IV-30		124°43.5'W	439				
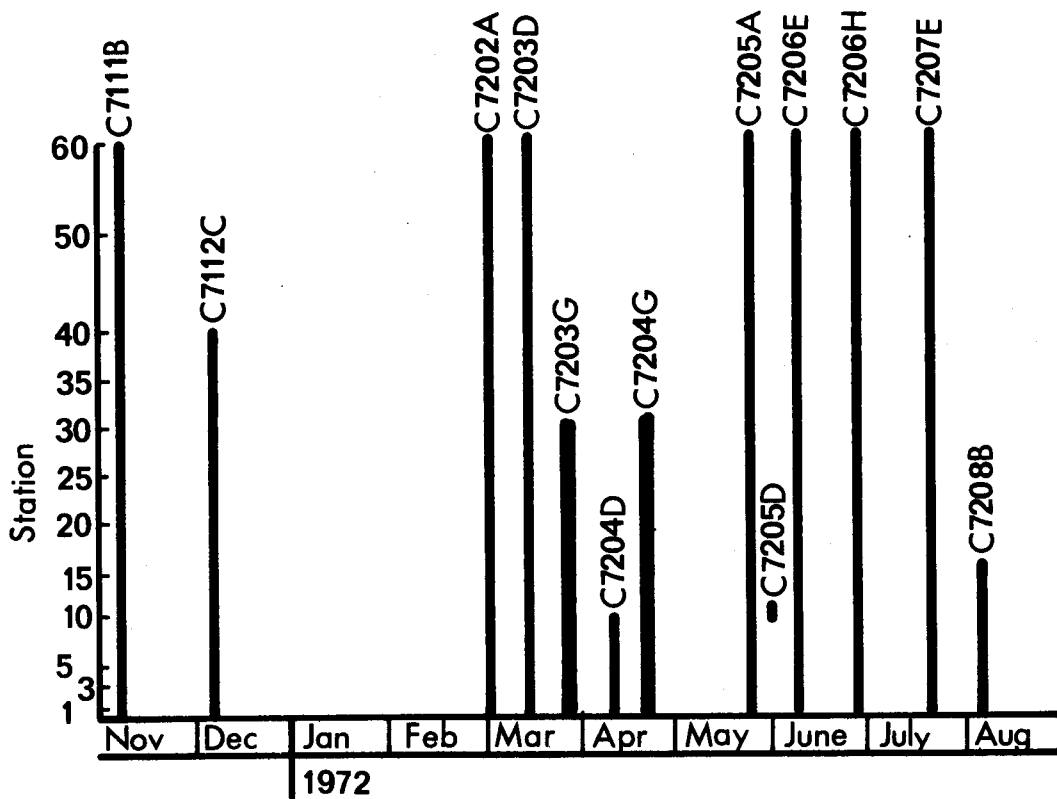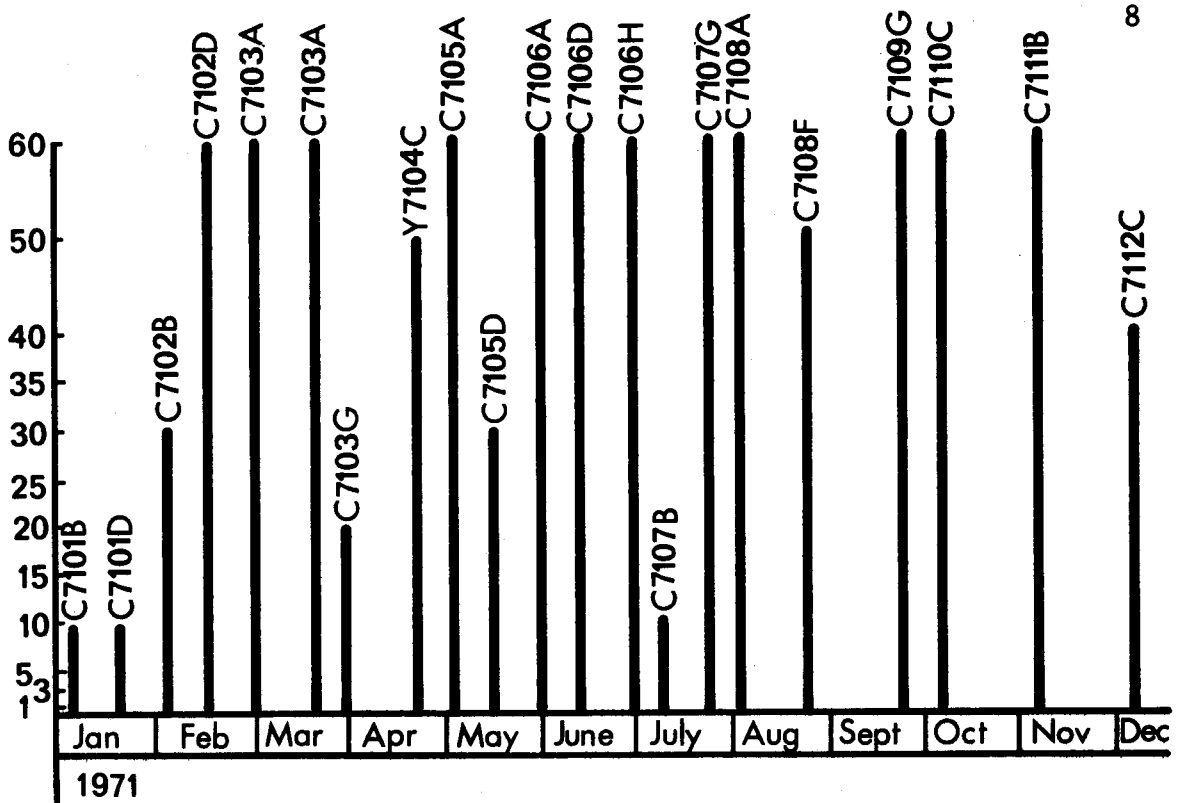
Figure 3. Date and extent of 34 Early Life History cruises, from January, 1971 - August, 1972.

Table III. Date, number and station of drift bottle releases on 1972 cruises.

Cruise	Date	Release area	No. /station	No. /cruise
C7202A	3, 4 March	NH 1-60	12	144
C7203D	15, 16 March	NH 1-60	12	144
C7203G	27-30 March	I-1 - VII-30	12	576
C7204D	11 April	NH 1-10	12	48
C7204G	19-22 April	I-1 - VI-30	24	1008
C7205A	22, 23 May	NH 1-60	24	288
C7206E	11, 12 June	NH 1-60	24 (+120 @ NH-60)	408
C7207E	21, 22 July	NH 1-60	24	288
C7208B	5 August	NH 1-15	24	120

drift bottle returns were compiled and analyzed by William Gilbert, OSU Oceanography.

After the hydrographic sampling was completed, plankton tows were undertaken using tandem sets of bongo nets (Figure 4). The small (0.2 m) bongos had cylinder/cone nets 1.8 m in length made of 0.233 mm and 0.571 mm Nitex mesh with an effective filtering area to mouth area ratio of 10:1. The large (0.7 m) bongos had two cylinder/cone nets 5.1 m in length of 0.571 mm Nitex on both sides, with an effective filtering area to mouth area ratio of 8:1. A scope to depth ratio of 2:1 was maintained by using a 40 kg multiplane kite-otter as a wire depressor (Colton, 1959). The water column was divided into three to five levels depending on depth. The nets were lowered to near bottom or 150 mm and held for three to five minutes at that level and then raised to the next level for an equal period of time. This resulted in stepped-oblique tows. A time-depth recorder trace was obtained for each tow. The tows lasted from 10-25 minutes depending on the depth of the station. Replicate tows, as well as day/night collections, were made on several occasions. A speed of 2-3 knots was maintained by cruising into the prevailing sea. All nets contained TSK flowmeters (Tsurumi-Seikikosakusho Co. Ltd., Yokohama, Japan). Meters were calibrated infrequently both at sea and in swimming pools by towing the meters known distances repeatedly. Because of infrequent calibration, a regression line was fitted to the
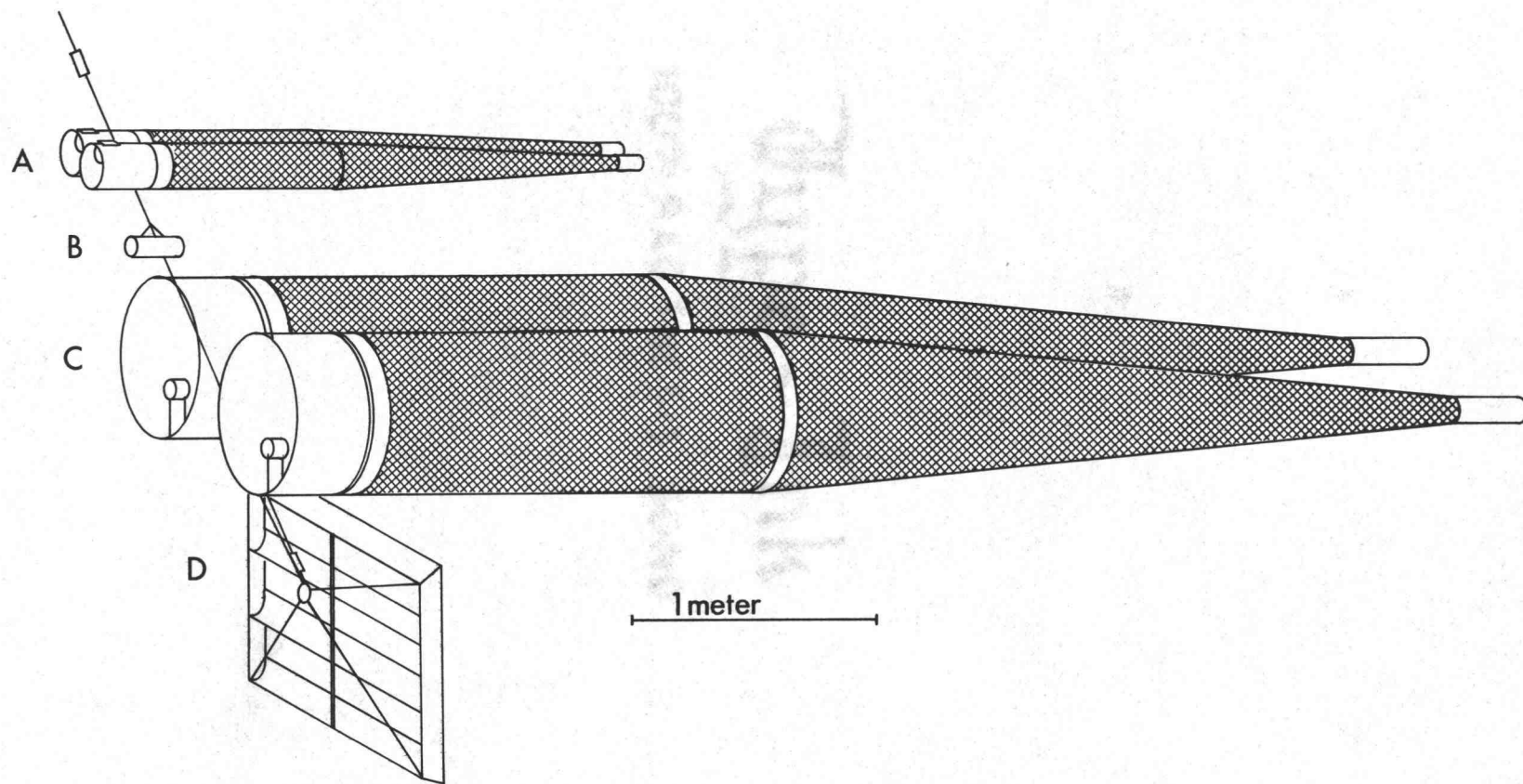
Figure 4. A. Small (0.2 m) bongo nets, B. time-depth recorder, C. large (0.7 m) bongo nets, D. multiplane kite-otter wire depressor.

calibration factors for the different calibration times, and an estimated calibration factor was taken from that line for each cruise. All samples were immediately preserved at sea with 10% formalin. They were then condensed and buffered with sodium borate on shore within one week of fixation. Only the sample from the port side of the large bongos was analyzed. Because of the low density of the larvae, this entire sample was sorted. No subsampling was done. A total of 367 samples was sorted for shrimp larvae from the two years of sampling.

An epibenthic sampler (EBS, Figure 5) was designed and used to capture larval and juvenile shrimp on or near the sea floor. A box with a spring-loaded door was mounted on the sled at a variable height above the bottom (ca. 25 cm). Upon contact with the sea floor a shoe attached to the door was depressed, which held the door open allowing water to pass through the tox, flowmeter and plankton net. As soon as the sled was lifted from the floor four heavy springs closed the door, stopped the flow of water through the box and held it shut on the return to the surface. In this manner quantitative samples of animals on or just above the sea floor could be sampled without contamination from plankton higher in the water column. The EBS was used systematically on cruises C7204G and C7205D. The EBS was irreparably damaged in use before a more extensive sampling program could be completed.

A

B

C

1 meter
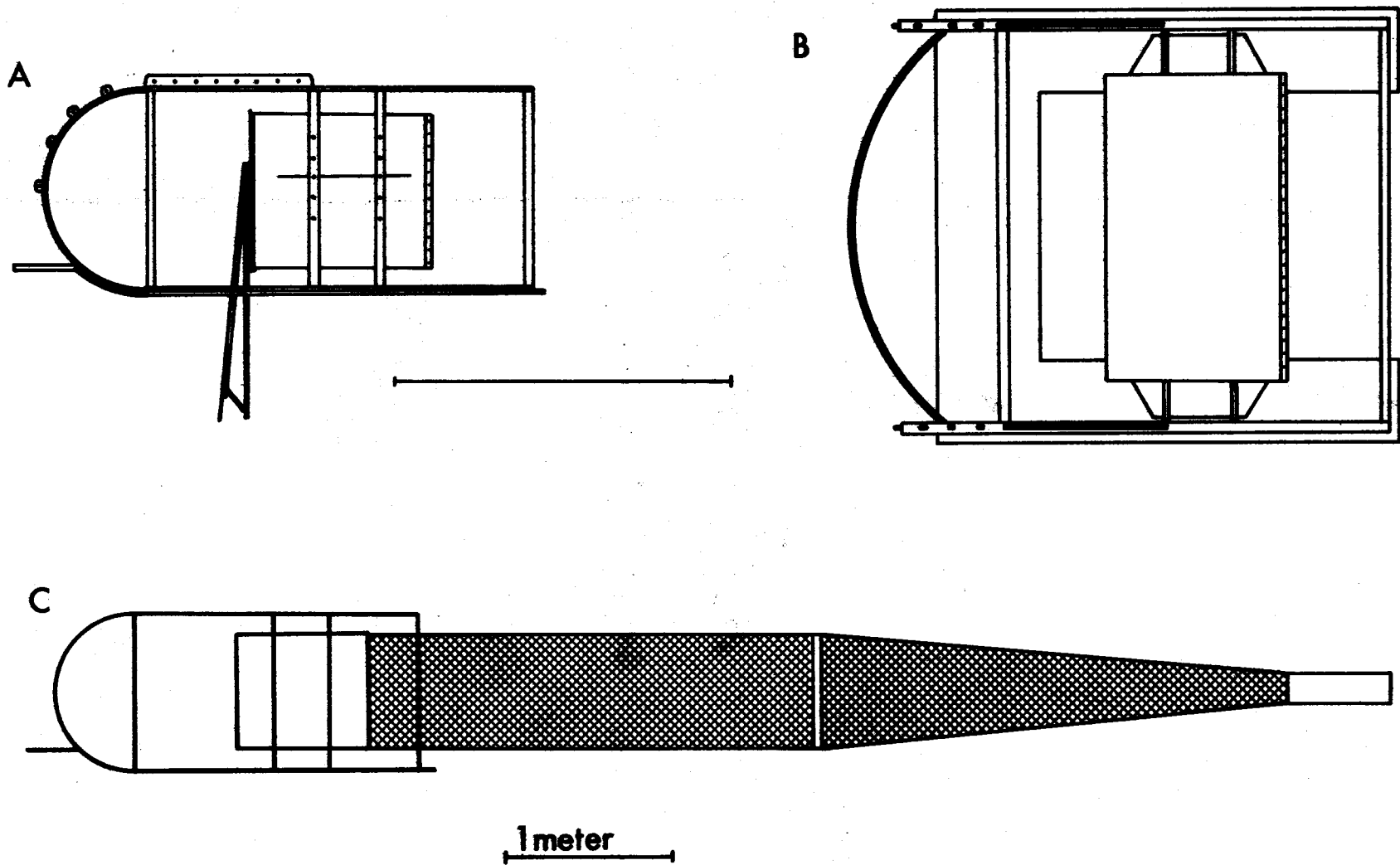
Figure 5. Epibenthic sampler. A. side view, B. top view, C. sampler with net attached.

On several cruises a 16' (4.9 m) semi-balloon otter trawl

(Marinovich Trawl Co., Inc., Biloxi, Mississippi) was used to assess

abundance of adult shrimp and the percentage of ovigerous females at

selected stations. Live ovigerous females to be used in the larval

rearing experiments were also collected with this trawl.

Hourly wind data were supplied by William Gilbert, School of

Oceanography, Oregon State University. The data were gathered by

the National Weather Service from a recording anemometer located at

the base of the south jetty at Newport, Oregon. The data are stored

as a scaler (kilometer-miles) divided into north-south and east-west

components. The resultant vectors from the daily means for 1971 and

1972 were plotted as progressive vector diagrams by Dr. C.B. Miller,

School of Oceanography, Oregon State University.

Laboratory Experiments

The major emphasis of the laboratory work was to find tempera-

ture and salinity tolerances and optima for growth and survival of

P. jordani larvae. A 5 x 5 factorial design was employed with tem-

peratures of 5, 8, 11, 14 and 17°C and salinities of 26, 28, 30, 32

and 34‰ . The ranges of temperature and salinity were chosen to

encompass those in the field during the period of larval development.

Twenty-five larvae were placed in each polyethylene container with

600 ml of filtered seawater. Four such containers were placed in

each of the 25 temperature/salinity combinations. Table IV summarizes the factorial design and the order in which it was filled.

The percent survival to each larval stage was analyzed by response surface methodology as reviewed by Alderdice (1972). The surface is described by the quadratic:

$$Y = b_0 x_0 + b_1 x_1 + b_2 x_2 + b_{11} x_1^2 + b_{22} x_2^2 + b_{12} x_1 x_2$$

where Y = percent survival, x_1 = temperature (${}^{\circ}$C), x_2 = salinity (‰), and b_0 = constant, b_1 = linear effects of temperature, b_2 = linear effects of temperature, b_{11} = quadratic effects of temperature, b_{22} = quadratic effects of salinity, b_{12} = interaction effect of temperature and salinity (Box and Youle, 1955). The equation was fitted for each larval stage using multiple regression. The resulting equations were used to generate response surface estimates of percent survival.

Seawater was brought from offshore because of the low salinity and suspect water quality of the Marine Science Center water supply during times of high river flow. One-half of the animals (two containers) at each temperature/salinity combination were checked daily. Therefore, each container was inspected every other day, the number of larvae surviving, the number of molts and stage of development of each individual were recorded (see Appendix for details of larval staging). The water was changed, and fresh food was added. Artemia salina nauplii hatched from San Francisco Bay brine shrimp

Table IV. Factorial design: temperature, salinity, and the order and extent to which the design was filled.

Temperature (°C)	Salinity (‰)											
	26		28		30		32		34		growth	
5	2	2	2	2	2	2	2	2	2	2	2	2
	2	2	2	2	2	2	2	2	2	2	2	x
8	1	1	1	1	1	1	1	1	1	2	2	2
	2	2	2	2	2	2	2	2	2	2	2	2
11	1	1	1	1	1	1	1	1	1	1	1	1
	2	2	2	2	2	2	2	2	2	2	2	2
14	2	2	2	2	2	2	2	2	2	2	2	2
	2	2	2	2	2	2	2	2	2	2	2	2
17	2	2	2	2	2	2	2	2	2	2	2	2
	3	3	3	3	3	3	3	3	x	x	x	x

25 larvae/container with 600 ml filtered seawater

Numbers indicate date of initiation: 1 = 16 March, 1973; 2 = 17 March, 1973; 3 = 18 March, 1973

x = Containers not filled due to insufficient numbers of larvae

eggs (San Francisco Fish Farms, Inc., Menlo Park, California) were used exclusively for food. As the P. jordani larvae grew, the Artemia larvae were reared to larger sizes by holding them in seawater containing heavy concentrations of the chrysophyte Isochrysis galbana Parke (Indiana University, LB 987). Mixed sizes (1, 2, and 3 days after hatching) of Artemia nauplii were fed to the P. jordani uniformly at all temperatures and salinities. No attempt was made to quantify the food input except to ensure that food would still be present at the next inspection two days later.

Temperature was maintained within $0.1^{\circ}C$ by using thermostatically controlled water baths. Experimental salinities were attained either by dilution with double glass distilled water or the addition of evaporated seawater brine volumetrically. Accuracy within 0.1‰ could be obtained with this method and was checked frequently with the CSIRO inductively coupled salinometer.

In addition to the factorial design experiment, 100 larvae were maintained as above, at 32‰ at each of the five temperatures for analysis of growth rates and morphometric studies. Five larvae were preserved from each temperature at each zoeal stage.

RESULTS AND DISCUSSION

Field Sampling

General Distribution and Abundance--1971

The temporal and spatial distribution and abundance of P.

jordani larvae collected in 1971 are graphically summarized in

Figure 6. Early zoeae (I, II and III) were found on 16 February, when

they were widely distributed but most abundant at 5, 10 and 15 nauti-

cal miles. In early March all larvae were within 20 nautical miles

with the highest density at NH 5. Most of the larvae were recently

hatched but there were some Stage II's, III's and IV's. The cruise on

20 March coincided with what appeared to be the peak of larval hatch-

ing, since Stage I's predominated and were most abundant within 20

nautical miles of shore. The late March cruise was abbreviated

because of bad weather. However, all larvae found were Stage I's at

the 3 and 5 nautical mile stations. By 22 April the P. jordani larvae

were dispersed from NH 5 to NH 50, with the peak of abundance at

NH 5, consisting mostly of Stage II and III. A few Stage VI's and

VII's were present at NH 15. In early May the distribution of larvae

appeared to have one center at NH 5 and another at NH 50. Young

stages predominated at both centers. Samples collected on 14 May

contained small numbers of intermediate and later larvae between

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STAGE XI-JUV.
STAGE VI-X
STAGE I-V

NO./1000M³

10^3
10^2
10

STATION

60 50 40 30 20 10 5 1

16-II
1-III
20-III
30-III
22-IV
3-V
14-V
1-VI
12-VI
28-VI
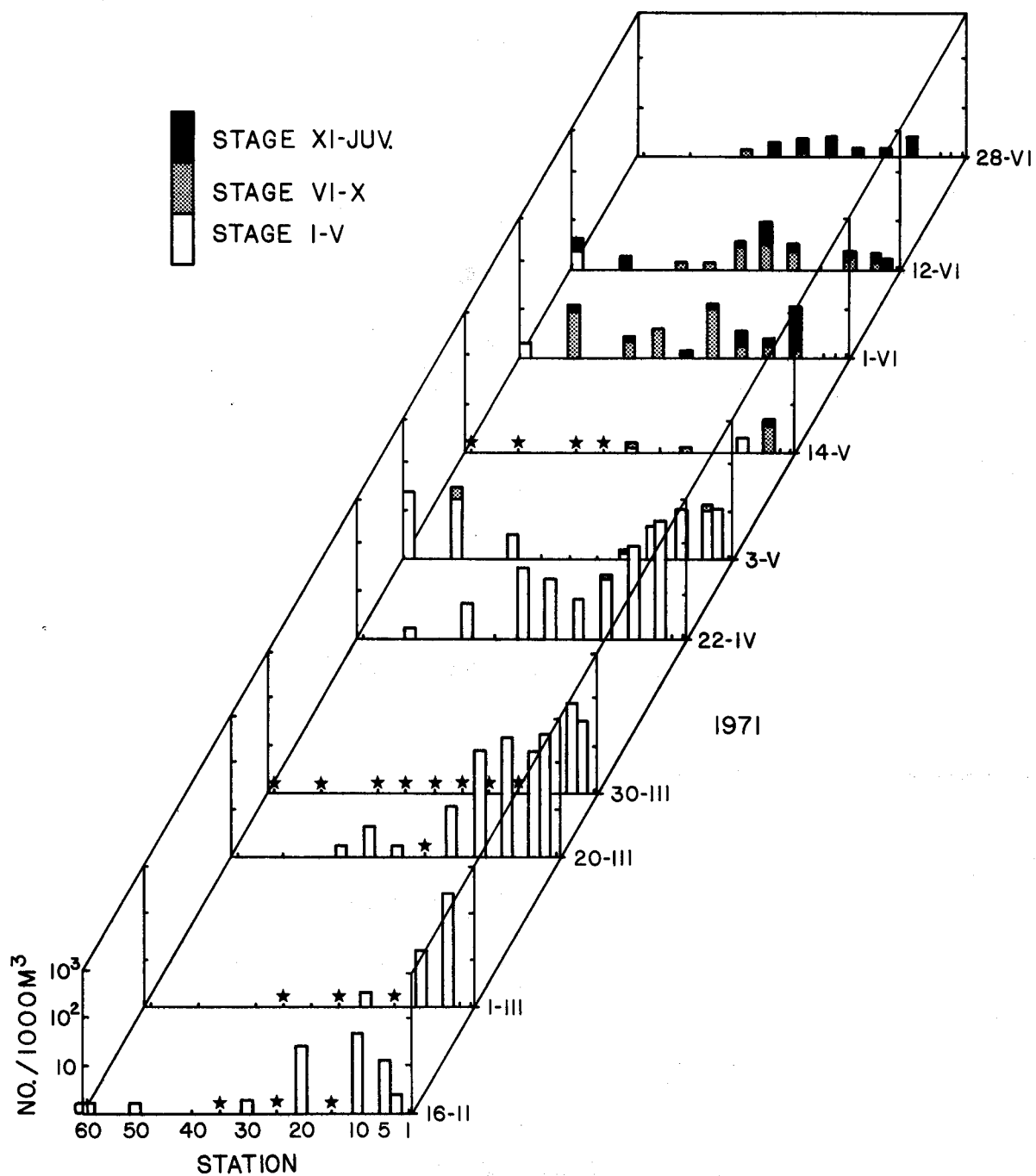
1971

Figure 6.   Three dimensional display of larval distribution and
abundance with time for 1971.

NH 5 and NH 30. On 1 June larvae were more widely distributed between NH 10 and NH 60, and were intermediate to late in development (VI - XIII). Larval abundance, though greater than in mid May, was still low. On the 12 June cruise the larvae were even more dispersed (NH 3-60), well developed and had a peak of abundance at NH 25. On the 28 June cruise the only juvenile of the season was found at NH 15. Other larvae were found between 10 and 40 nautical miles from shore and were in very late stages of development (Stage X - XVI). No larvae or juveniles were found in the water column on the 6 July and 21 July cruises.

Stage Specific Larval Distribution--1971

In order to gain an understanding of spatial distribution of individual larval stages, abundances of larvae (no. /1000 m^3) in a given stage were summed for each station over all cruises. Figure 7 summarizes this information. In 1971 Stage I, though most abundant inshore, was scattered over the entire length of the 60 mile transect. This trend continued for later larval stages (II - V). A large number of these larvae were found at NH 50 and 60. By the time larvae reached Stage VI numbers were much diminished and most larvae were outside NH 15 and present as far offshore as NH 60. This trend was apparent through Stage XII. Numbers of larvae collected that were Stage XIII and older were extremely small, making generalizations
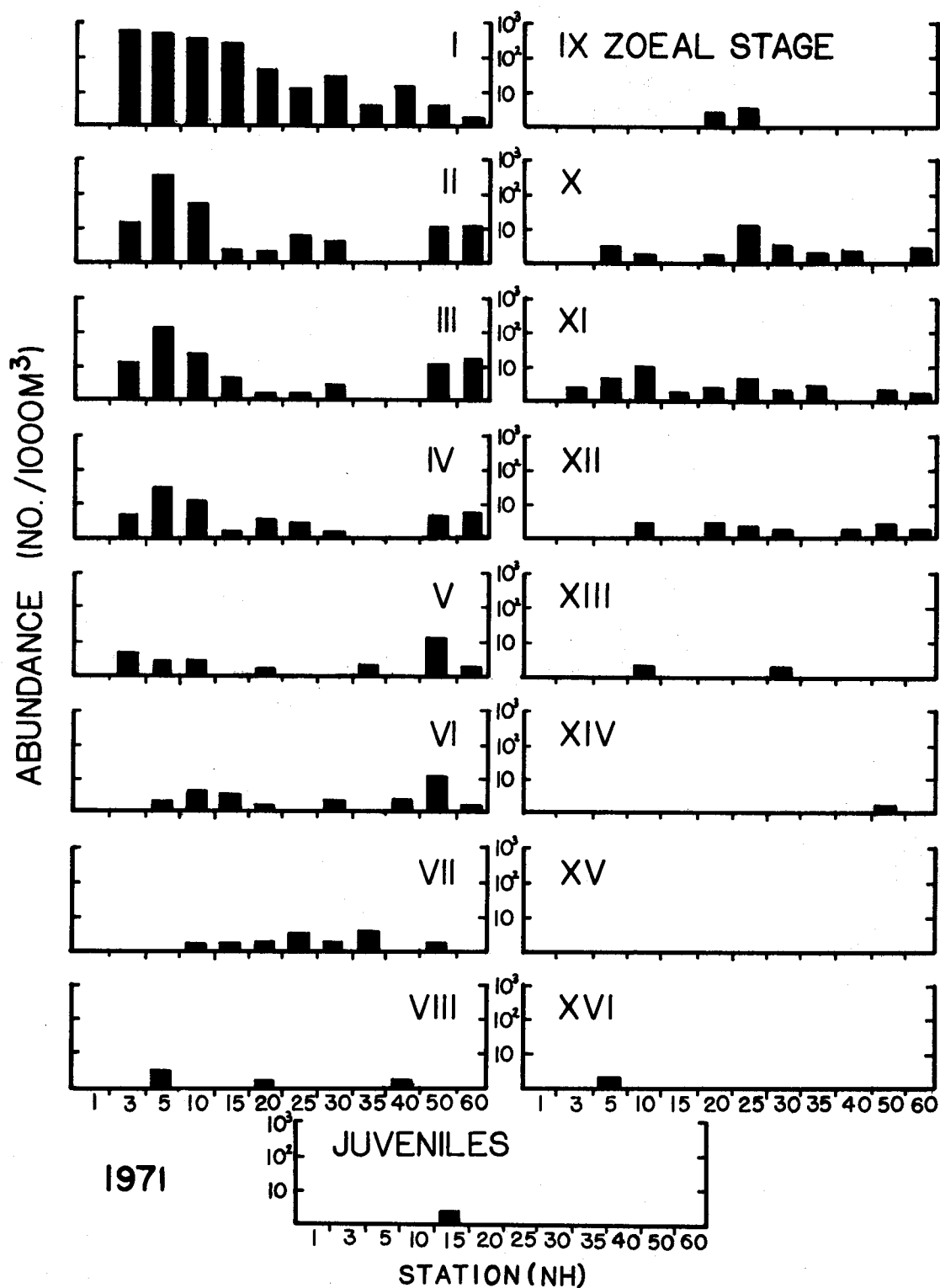
Figure 7. Stage specific larval distribution. Distribution and abundance summed within larval stages over all cruises in 1971.

about their distribution very tenuous. Very few late larvae and only

one early juvenile were captured at NH 5 and 15.

General Distribution and Abundance--1972

The temporal and spatial distribution and abundance of P.

jordani larvae collected in 1972 are graphically summarized in

Figure 8. No cruises were made until 4 March, when small numbers

of young (I and II) larvae were found between NH 3 and NH 15. On

16 March there were large numbers of Stage I zoeae at NH 3 and 5

and lower numbers farther offshore. Small numbers of Stage II's and

III's were also present. In late March a 30 mile transect on the

Newport hydro-line showed that the center of the larval distribution

was at NH 10 and that the dominant stage was Stage III. This indi-

cated that the peak of larval hatching had occurred by this time.

Larvae were present at NH 1 for the first time and were also present

at each station out to NH 20. This contrasts with 1971 when P.

jordani larvae were never found at NH 1. The 11 April cruise was

curtailed at NH 10 because of rough seas; however, larvae were

abundant within 10 nautical miles with peak numbers at NH 10. The

most abundant larval stages were III's and IV's; larvae present

ranged from Stage I - VIII. On 20 April, larvae were scattered

between 5 and 30 nautical miles offshore. Stages I - XI were present

with stages VI, VII and VIII the most common. After a full month, the
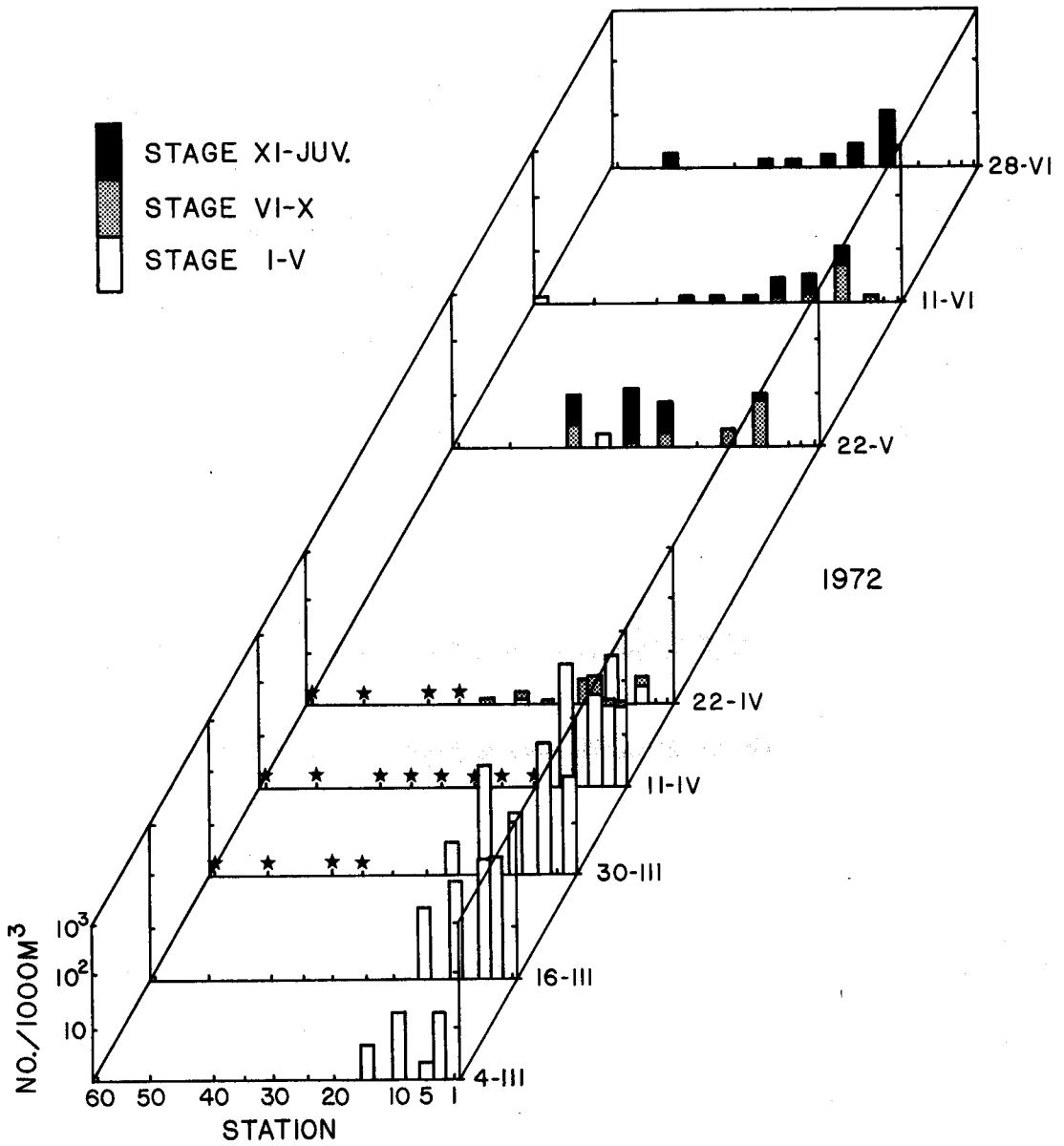
Figure 8. Three dimensional display of larval distribution and abundance with time in 1972.

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larval distribution on 22 May was displaced offshore, and was spread between NH 10 and NH 45. Larval development was well advanced and the first juveniles of the season were found at NH 25. The model stage was between X and XII. The cruise on 11 June showed a distribution of larvae similar to that in late May. Larvae were at an advanced stage of development (older than XI) and more distributed between NH 5 and NH 60 with most of the larvae collected at NH 10, 15 and 20. A large number of juveniles were caught in a night tow at NH 15.

Stage Specific Larval Distribution--1972

The stage specific larval distribution in 1972, though similar to 1971, was more restricted (Figure 9). Early stages (I - IV) were found only inside NH 15 and extended into NH 1. Older larvae were found farther offshore, rarely extending beyond NH 40. Late larvae (XIII - XVI) and early juveniles, though present in small numbers, were more abundant than in 1971 and were most abundant between NH 15 and 30.

Seasonal Wind and Current Regimes--1971 and 1972

Progressive vector diagrams (Figure 10) have been used to show the direction and intensity of the wind from January through July in 1971 and 1972. The two years differed in several respects. In
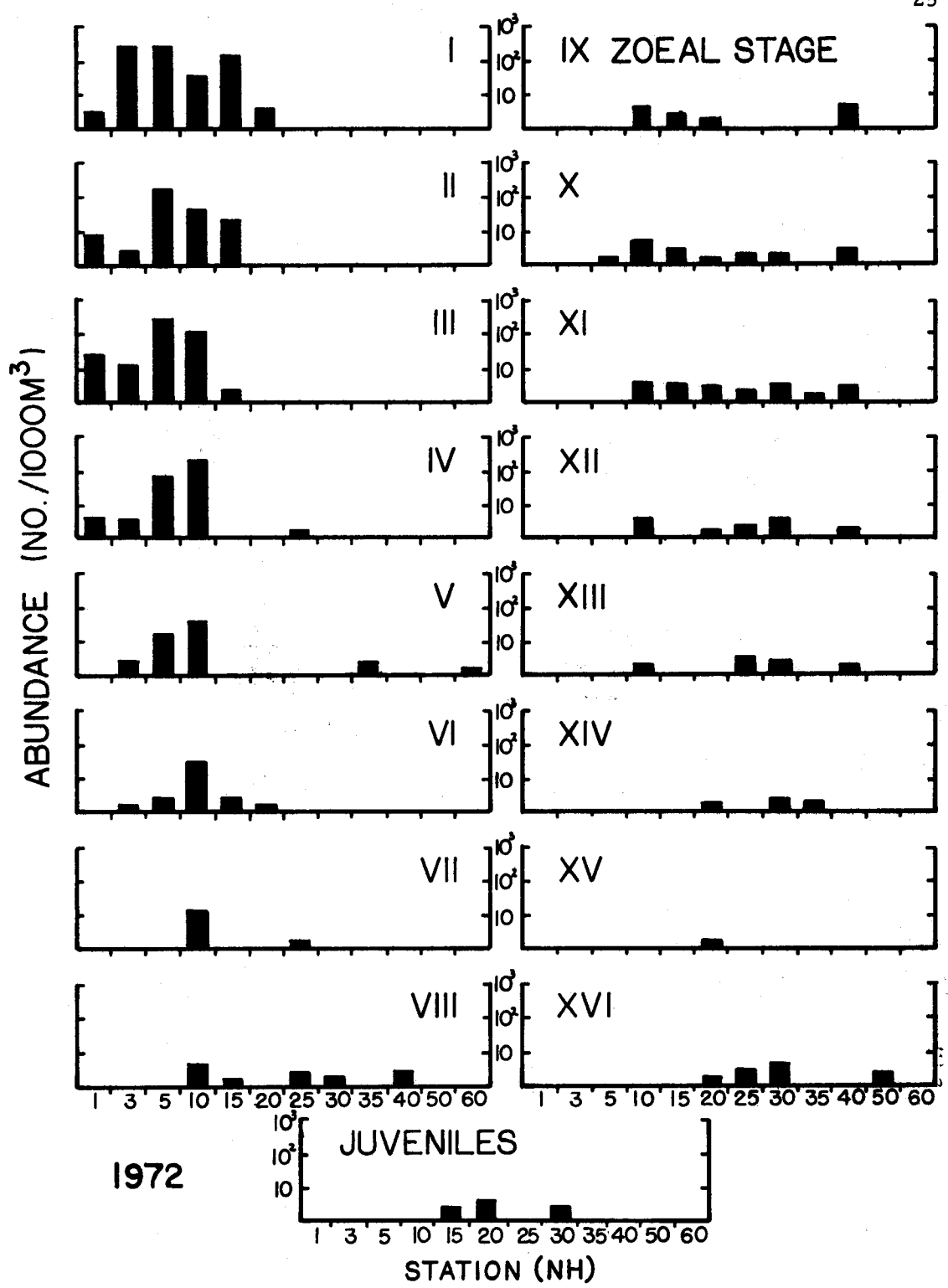
Figure 9. Stage specific larval distribution. Distribution and abundance
summed within larval stages over all cruises in 1972.
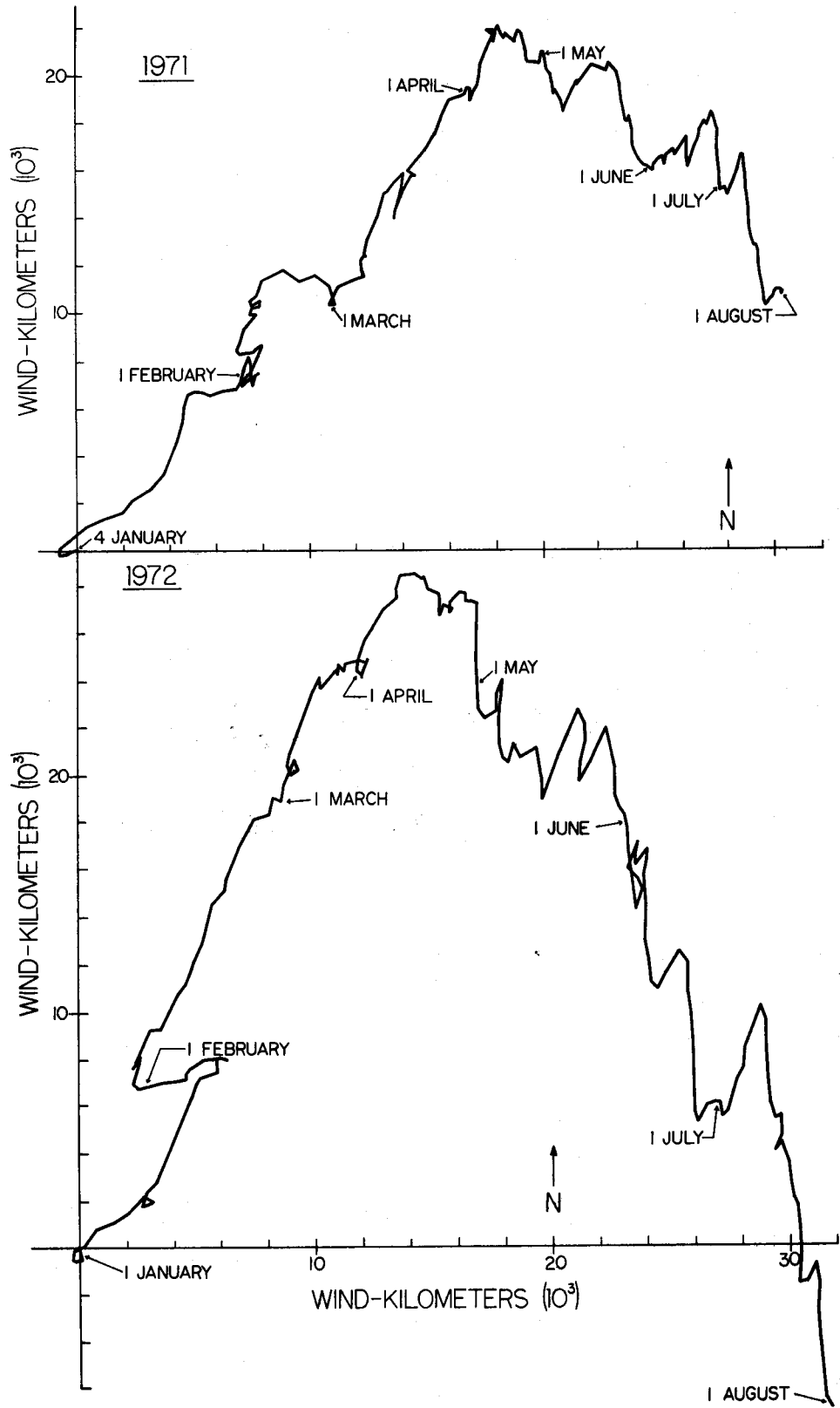
Figure 10. Progressive vector diagrams for winds at Newport, Oregon, 1971 and 1972.

February 1971 the winds were very mixed, while in 1972 the winds blew almost steadily from the southwest. March of 1971 was dominated by southwest wind with a one week pulse of northwest wind from 15-21 March. In 1972 the March winds were less intense, and almost all from the southwest, with only a few one day pulses of northwest wind. April in both years was transitional. The early part of the month had southwest winds. By mid April the winds were mixed. In both 1971 and 1972 a short pulse of northwest wind occurred in late April. The winds of the upwelling season, May through August, were stronger in 1972 than in 1971.

In order to put the two years in perspective, the upwelling indices for 1971 and 1972 were compared with a 25 year average, 1946-1971 (Bakun, 1973 and pers. comm.). These monthly indices estimate the magnitude of the offshore component of the Ekman transport (units are metric tons per second per 100 m of coastline). They were calculated from an estimate of the mean monthly sea surface wind stress, which was based on geostrophic wind calculated from pressure field data. The anomalies or deviations from the long-term mean values of the index were higher in both the first and third quarter of 1971 than 1972 (Table V). This can be interpreted as implying that the amount of surface water flowing onshore in the first quarter of 1971 was below average (first quarter anomaly = 20), while in 1972 it was near normal (anomaly = 3). The degree of upwelling in 1971 was

Table V. Upwelling indices by year and quarter for 1971 and 1972 along with the anomalies from a 25 year average (from Bakun, 1973, pers. comm.).

	1971		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

below normal (third quarter anomaly = -15) while the degree of upwelling in 1972 was higher and only slightly below the long term mean (anomaly = -5).

Surface Current Regime--1972--Drift Bottle Analysis

Drift bottles were released in various numbers on almost all cruises from early March through early August 1972 (see Table III). Returns were processed by William Gilbert, School of Oceanography, Oregon State University, Corvallis, Oregon. The presence of the northward flowing Davidson Current was well documented by the northerly drift of bottles in March and early April. Coincident with the northerly flow of surface water is an onshore component that helps account for the very high return rates in these months (mean return rate for cruises C7203A, 3D, 3G and 4D = 46.65%) (Figure 11). By
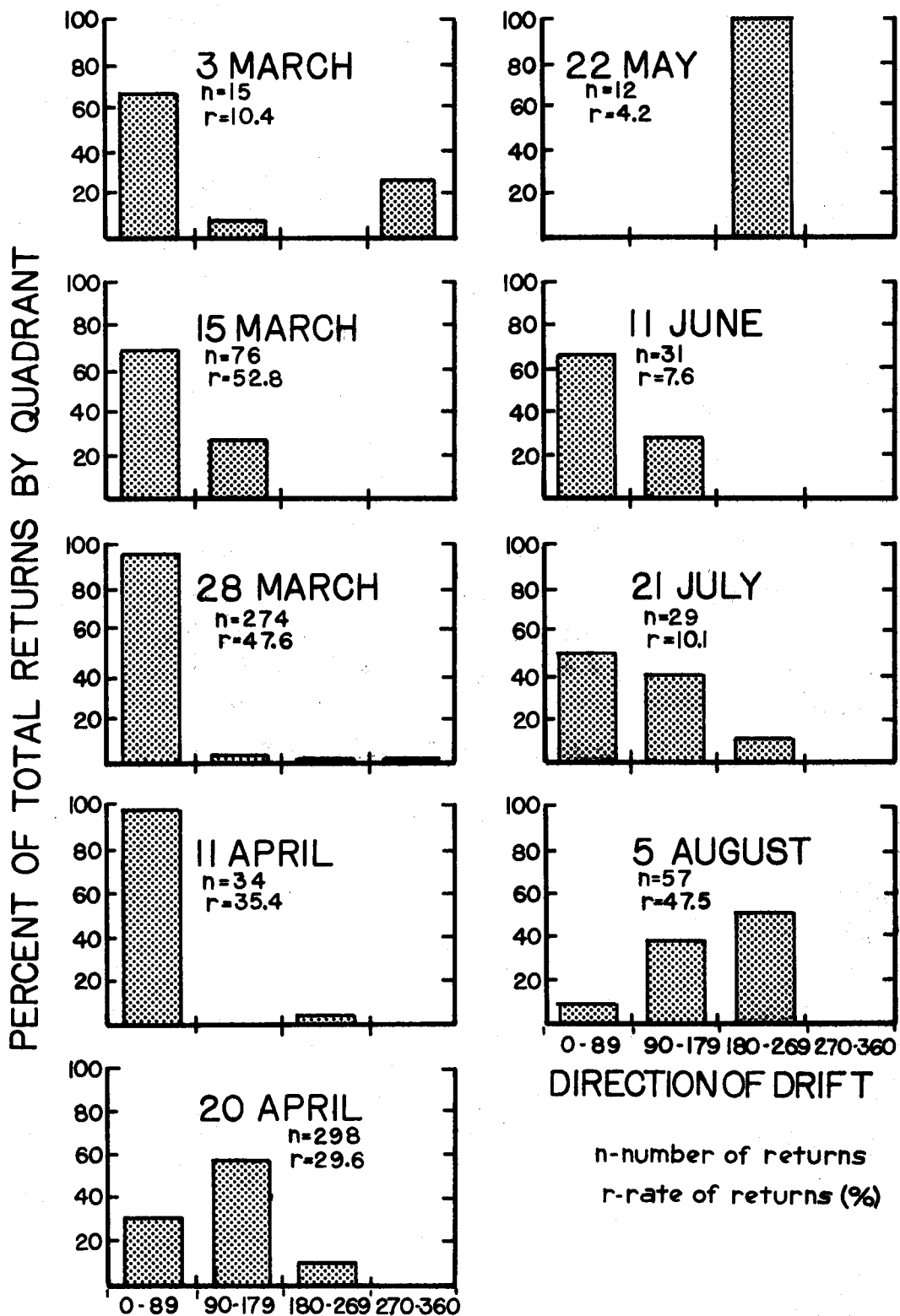
Figure 11. Drift bottle returns, 1972: number, rate of return and
direction of drift summarized by quarterly components
(from data supplied by M.J. Hosie, FCO and W. Gilbert,
OSU School of Oceanography).

late April currents were transitional with a large southerly component.
The presence of an offshore component was indicated by the lower
return rates (mean return rates for cruises C7204G, 5A, 6E, 7E and
8B = 19.8%) (Figure 11). Surprisingly, a considerable northerly
component remained in all months except late May and early August.
Most of these returns, however, are from the nearshore stations
(NH 1 - 5).

The different wind and resultant current regimes of 1971 and
1972 are reflected in the larval distributions for the two years. The
analysis is somewhat tenuous because of the extrapolation of the wind
data from the shore station to the distribution of larvae in the water
column 30-40 km from shore. The widespread distribution of early
larvae (NH 3 - 40, Figure 6) in early and mid March 1971 can
probably be attributed to the mixed winds in February and to the pulse
of northwest wind in mid March. More dramatic displacement was
seen in early May, 1971 when numbers of larvae were found in
abundance at NH 50 and 60. In May the wind was predominantly from
the northwest. It is interesting to note that larval numbers decreased
markedly after this time. This attrition was probably due to many
factors, a major one being this extensive offshore displacement. The
degree of offshore displacement of early larvae was more limited in
1972. This was probably due to the stronger, more consistent
southwest winds during February and March, 1972. Older larvae were

found offshore to a more limited degree in 1972 than in 1971. The

displacement caused by upwelling was probably influenced by the

exact time at which upwelling occurred during the larval period. The

present study (see vertical distribution section) and a more limited

one on P. danae by Berkeley (1930) have shown a definite gradient of

age with depth. Younger larvae, which are strongly photopositive

(personal observation), were found closer to the surface, where they

were more susceptible to the offshore surface component of northwest

winds. Later in the larval season, when older larvae were deeper in

the water column, the magnitude of the offshore component was

lessened and, therefore, displacement was reduced. In 1972 when

upwelling started in late April the larvae were older than those of the

same period in 1971 (see growth rate section), presumably deeper in

the water column, and, therefore, their displacement offshore was

more limited. A more thorough knowledge of subsurface currents,

during upwelling, is necessary before this hypothesis can be tested.

The movements of adult P. jordani associated with reproductive

events have not been well defined. Dahlstrom (1970) found P. jordani

at Morro Bay, California moved offshore 3-5 km in the winter to

spawn. There was no evidence of a comparable inshore migration

prior to hatching. Lukas and Hosie (1973) reported that female shrimp

left their study area (10-20 nautical miles off Tillamook Head, Oregon)

in the fall. The numbers of females increased in March, the increase

occurred from south to north across their station grid. There was no further movement inshore associated with larval hatching.

Several species of pandalids have been shown to make migrations as adults, when they are spawning or when larvae are hatching from eggs on the pleopods. The best documented studies have been on P. borealis in the North Atlantic (Haynes and Wigley, 1969; Horsted and Smidt, 1956). Haynes and Wigley (1969) found that only ovigerous females migrated from deep water to shallower near-shore depths from the time of spawning in October until just before hatching in March and April (mean depth of females: October, 231 m; November, 213 m; January, 164 m; February, 140 m; March, 23 m). Apollonio and Dunton (1969) found larvae hatched in late March and early April and were confined to the nearshore pelagic environment within 10 nautical miles of the coast. Furthermore, they found very little offshore displacement of the larvae (Stages I - IV) but the extent of their sampling was limited. They did find, however, 0 and I age shrimp in shallower water for the first 18-20 months of life. A follow-up study by Rinaldo (1972) failed to define the distribution and abundance of the older stages (IV - VI) of P. borealis in the Gulf of Maine.

Pandalus montagui in the eastern North Atlantic has been shown to move offshore to spawn in November-March (Mistakidis, 1957) and then to move inshore in April-October to hatch larvae (Lebour, 1939, 1947; Allen, 1963).

Off Newport, Oregon, the highest concentrations of adult P.

jordani were found between NH 20 and 25. There was no evidence of

a shoreward movement of ovigerous females during the period of

hatching in March. The nearshore concentration of larvae in March

1971 was probably caused by the shoreward component of the dominant

southwest winds during February and March. This pattern was even

more striking in 1972 when the winds were stronger and more con-

sistently from the southwest in February and March.

Distribution and Abundance along the Coast--GRIDS

On two extended cruises (C7203G and C7204G) a grid network of

stations was sampled along the northern and central Oregon coast.

This was done to compare the observations gained from the time

series of samples along the Newport hydro-line with a small number

of spatial surveys of P. jordani larval distribution and abundance. On

cruise C7203G, in late March, all seven 30-mile transects from

Tillamook Head to the Siuslaw River were completed. Due to bad

weather the southernmost transect was not sampled on cruise C7204G

in late April. Figure 12 summarizes the total larval distribution and

abundance for March and April in a three-dimensional manner. As

on the Newport hydro-line, early larvae were most numerous within

15 nautical miles, extending into the one mile station in March. This

trend was consistent for the entire length of the sampling area
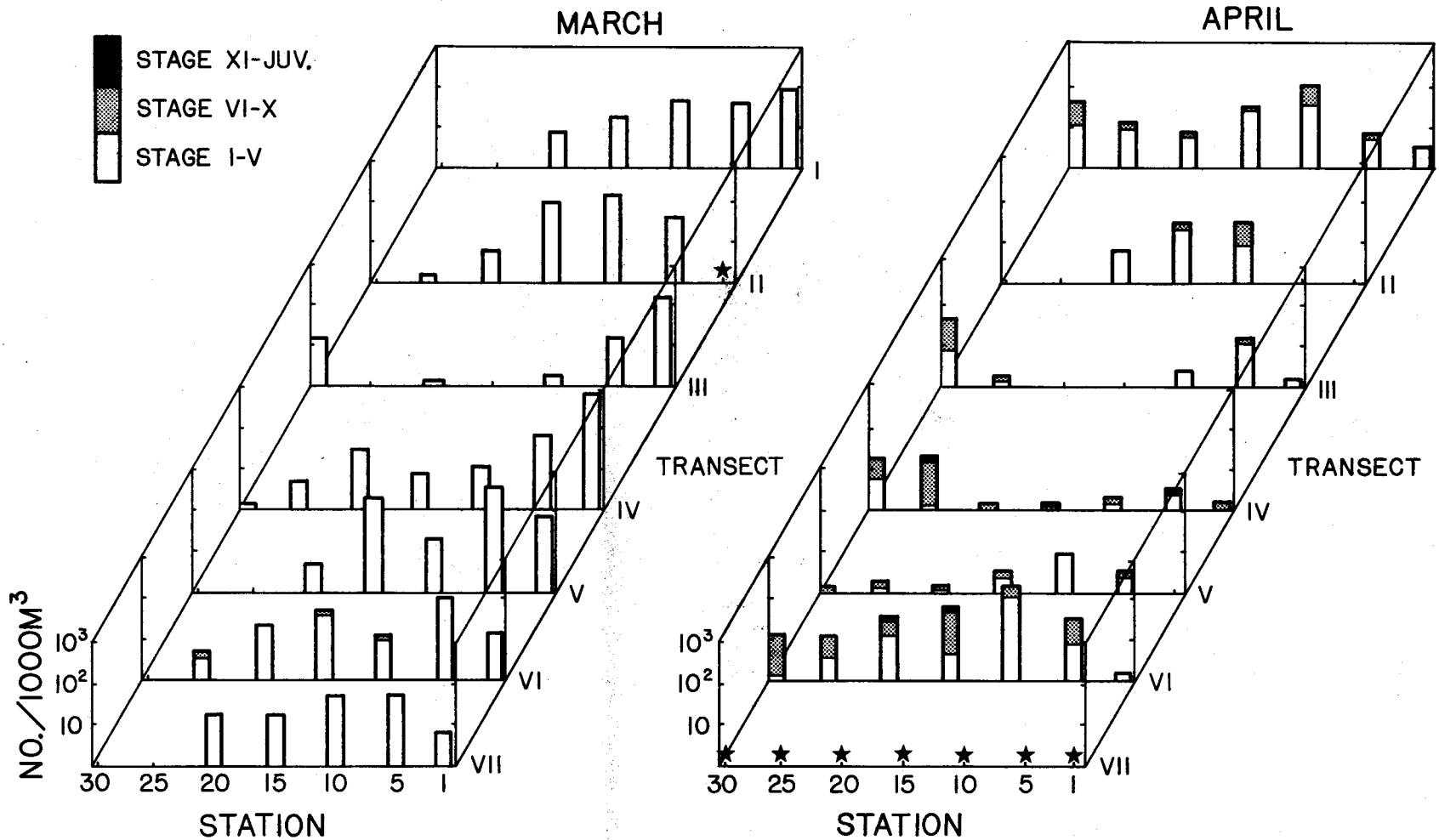
Figure 12. Three dimensional display of larval distribution (both alongshore and offshore) and abundance in March and April, 1972.

(Table VI). A concordance analysis (Tate and Clelland, 1957) showed that larvae were not uniformly dispersed and that for most transects larvae were most numerous at the 1 and 5 nautical mile stations ($W = 0.62**$, $W_{0.01, 7, 7} = 0.36$). Overall larval abundance also varied between transects. Transects IV and V had considerably higher total numbers of larvae than the average of the other transects (1093.2 and 717.5 respectively, versus ca. 250).

Figure 12 also summarizes the April larval abundance and distribution. Offshore displacement and dispersion of the larvae were evident and larvae were usually most numerous at the 10 nautical mile station. Large numbers of larvae were collected out to 30 nautical miles on almost all transects. A concordance analysis substantiates this dispersal trend with a value of $W = 0.43**$, still highly significant ($W_{0.01, 6, 7} = 0.39$) but not as large as the March cruise. In late April there was also variation in total larval numbers between transects. Larval numbers were lower in general; however, unlike March, transects VI and I had the most numerous larvae (418.0 and 232.3 respectively, compared to < 100 in each of the others) (Table VI).

Stage Specific Coastal Distribution and Abundance

In order to ascertain if there was a gradient of larval age along the coast the abundance of larvae in each stage was summed

Table VI. Distribution and abundance (no. /1000 m^3) of Pandalus jordani larvae in late March and late April. Paired numbers indicate replicate tows.

Transect	Station							$\Sigma \frac{\text{no.}}{1000 \text{ m}^3}$
	1	5	10	15	20	25	30	
				March - C7203G				
I	98.0	50.2	63.7	24.7	8.1	0	0/0	244.7
II	-	55.4	156.2	96.6	7.9	0.8/0.9	0	317.4
III	222.0	17.8	2.0	0	0/1.1	0	16.5	259.4
IV	955.2	79.2	12.0	10.1/7.2	31.0	6.2	1.1	1093.2
V	80.0	469.2	12.2/33.6	138.4	6.9	0	0	717.5
VI	14.0	155.7/106.2	12.2	69.0	34.2	7.0	0	261.9
VII	11.6/5.2	74.0	118.8	18.2	22.6	0	0	245.2
				April				
I	3.6/3.0	7.5	108.6	44.2	8.9	12.0	47.7	232.3
II	0	0/0	35.8	43.5	8.7	0	0	88.0
III	1.3	19.2	2.4/6.4	0	0	3.2	51.5	79.6
IV	1.6	4.1	2.9	2.1/1.0	1.0	26.8	24.1	62.0
V	0	4.2	9.8	4.3	1.1/1.2	2.5	1.3	23.2
VI	1.6	41.3	213.3	83.4	48.8	-/14.4	15.2	418.0
VII	-	-	-	-	-	-	-	-

within transects. This analysis is summarized in Figure 13. The median stage of all larvae found on the transect was calculated and plotted. In March no consistent gradient was seen, but there were considerable differences in median stage of development between transects. Transects V and VI had median stages of 3.28 and 3.43 respectively while the others averaged 2.0. By April the stage distribution between transects was more uniform. Median stage of development in April was 4.9 with a low of 4.2 and a high of 5.8. This is an increase of 2.38 stages from March. There was also more variability in larval stages in April than in March, with a slight increase in the occurrence of older larvae in the lower transects (IV - VI).

Onshore-offshore age distribution was analyzed by summing each stage abundance between transects for each cruise. This information is given in Figure 14. In March Stages I - IV predominated and were most abundant within 15 to 20 nautical miles. By April the older larvae were dispersed outside 5 nautical miles. The peaks of abundance for these older larvae were either 10 nautical miles for stages I - VI or 15 nautical miles for Stages VII - XI.

The grid sampling in March and April, 1972 relieved apprehension that the intensive sampling done on the Newport transect might not be representative of the distribution and abundance patterns of P. jordani larvae coast-wide. The Newport line is near the southern
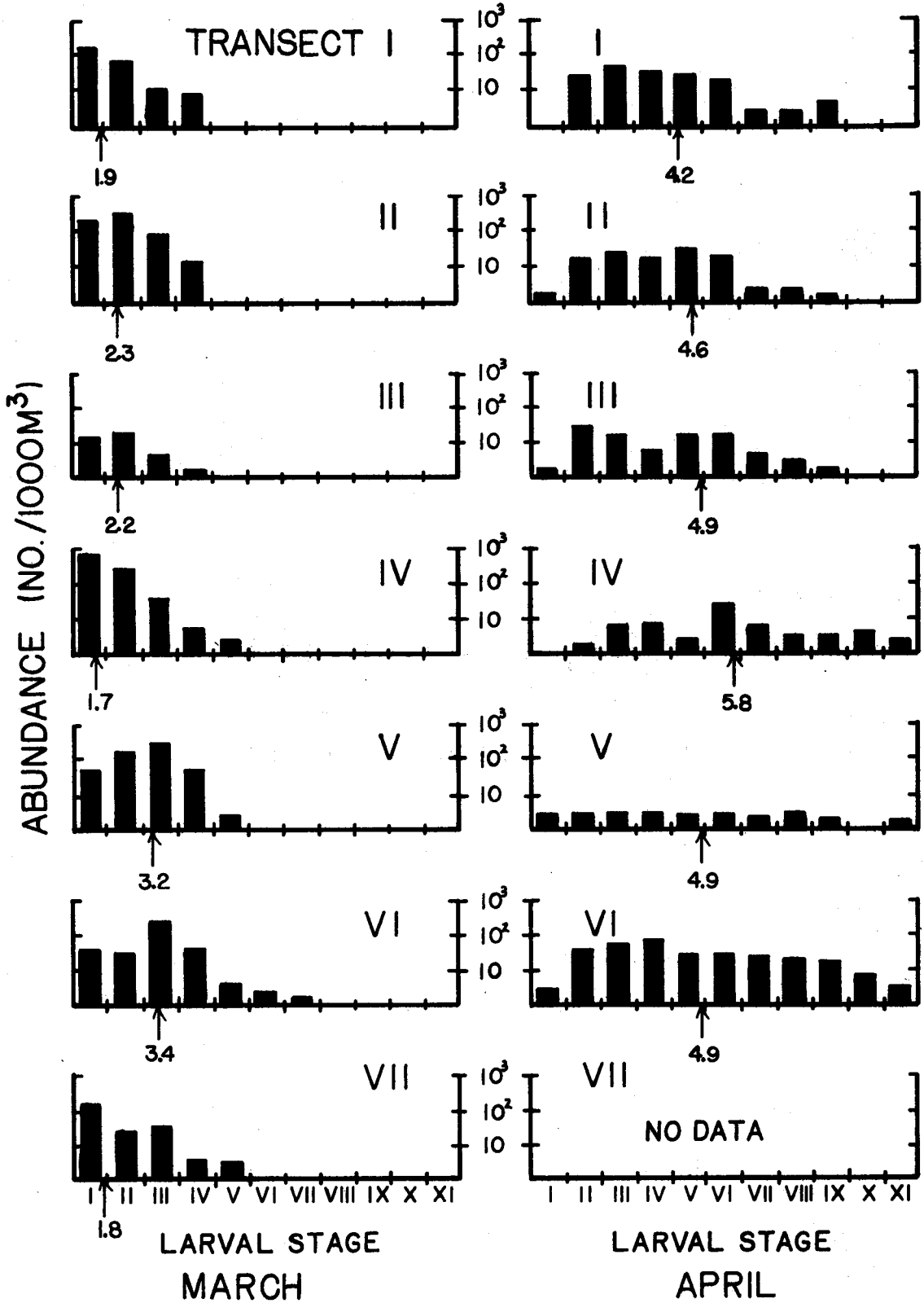
Figure 13. Stage specific larval distribution. Larval abundance summed by stage within transects.
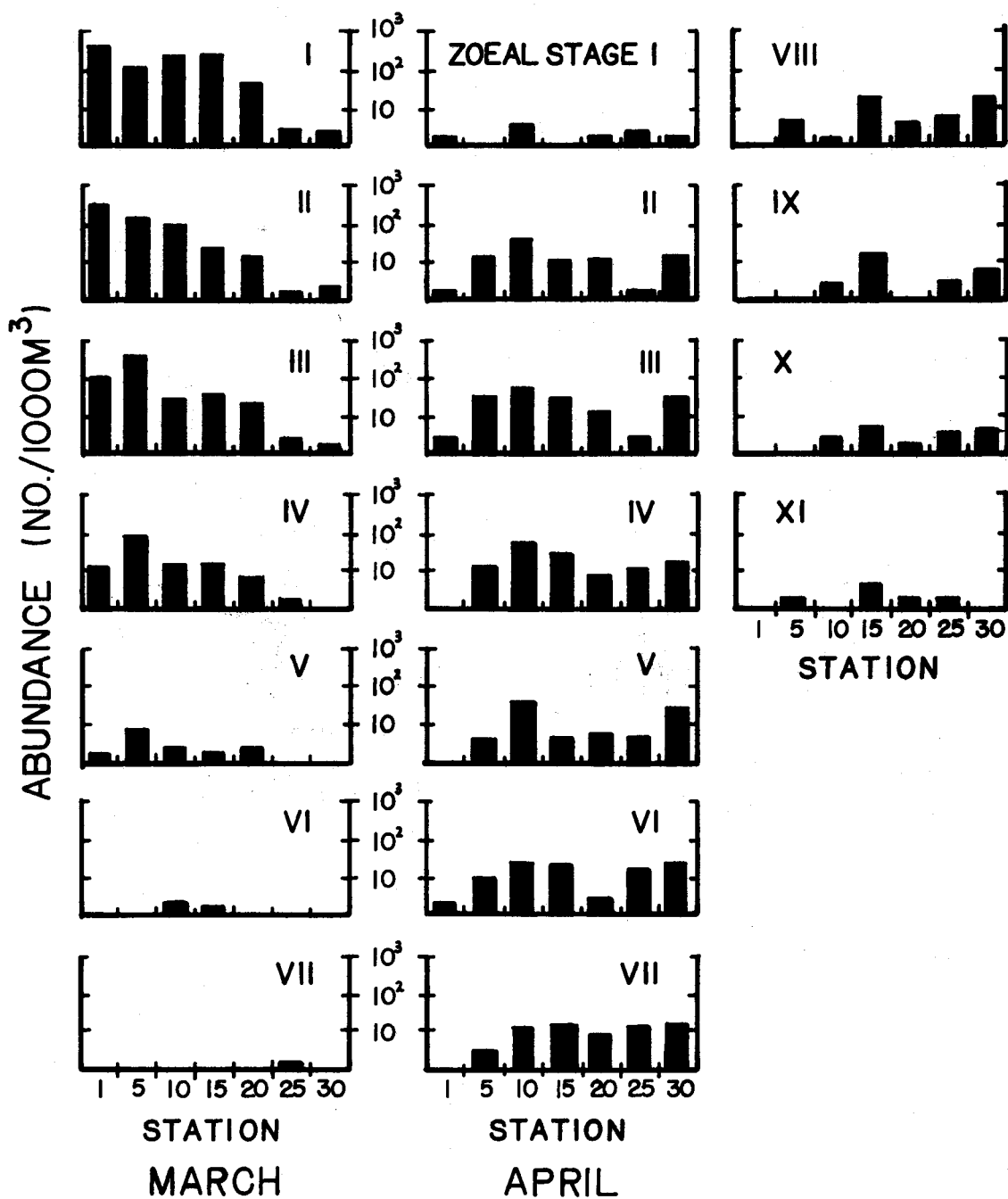
Figure 14. Stage specific larval distribution. Larval abundance summed by stage over all transects.

extreme of the extensive northern shrimp beds centered off Tillamook

Head, and is separated from the southern Oregon fishery by a

formidable rocky outcrop, Heceta Bank. From the extent of the

sampling on the grid cruises, it is believed that the dynamics of P.

jordani larval distribution and abundance are uniform along the entire

coast and are not restricted to the more limited shrimp beds.

Rasmussen (1953) and Horsted and Smidt (1956) found north-

south differences of several months in the time of oviposition, length

of ovigerous state and therefore the time of larval hatching in

P. borealis along the coast of Norway. Dahlstrom (1970) noted

smaller differences in spawning times between British Columbia,

Washington, Oregon and California populations of P. jordani. A

gradient in occurrence of early larvae or age with latitude was not

seen in the present study. The time difference in hatching of larvae

between Tillamook Head and Coos Bay is only one to two weeks

(Robinson, 1971). The sampling effort in the present study could not

resolve a gradient that small. A more extensive grid, over a wider

latitudinal range, with simultaneous sampling at the extremes would

be necessary.

Field Estimates of Larval Growth Rates--1971 and 1972

Figure 15 summarizes the surface seawater temperatures from

February through July in 1971 and 1972. In February, March and
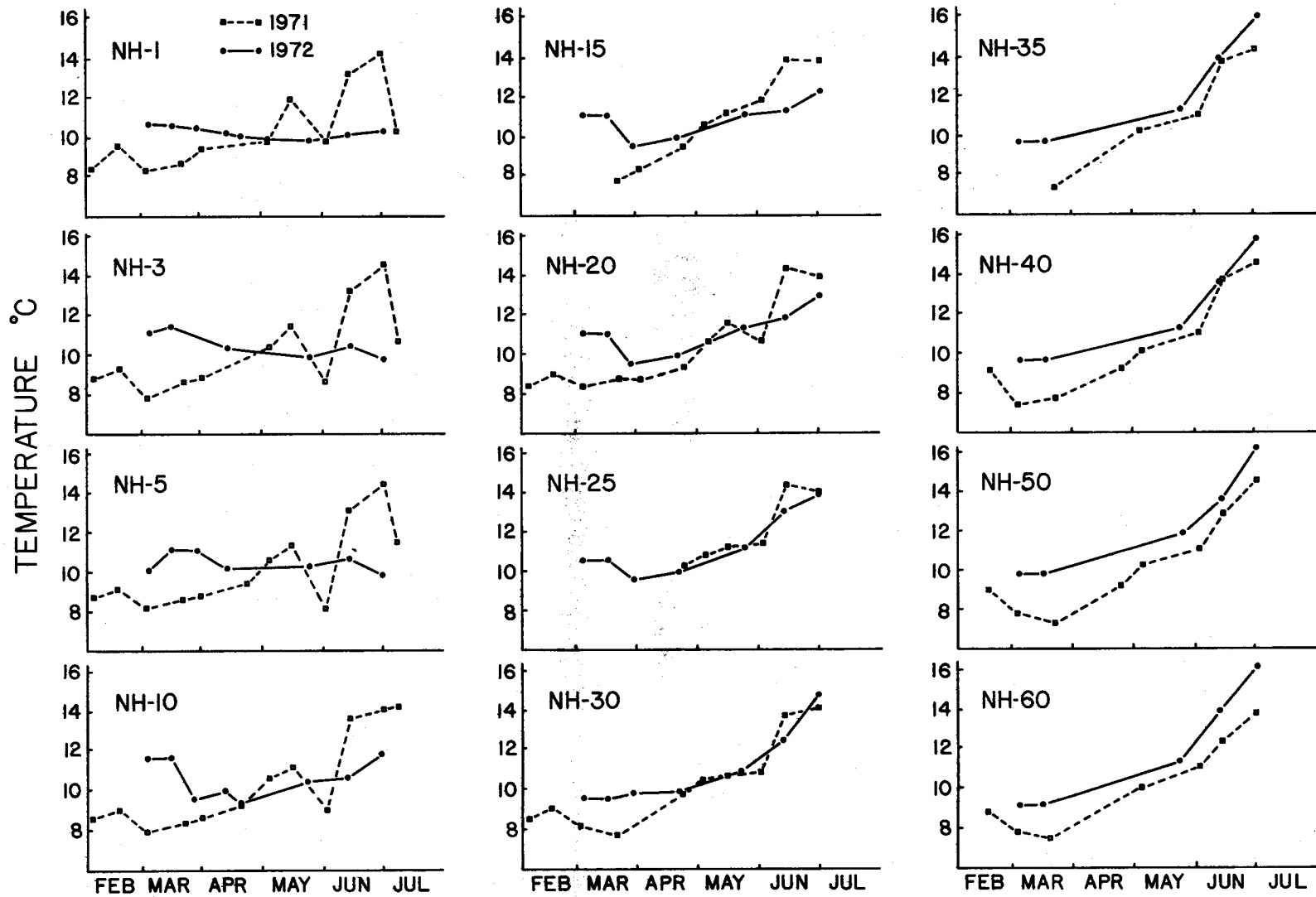
Figure 15. Surface seawater temperatures at the 12 Early Life History sampling stations for 1971 and 1972.

April, 1971, temperatures were somewhat variable and were between 8 and 10°C inside NH 20. From late April through July temperatures increased sharply to between 14 and 15°C, due to increased solar radiation and lack of strong upwelling. The sharp temporary decrease in temperature seen in early June corresponded to a pulse of upwelling in late May (see Figure 10). The surface seawater temperatures were very different in 1972. Nearshore, the temperatures were more constant and warmer in the early part of the larval season of 1972 than in 1971, ranging between 10 and 12°C. This was due to the strong onshore flow of the well developed Davidson current in 1972. Temperatures rose slightly in late spring but were held well below the high temperatures reached in late June of 1971 by the strong upwelling conditions in 1972.

The histograms in Figure 16 compare the abundance of individual larval stages for 1971 and 1972, for each cruise, spaced on a time scale.

The sampling frequency (approximately bimonthly) in the present study made it difficult to pinpoint the time of hatching. The peak of larval hatching usually occurs in the last two weeks in March off central Oregon (Robinson, 1971, his Table 3, p. 16). In both 1971 and 1972 the peak of hatching appeared to be in this period, but there were considerable numbers of larvae present in mid-February when sampling began in 1971 and in early March when sampling began in
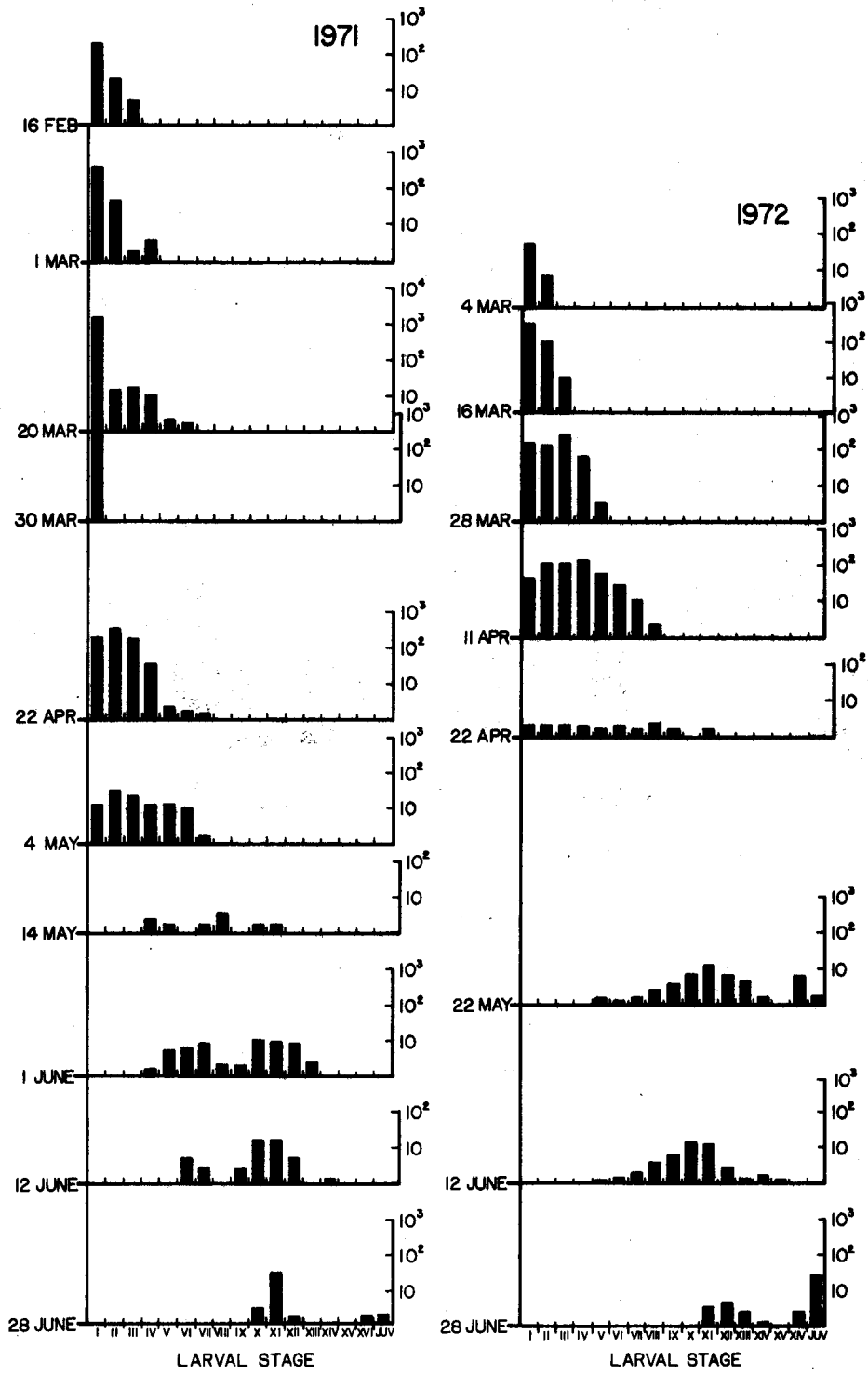
Figure 16. Histogram showing stage and abundance of <u>Pandalus</u>
<u>jordani</u> larvae in 1971 and 1972. Histograms are spaced
on a time scale to represent growth rate.

1972. Therefore, an estimate of the time of initial hatching cannot be accurate. For this reason the median stage of larval development was not adequate to characterize the "age" of a larval sample pooled over all stations from a given cruise. Without an accurate estimate of larval age on successive cruises a quantitative approach to larval growth rate was not possible, and a more simplified, descriptive approach was adopted. Nevertheless, differences in the change in age structure with time ("growth rate") in the two years of sampling were apparent.

The change in age structure from 16 February to 30 March 1971 was almost insignificant in that Stage I larvae predominated throughout. At the same time, water temperatures within 20 miles were between 8 and $10^{\circ}C$. The rapid increase in median stage between 22 April and 1 June 1971 coincided with the rapid increase in surface temperature from April to the first part of June. The brief period of upwelling in June with resulting lower temperatures was reflected in slower growth of the larval population through the month.

In 1972 larval growth rate appeared to be relatively constant from the peak time of hatching in mid March through the month of May. This corresponded to the relatively constant and warmer temperatures during that time. The faster growth in 1972 was evident from the change in age structure and earlier appearance of older larvae and juveniles than in 1971. The onset of upwelling and colder

surface seawater temperature was again in June and the rate of change in age structure was slowed as in the previous year.

Berkeley (1930) noted a change in age structure with time of a limited number of P. danae samples taken in British Columbia waters. Very little increase in the median stage of the samples was noted between samples taken on 22 March and 6 April. By 18 May the larvae were still in the first and second stages. A dramatic change in the age structure of the larvae occurred between 18 May and 6 June, by which time the larvae were in the last four stages. P. danae has only six larval stages. By 27 June the larvae had left the water column. The numbers of larvae in Berkeley's study were very small, and there were no temperature data supplied with the results. Therefore, interpretation of the fluctuations in apparent growth rate with respect to temperature are conjectural. Undoubtedly, water temperatures had increased in late May leading to more rapid molting of the larvae. In another limited study of P. borealis larvae in the Gulf of Maine (Apollonio and Dunton, 1969), the development of larvae with each successive cruise from 3 April to 3 May was more regular than that demonstrated by Berkeley. In the one month of Apollonio and Dunton's survey the majority of the larvae had passed through the first three larval stages before disappearing from the study area. Again, no hydrographic data were supplied with the larval abundance results.

Vertical Distribution of Larvae--Day/Night Differences

On 30, 31 May 1972 a series of quasi-vertically stratified samples was taken at grid station IV-10 (Lat. 45°04.0'N, Long. 124° 15.1'W). The 160 m water column, divided into four horizons (0-10, 11-50, 51-100, 101-150 m), was sampled with the open bongo nets, and a bottom sample was taken with the opening/closing epibenthic sled. Replicate tows (bongos or sled) were taken at each depth interval, both day and night. Contamination in the open bongo nets was minimized by lowering to the depth interval as fast as possible, doing a stepped-oblique tow through the horizon and then raising the net as quickly as possible. Contamination was greatest at the 101-150 m interval because of the length of time needed to get the nets to depth and to recover them. The towing time at depth, however, was long enough to keep the period of contamination below 20% of the total sampling time. Contamination at the intermediate depths (51-100 and 11-50 m) was less than 10% (Table VII).

Figure 17 graphically summarizes the vertical distribution of P. jordani larvae and juveniles during one 24-hour period. During the day larvae were distributed throughout the water column and were most abundant in the 0-10 m depth interval. A trend of increasing age with depth was evident. The sled tows revealed a very high concentration of early juvenile P. jordani (284.1 and 290.2/1000 m^3) on the

Table VII. Sampling depth interval, percent of time within interval and number of larvae and juveniles caught within the depth interval for the quasi-stratified sampling on Cruise C7205D.

Depth interval, tow number, day/night	Percent of time within depth interval	Larval abundance (no. /1000 m^3)
150-1-D	84.6	5.33
150-2-D	85.9	8.50
150-3-N	83.8	4.58
150-4-N	80.3	11.38
100-1-D	87.3	9.14
100-2-D	91.4	7.70
100-3-N	91.9	18.00
100-4-N	93.2	9.27
50-1-D	94.5	7.07
50-2-D	93.5	2.59
50-3-N	93.1	8.80
50-4-N	93.1	9.99
10-1-D	100.0	11.79
10-2-D	100.0	19.73
10-3-N	100.0	12.24
10-4-N	100.0	12.48
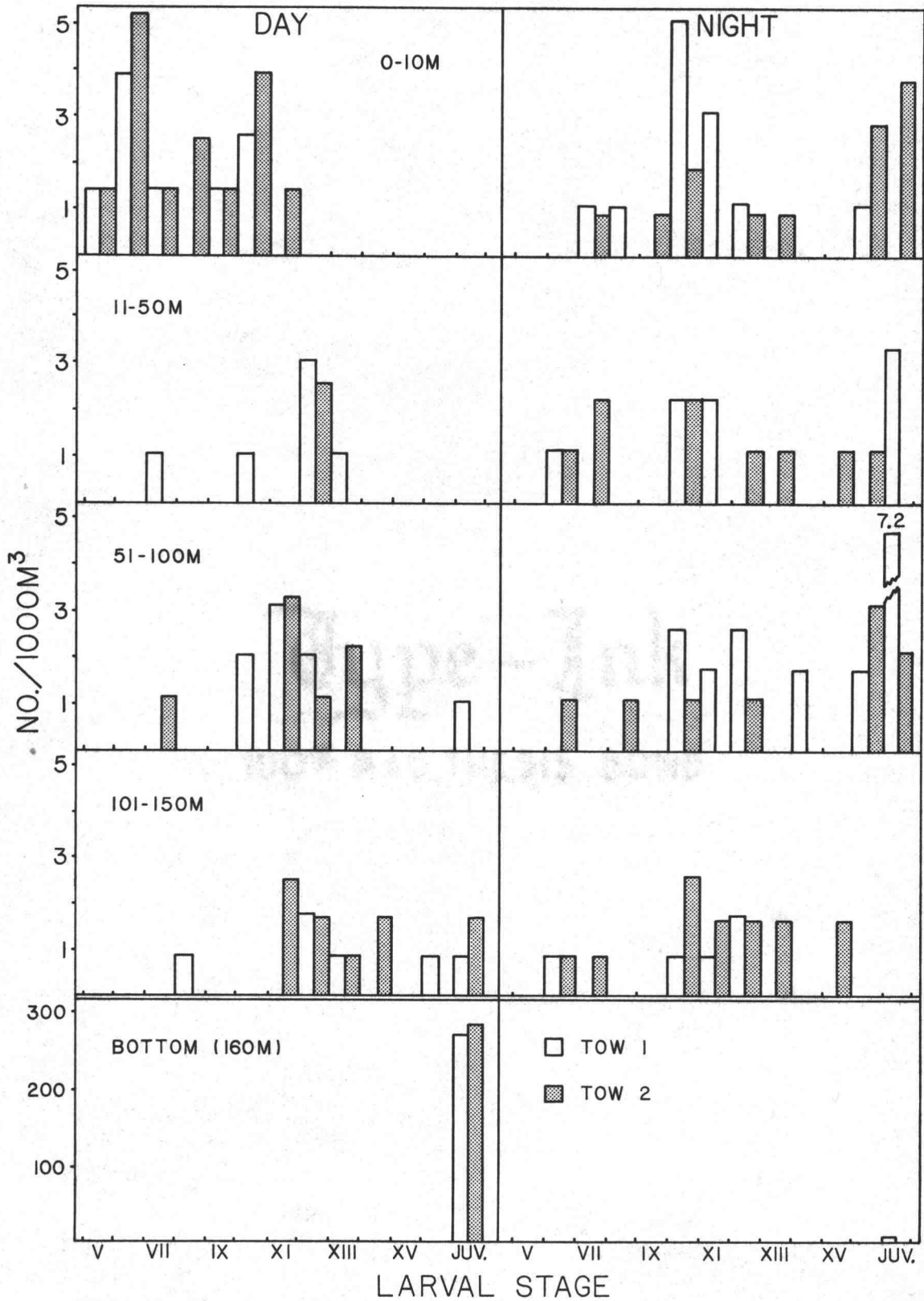
Figure 17. Vertical distribution of larvae and early juveniles during one day and one night period. All tows were replicated.

bottom during mid-day. At night larval shrimp were still uniformly

distributed through the entire water column. The younger stages (V

and VI) found in some abundance in the 0-10 m sample during the day

disappeared at night and did not appear in large numbers at other

depths. Furthermore, the age gradient with depth was no longer

present. This was due, in part, to an upward movement of late larvae

(XVI) from the 101-150 m horizon to the upper layers. The most

dramatic feature of the night distribution was the vertical migration of

early juveniles. Samples obtained from sled tows indicated that they

were virtually absent on the bottom (0 and $3.7/1000 \ m^3$). Further-

more, they were absent from the lower portion of the water column

(100-150 m) and migrated into the upper 100 m including the top 10 m.

Adult P. jordani have been shown to undergo regular diel

changes in vertical distribution (Tegelberg and Smith, 1956; Alverson

et al., 1960; Pearcy, 1970, 1972; Robinson, in press). Pearcy (1972)

has shown day/night differences in density of adult P. jordani on the

bottom by sampling with beam trawls and photographically with deep

sea cameras ($2.3/m^2$ during daylight versus $0.01/m^2$ at night).

Furthermore, midwater trawls never contained P. jordani adults

during the day while there was an average of 22/1-2 hour tow at night

using a 3 m Isaacs-Kidd midwater trawl at inshore stations.

In this study, the vertical distribution of P. jordani larvae was

described, the ontogeny of vertical migratory behavior traced and

the point at which shrimp are recruited to the bottom established. The larvae were found throughout the water column, including the top 10 m, and an age gradient with depth was evident similar to that observed on a more limited scale (7-34 m) by Berkeley (1930) for P. danae. From the one sampling of a 24 hr period, there is no evidence that larvae younger than Stage XVI migrate to any extent.

The difference in distribution between the last larval stage and the first juvenile instar is interesting because both are morphologically equipped to migrate and do so over the full extent of the 160 m water column. The only morphological differences between the two stages are that larval Stage XVI still has small buds at the base of the periopods which are remnants of the exopodites, and the supra-orbital spine is still present on the carapace. In the molt from Stage XVI to first juvenile instar both of these very minor morphological features are lost. The primary ecological difference is that juveniles are fully recruited to the bottom during daylight while Stage XVI larvae are not.

Pearcy (1973) has published the only information on day/night differences in benthic occurrence of juvenile P. jordani. The data were collected during one cruise in late April, 1971, 8-18 nautical miles off Tillamook Head. He found, using a plankton net mounted above a beam trawl, that juveniles (< 7.0 mm in carapace length) were more abundant near the bottom during daylight than at night

(mean abundance for four daylight trawls = 121.4/1000 m^3, versus

57.3/1000 m^3 mean abundance for six trawls at night). Plankton

tows taken by Pearcy using the same 0.7 m bongo nets as used in the

present study were not vertically stratified or separated by day and

night. They simply showed that the oblique tows to one-half of the

station depth caught more larval and juvenile P. jordani than the

surface tows (6.1 versus 0.8/1000 m^3), and both caught less than the

net mounted on the beam trawl (6.1 versus 86.4/1000 m^3). All esti-

mates of abundance from the beam trawl plankton net were subject to

contamination from the overlying water column.

Laboratory Experiments

The Combined Effects of Temperature and Salinity
on Survival of Laboratory Reared Larvae

Pandalus jordani larvae were successfully reared through 16

larval stages and several juvenile instars. Response surface estima-

tion of the combined effects of temperature and salinity on larval

survival to Stage II is shown in Figure 18. Optimal survival occurred

at all salinities between 9 and 10°C. Only the linear and quadratic

effects of temperature were statistically significant (Table VIII). The

effect of temperatures on survival in the upper part of the environ-

mental range was more marked than the effect of lower temperatures

as evidenced by the lower survival at 17°C than at 5°C. This ridge
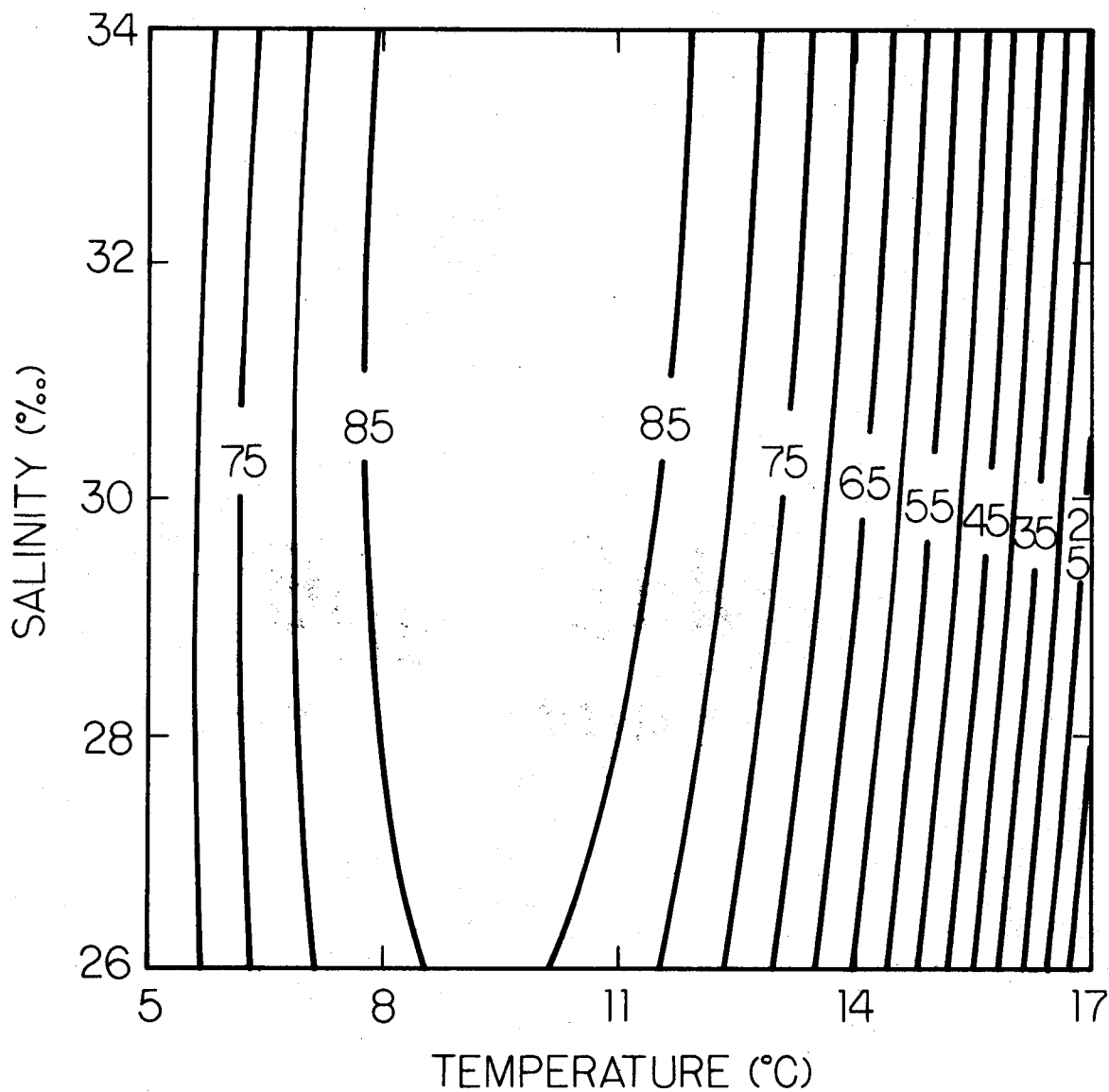
Figure 18. Response surface estimation of percent survival to larval stage II at 25 temperature and salinity combinations for _Pandalus jordani._ The equation incorporating all variables explained 67.29% of the variation: $Y\%_{survival} = -66.27 + 17.61(T) + 4.21(S) + 0.18(TxS) - 1.19(T^2) - 0.09(S^2)$.

Table VIII. Significance of linear effects of temperature and salinity, quadratic effects of temperature and salinity and the interaction of temperature and salinity in explaining the variability of larval survival at Stage II, VI, X and XI.

Stage	Variable	t (94 d.f.)	Significance level
II	T	6.82	.01
	S	0.22	N.S.
	TxS	0.62	N.S.
	T^2	-15.01	.01
	S^2	- 0.28	N.S.
VI	T	6.70	.01
	S	1.60	.20
	TxS	- 0.43	N.S.
	T^2	-12.60	.01
	S^2	- 1.52	.20
X	T	4.78	.01
	S	0.15	N.S.
	TxS	- 0.19	N.S.
	T^2	- 8.69	.01
	S^2	- 0.06	N.S.
XVI	T	2.33	.05
	S	- 1.48	.20
	TxS	0.58	N.S.
	T^2	- 5.32	.01
	S^2	1.56	.10

configuration also characterized the response surface estimation of

survival to Stage III.

The response surface estimation for survival to Stage VI is

seen in Figure 19. These curves are similar in shape to the surfaces

for larval Stages IV - VIII. Maximum survival (> 50%) occurred at

11°C and 31‰ . Linear and quadratic effects of temperature were

significant at the .01 level. The linear and quadratic effects of

salinity were less significant (.20) and affected survival only at the

lower salinities (Table VIII).

Figure 20 shows the response surface estimation of percent

survival to larval Stage X. Larval Stages IX, XI and XIII showed a

similar response to the combined effects of temperature and salinity

on survival. During these stages only the linear and quadratic effects

of temperature are significant (Table VIII). Maximum survival

(>23%) extends almost the entire range of salinity, and was reduced

only at the lowest salinities. The optimal temperature was slightly

above 11°C.

Figure 21 shows the response surface estimation of survival to

the last larval Stage XVI. Temperature and salinity affected the

shape of the survival curves at Stages XII, XIV and XV in a similar

fashion. Highest survival occurred between 11 and 13°C and at the

higher salinities (>32‰). The linear and quadratic effects of

temperature on survival were significant at the .05 and .01 levels
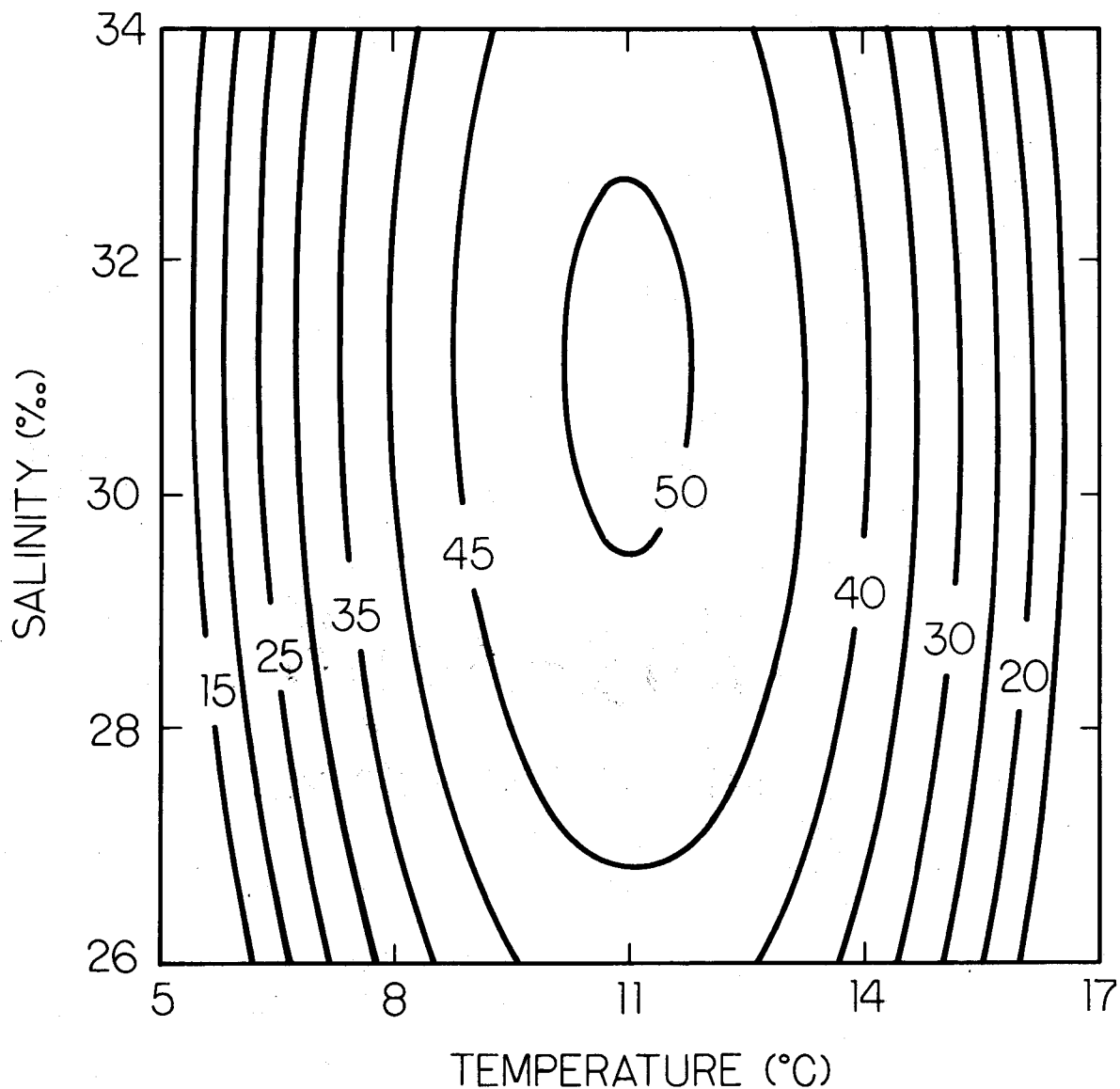
Figure 19. Response surface estimation of percent survival to larval
stage VI at 25 temperature and salinity combinations for
Pandalus jordani. The equation incorporating all variables
explained 63.47% of the variation: $Y_{\%surv.}$ = -407.14 +
26.78(T) + 20.01(S) - 0.05(TxS) - 1.15(T^2) - 0.31(S^2) .
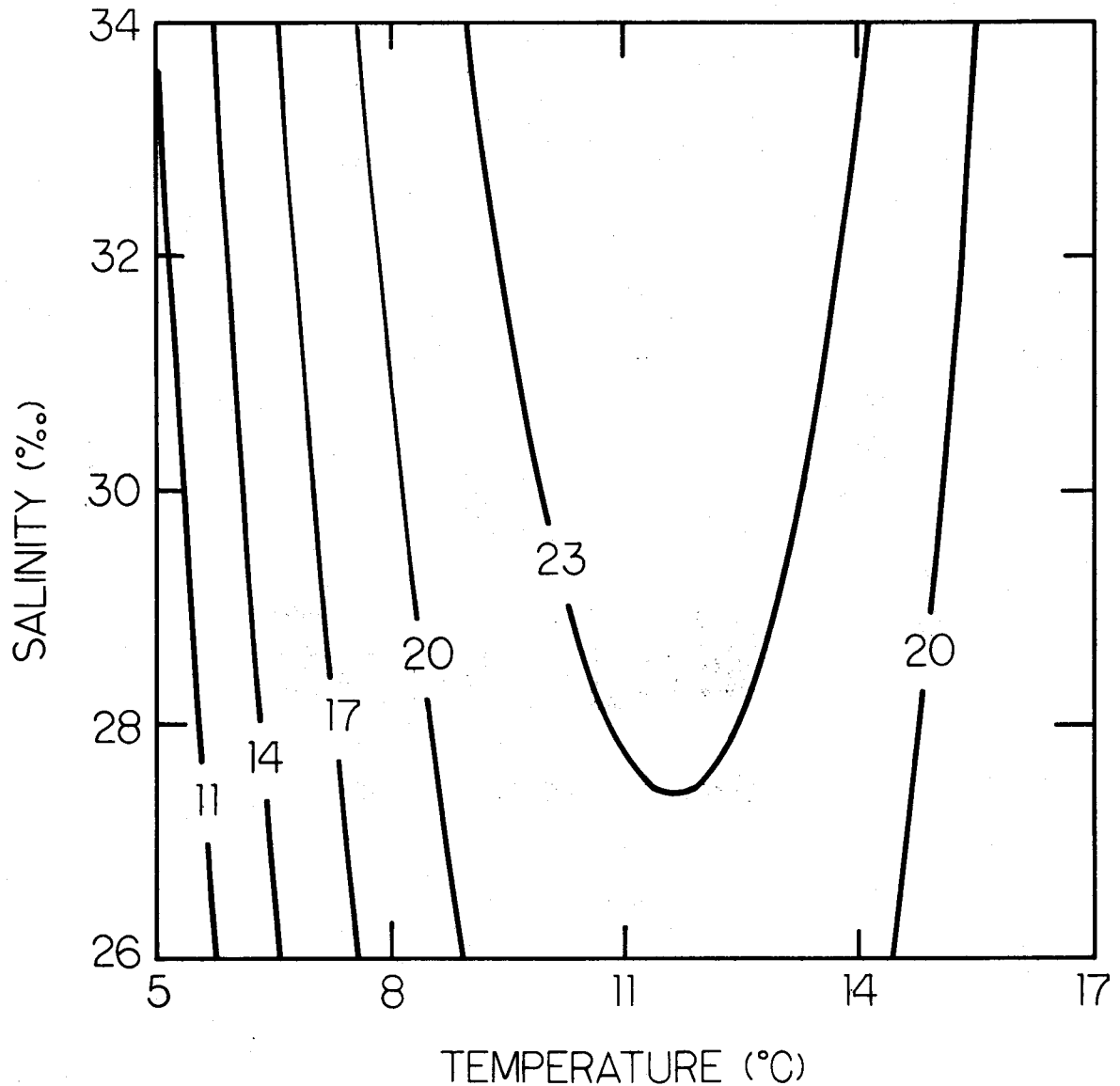
Figure 20. Response surface estimation of percent survival to larval stage X at 25 temperature and salinity combinations for <u>Pandalus jordani</u>. The equation incorporating all variables explained 48.07% of the variation: $Y_{\% surv.}$ = -83.15 + 13.28(T) - 1.27(S) - 0.01(TxS) - 0.55(T^2) - 0.01(S^2) .
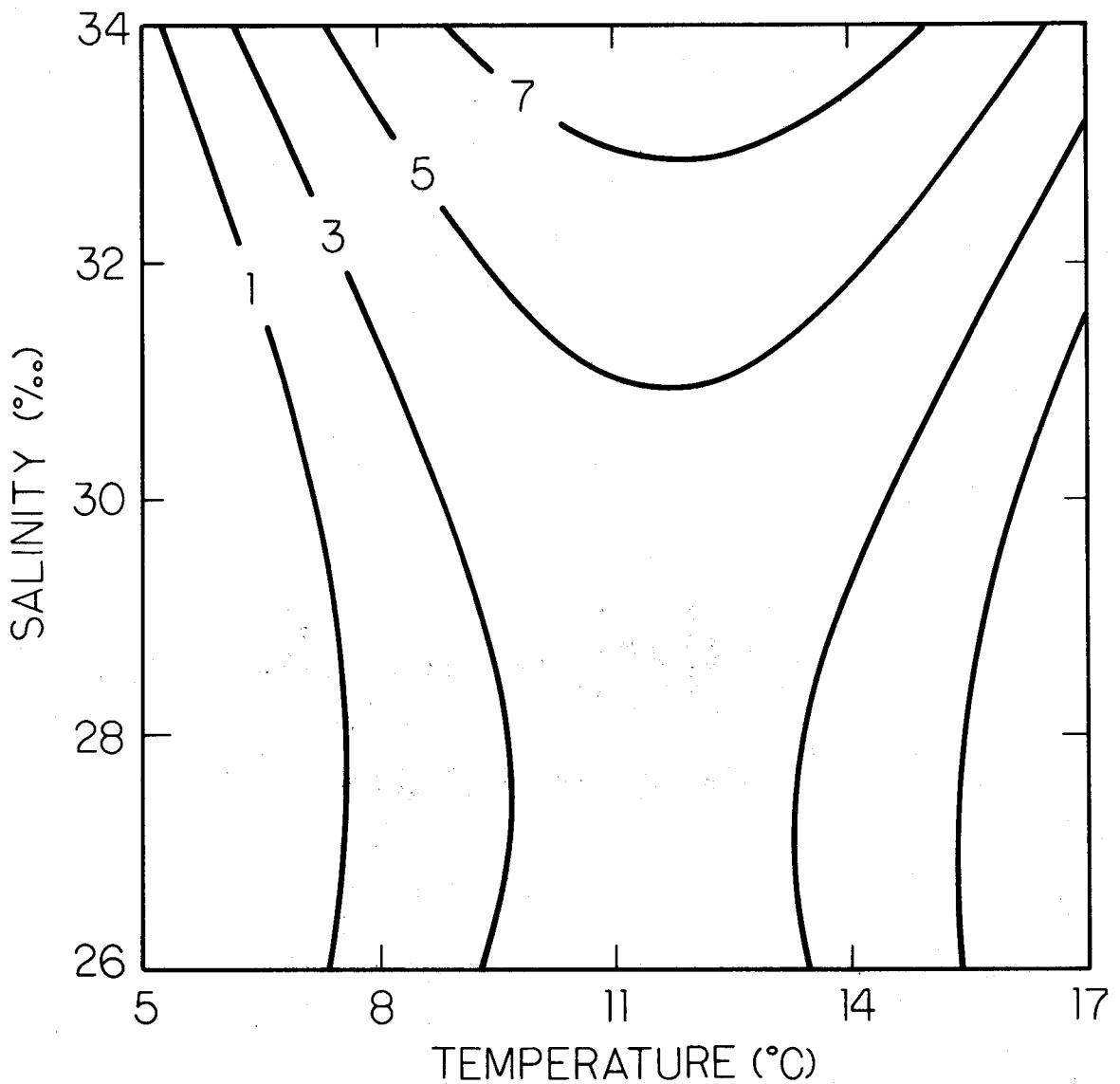
Figure 21. Response surface estimation of percent survival to larval stage XVI at 25 temperature and salinity combinations for _Pandalus jordani_. The equation incorporating all variables explained 33.44% of the variation: $Y_{\% surv.} = 72.6 +$ $3.23(T) - 6.34(S) + 0.02(TxS) - 0.16(T^2) + 0.11(S^2)$.

respectively. The linear and quadratic effects of salinity were significant at low levels (.20 and .10 respectively) (Table VIII).

Table IX summarizes the analyses of variance for Stages II, VI, X and XVI and the computed R^2 values for the complete regression equations at each stage. With larval development, the equations explain a decreasing amount of the variability in the combined effects of temperature and salinity on survival of P. jordani under laboratory conditions.

Table IX. Analyses of variance table, with mean square values at larval stages II, VI, X and XVI. R^2 values at each larval stage are included.

Source	Degrees of freedom	Analyses of variance			
		Mean square$_{II}$	Mean square$_{VI}$	Mean square$_X$	Mean square$_{XVI}$
Total	99	801.73	429.15	167.59	32.44
Regression	5	10679.89	6184.80	1595.08	214.81
Residual	94	276.30	189.35	91.66	22.74
R^2		0.6729	0.6347	0.4807	0.3344

The importance of considering the effects of temperature and salinity on survival of marine larvae has been stressed by many investigators (Bishai, 1961; Costlow, Bookhout and Monroe, 1960, 1962, 1966; Crisp and Costlow, 1963; Kinne, 1964; Lough and Gonor, 1973a, b; Sandoz and Rogers, 1944; Zein-Eldin and Aldrich, 1965). Most species considered in the above investigations inhabit estuaries,

where both temperature and salinity may change drastically, during all or part of the life cycle. It may, however, also be important to know the roles of these factors in the coastal ocean where the fluctuations are definite, but less extreme. The hydrographic conditions off Oregon fluctuate considerably (Bourke et al., 1971). The planktonic larval existence of P. jordani encompasses a period of hydrographic flux caused by seasonal, as well as daily shifts in wind, currents and hydrography. It was, therefore, of interest to test the combined effects of temperature and salinity on the survival of larval P. jordani over a range of conditions they are likely to encounter during their planktonic existence. A monofactorial analysis may lead to conclusions that are ecologically invalid and should be replaced wherever possible by a bi-, tri-, or polyfactorial approach (Kinne, 1963). Response surface methodology, as used in the present study, extends the inferential power of such laboratory analysis of multidimensional ecological processes (Alderdice, 1972).

In early larvae (I - III) the linear and quadratic effects of temperature were the only significant factors affecting larval survival. As larvae developed, the optimal temperature increased slightly (9-12°C) while salinity still did not have a significant effect on survival. Salinity did affect survival in older larvae (IV - XVI) to a small degree (P < .20), but only at the lower salinities within the optimal range of temperature.

From these laboratory findings it was inferred that P. jordani larvae are euryhaline over a limited salinity range and relatively stenothermal. It also appeared that the optimal temperature for survival increased a few degrees over the period of development. It is apparent that changes in hydrographic factors, especially temperature, that occur seasonally off the Oregon coast are factors affecting larval survival.

Laboratory Growth Rates

Laboratory growth rates were calculated from estimates of the median time for individuals within a temperature-salinity combination to complete a larval stage. There were no significant differences between the four replicates within the temperature-salinity combinations and therefore, numbers within combinations were pooled. Furthermore, it was found that salinity had no significant effect on larval growth rates. Therefore, the larvae at each salinity were pooled for each temperature. By pooling all individuals at each temperature, the number of larvae (about 500 initially) was large enough to compute median completion times for each stage and thereby gain more precise estimates of the effect of temperature on growth rate. The larvae at 17°C died so rapidly that there were not enough individuals for analysis at any stage after Stage I. Resolution was limited to two days, the interval between observations.

Figure 22 shows the fitted regression lines of median time to complete stage vs. larval stage and Table X contains the equations used to fit the lines. The estimate of time to complete a larval stage at each temperature was not independent, because the same individuals were used for estimation at each subsequent molt. The lack of independence in these estimates resulted in a tendency for a series of points to run above the fitted regression line followed by a series of points running below the line.

The differences between slopes at each temperature were quite uniform except for the $5^{\circ}C$ line which was displaced downward. At $14^{\circ}C$ and to a lesser extent at $11^{\circ}C$, there appeared to be a change in the molting rate, large enough to warrant fitting two lines to the observed values at these two temperatures. Older larvae (above VI) molt at a slower rate. A noticeable shift in food preference was seen in the laboratory animals shortly after this molt. After Stage VI a diet comprised solely of recently hatched Artemia nauplii was no longer suitable. This was apparent because large numbers of Artemia were still swimming in the experimental containers two days after their introduction. There was also a slight increase in larval mortality. Artemia nauplii reared for 4-6 days on Isochrysis galbana were added to the ration. This mixture of older (larger) Artemia as well as the recently hatched nauplii appeared to be adequate.
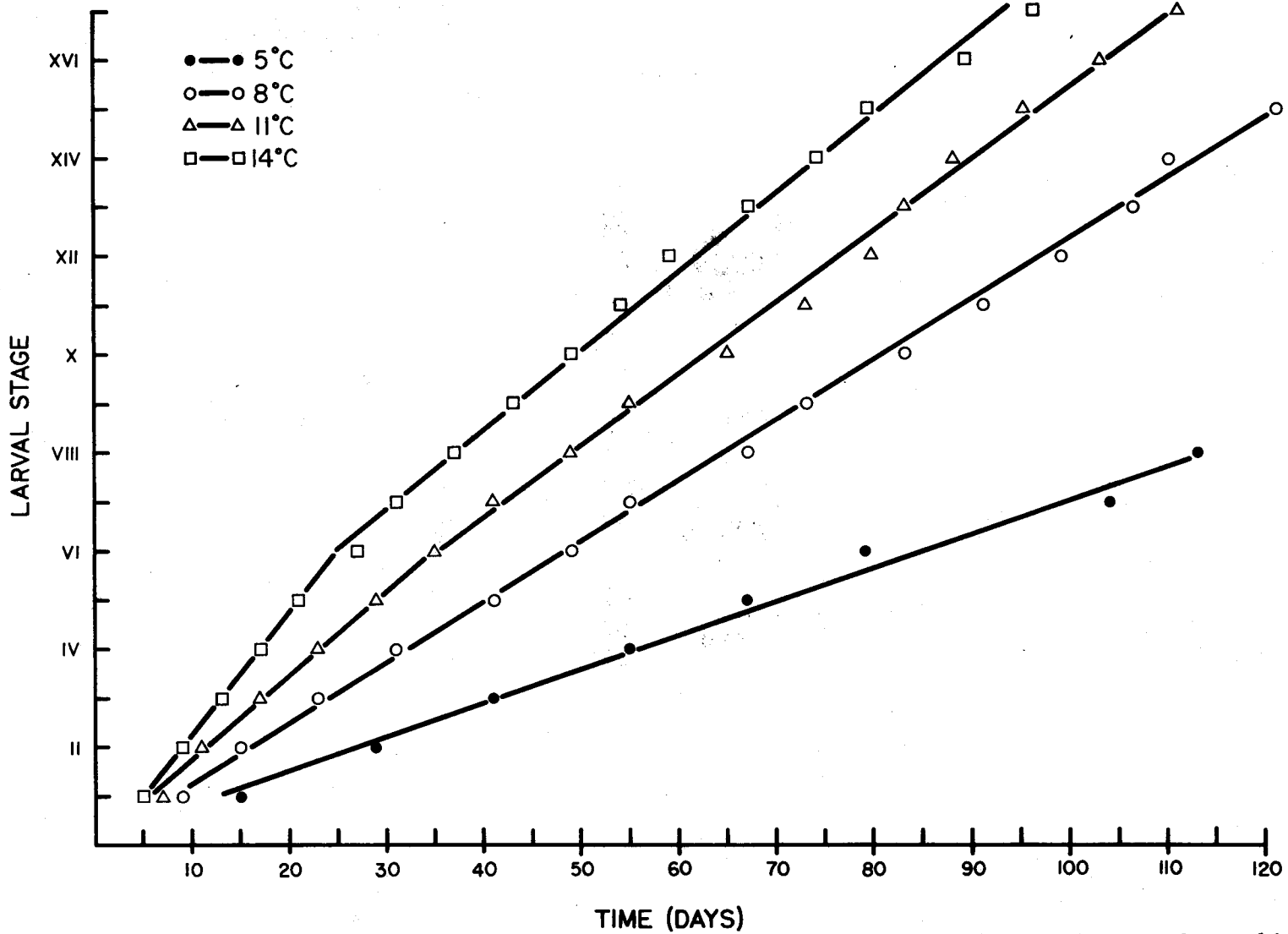
Figure 22.   Effects of temperature on growth.   Measured by the time for the median number of larvae to complete a given larval stage.

Table X. Regression equations for the effect of temperature on the
median time to complete a larval stage at four experi-
mental temperatures and a general equation for the effect
of temperature and stage on the median time to complete a
larval stage.

Temperature (°C)		Regression equations

5		$Y^a = -1.7 + 14.46$ (zoeal stage)
		$r = 0.9951 \quad r^2 = 0.9902$
8		$Y = 0.038 + 8.078$ (zoeal stage)
		$r = 0.9988 \quad r^2 = 0.9976$
11	(early)	$Y = 0.14 + 5.78$ (zoeal stage)
		$r = 0.9988 \quad r^2 = 0.9977$
	(late)	$Y = -3.05 + 6.64$ (zoeal stage)
		$r = 0.9968 \quad r^2 = 0.9936$
14	(early)	$Y = 1.00 + 4.00$ (zoeal stage)
		$r = 1.00 \quad r^2 = 1.00$
	(late)	$Y = -12.97 + 6.25$ (zoeal stage)
		$r = 0.9971 \quad r^2 = 0.9942$
General		$Y = 53.78 + 6.80$ (stage) $- 5.12$ (temperature)
		$r = 0.9654 \quad r^2 = 0.9321$

[a] Y = median time to complete a larval stage

Table XI summarizes the median time to complete each larval stage, as well as the intermolt period for each larval stage at the four experimental temperatures analyzed. The mean intermolt period for each temperature was computed from the observed values and compared with the slopes of the fitted regression lines.

A general regression equation incorporating both larval stage of development and the effect of temperature on the median time to complete a given stage was also computed (Table X).

It is generally recognized that temperature, acting either independently or simultaneously with other environmental factors, is one of the major physical factors affecting survival, duration of stages, and distribution of meroplanktonic invertebrate larvae (Costlow and Bookhout, 1971; Kinne, 1970). In crustaceans, growth is closely correlated with molting. The effect of temperature on molting frequency therefore is important in assessing growth rate. Molting frequency has been shown to be directly influenced by temperature in a number of investigations on adult crustaceans (Bückmann and Adelung, 1964; Passano, 1960; reviewed by Kinne, 1970). Kinne (1953) found the molting frequency of newly hatched Gammarus deubeni was independent of temperature within its normal range, whereas in adults the frequency of molting was closely dependent on variations in ambient temperature.

Table XI. Median time to complete a larval stage and the intermolt period (in days) for the stage, for each experimental temperature.

| Stage | Temperature (°C) | | | | | | | |
| | 5 | | 8 | | 11 | | 14 | |
	time[a]	period[b]	time	period	time	period	time	period
I	15	15	9	9	7	7	5	5
II	29	14	15	6	11	4	9	4
III	41	12	23	8	17	6	13	4
IV	55	14	31	8	23	6	17	4
V	67	12	41	10	29	6	21	4
VI	79	12	49	8	35	6	27	6
VII	104	25	55	6	41	6	31	4
VIII	117	13	67	12	49	8	37	6
IX	-	-	73	6	55	6	43	6
X	-	-	83	6	65	10	49	6
XI	-	-	91	8	73	8	54	5
XII	-	-	99	8	77	4	59	5
XIII	-	-	103	12	83	6	67	8
XIV	-	-	110	17	88	5	74	8
XV	-	-	121	11	95	7	79	5
XVI	-	-	-	-	103	8	89	10
XVII	-	-	-	-	111	8	96	7

Mean intermolt period

5	8	11		14
14.65	9.00	early	5.83	4.50
(14.46)	(8.08)		(5.78)	(4.00)
		late	6.90	6.36
			(6.64)	(6.25)

[a]Median time to complete stage in days

[b]Intermolt period in days

Early larval stages (I-VI); Late larval stages (VII-XIII); numbers in parentheses indicate slope from regression formulae in Table X.

In the present study on larval P. jordani an increase in molting

frequency with increased temperature was seen. The slopes of the

fitted regression lines steepened and the intermolt period was

lessened with increasing temperature. Lasker (1966) has shown

temperature to be important in regulating the intermolt period of

Euphausia pacifica. In his study temperature was allowed to fluctuate

with ambient seawater between 6 and $15^{\circ}C$, with corresponding inter-

molt periods of 9 to 3 days respectively. Above $12^{\circ}C$ the intermolt

period was not further shortened from 3 days. In Lasker's study the

intermolt period at 8 and $11^{\circ}C$ was 7 and 4 days respectively, which

is only slightly faster than P. jordani larvae reared at those tempera-

tures in the present study ($8^{\circ}C$, 8.1 days; $11^{\circ}C \sim 6.0$ days). The

shortest intermolt period observed in P. jordani larvae was 4 days

for early larvae at $14^{\circ}C$ and those few Stage II and III larvae that

survived at $17^{\circ}C$.

At the lower temperatures (5 and $8^{\circ}C$) the molting frequency

appeared to be constant through all stages attained (VIII and XV

respectively). However, at the two higher temperatures (11 and $14^{\circ}C$)

there was a noticeable slowing in growth rate after Stage VI. In

larvae older than Stage VI, at these two temperatures, the intermolt

period was lengthened (Table XI). This pattern of longer intermolt

periods with age has been noted for a number of adult crustaceans

(Bückmann and Adelung, 1964; Kinne, 1970), the marine copepod,

Calanus helgolandicus (Mullin and Brooks, 1970) and larval Pandalus

platyceros (Wickins, 1972). However, the trend is usually a gradual

one with successive molts. In P. jordani larvae, reared in the

laboratory, this change in growth rate was first noticed at 14°C. The

larvae at this temperature were the first to reach this stage, at

which time a change in feeding habit was also noted. The feeding

regime was changed at this time. These larvae and all those at lower

temperatures were fed a diet of various sized Artemia nauplii.

Because larvae reared at 8°C had been fed mixed Artemia for several

days before they reached Stage VI, the effect of the transition was

probably damped, and at 8 and 5°C absent altogether. It would

appear, however, that the shift in feeding habit along with some

metabolic processes is not simply a laboratory artifact. Growth

increment measurements on several hundred larvae from field

samples in both 1971 and 1972 showed a transition in growth increment

at about the same stage.

Lasker (1966) estimated that laboratory growth rates for E.

pacifica were twice the field estimates of Ponomareva (1959, 1963)

and he believed this was probably due to the increased availability of

food in the laboratory. In this study, it was hoped that a comparison

between laboratory growth rates at various temperatures could be

compared with field growth rates. The field analysis did not lend

itself to the same type of analysis as was appropriate for the

laboratory data. An approximation, however, of the field growth rate from mid March to late May 1972 fell within the laboratory rates at 8 and 11°C, which corresponded to surface temperatures during that period. From this analysis it would appear that growth rates derived from laboratory rearing were reasonable approximations of the effects of temperature on growth rates of P. jordani in the field.

Effect of Temperature on Larval Size

Laboratory Estimates. At each experimental temperature, 50 larvae were reared apart from the temperature-salinity factorial design experiment in 32‰ seawater. These larvae were used to establish size/temperature relationships. Five larvae were pre-served and measured at each larval stage from all five temperatures when possible.

The relationship between total length attained at each stage and the temperature at which the larvae were reared is shown in Figure 23. The relationship between carapace length and temperature is shown in Figure 24.

Larvae reared at 5 and 17°C were smaller than those reared at 8, 11 and 14°C for every larval stage compared. Measurements were obtained on only three larval stages at 17°C due to the very high mortality at that temperature. At 5°C, mortality was not high but growth was so slow that only the fifth larval stage had been attained when the experiment was terminated after 120 days.
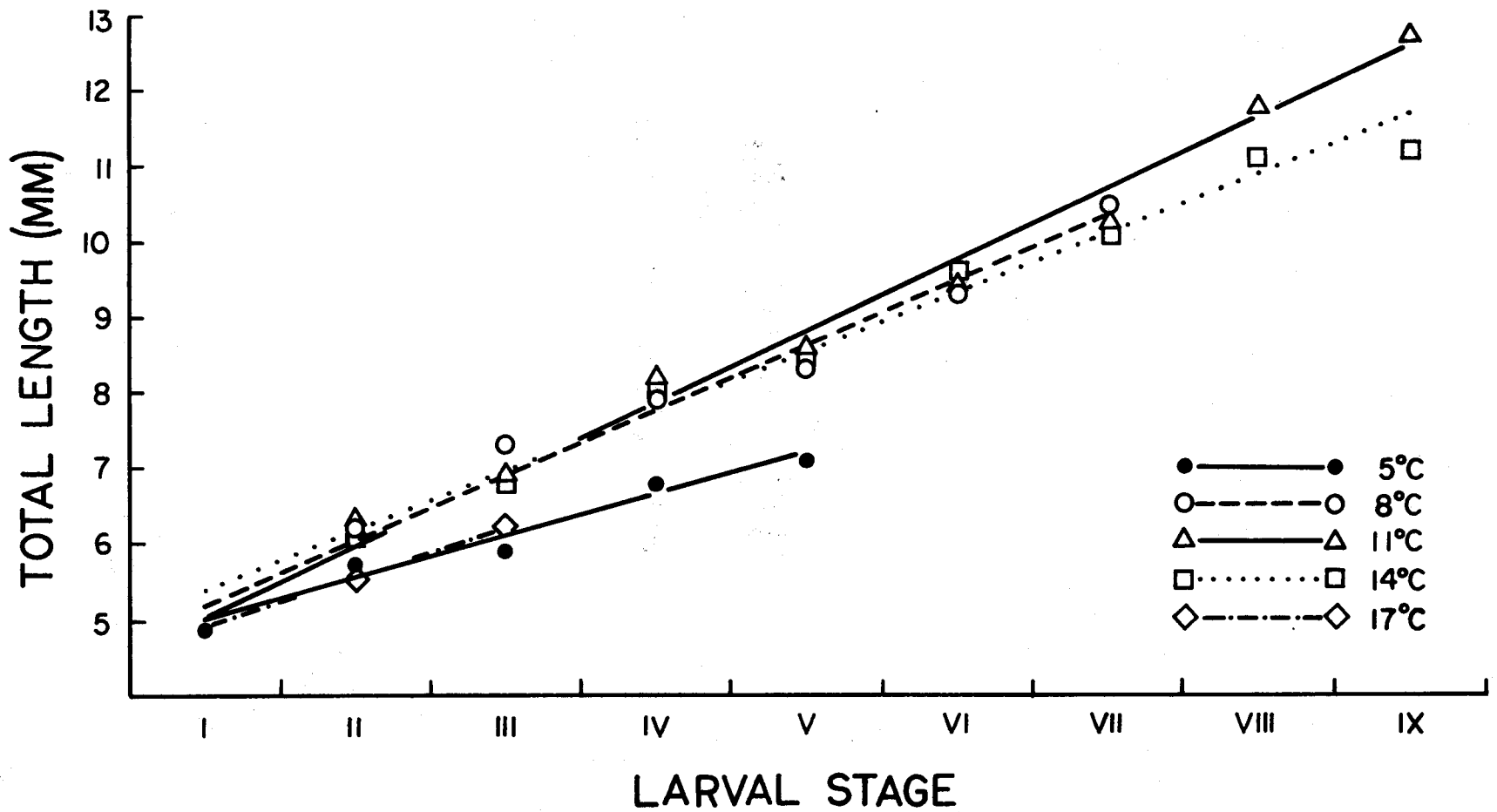
Figure 23. Relationship between total length and larval stage at five experimental temperatures.
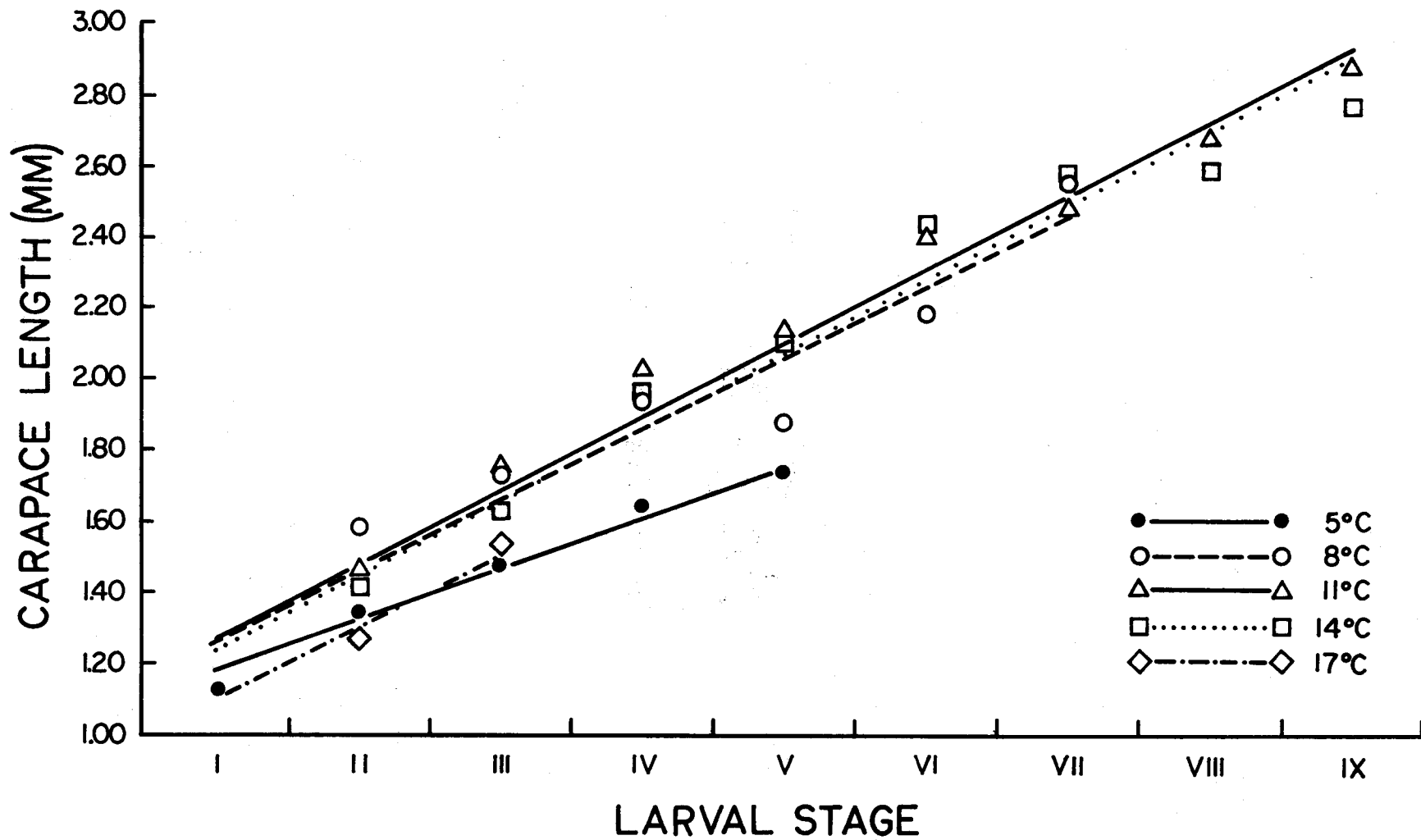
Figure 24. Relationship between carapace length and larval stage at five experimental temperatures.

Total lengths and carapace lengths of larvae reared at 8, 11 and 14°C were similar and were all larger than those for larvae reared at 5 and 17°C. Examination of Figures 23 and 24 and Table XII shows this similarity. Larvae reared at 11°C were slightly but not significantly larger than those reared at 8 and 14°C.

Many marine animals attain a larger final size in colder parts of their range. Large size at low temperatures is correlated with reduced rates of metabolism and growth, postponement of sexual maturity and prolongation of life (Kinne, 1963). There are, however, many exceptions to this. Pandalus jordani larvae reared under laboratory conditions did not show an inverse relationship between size and temperature. Larvae reared at the three intermediate temperatures were the largest, while larvae reared at the extremes (5 and 17°C) were the smallest. It may be that the effect of temperature is to change the conversion efficiency of food into body tissue and that the small size at the extremes of temperature in this study is a manifestation of lower efficiencies.

Field Estimate. Carapace length was the only measurement obtained from field samples. The first ten larvae of each stage encountered in every plankton sample were measured in 1971 (range: 174 Stage I's to 1 Stage XIV) and 1719 zoeae were measured in 1972 (range: 340 Stage I's to 5 Stage XV's).

Table XII. Summary of regression equations for total length and carapace length with zoeal stage for the five experimental temperatures.

Temperature (^{o}C)	Regression equations
	Total length
5	T.L. = 4.417 + 0.561 (zoeal stage)
	r = 0.9820 r^2 = 0.9644
8	T.L. = 4.331 + 0.859 (zoeal stage)
	r = 0.9888 r^2 = 0.9778
11	T.L. = 4.135 + 0.9327 (zoeal stage)
	r = 0.9949 r^2 = 0.9898
14	T.L. = 4.418 + 0.8135 (zoeal stage)
	r = 0.9918 r^2 = 0.9836
17	T.L. = 4.2567 + 0.655 (zoeal stage)
	r = 0.9940 r^2 = 0.9880
	Carapace length
5	C.L. = 1.000 + 0.1520 (zoeal stage)
	r = 0.9907 r^2 = 0.9815
8	C.L. = 1.044 + 0.2014 (zoeal stage)
	r = 0.9617 r^2 = 0.9248
11	C.L. = 1.058 + 0.2078 (zoeal stage)
	r = 0.9887 r^2 = 0.9778
14	C.L. = 1.020 + 0.2075 (zoeal stage)
	r = 0.9830 r^2 = 0.9663
17	C.L. = 0.8967 + 0.2050 (zoeal stage)
	r = 0.9882 r^2 = 0.9766

T.L. = total length; C.L. = carapace length, both in millimeters

The curvilinear relationship between larval stage and carapace length for 1972 is shown in Figure 25. Regression equations for both years are given in Table XIII. The size/stage relationship was virtually identical for the two years. Furthermore, the relationship seen in the field for Stages I - IX was very similar to the size/stage relationship for larvae reared in the laboratory at 8, 11 and 14°C.

Larval Growth Increment--Laboratory and Field Estimates

The growth increment (growth factor) for larval P. jordani is defined as the ratio of the lengths of successive stages:

$$\text{G. I. } Z_{i+1} = \frac{\text{length } Z_{i+1}}{\text{length } Z_i}$$

Both carapace length and total length of the laboratory reared larvae were used to make this calculation while only the carapace length measurements were used for the field estimates.

Laboratory Estimates. Table XIV summarizes growth increments, based on both total length and carapace length at the five experimental temperatures. Growth increments were quite variable within and between temperatures and stages. A relationship between temperature and growth increment was not observed. At all five temperatures the growth increment was greatest for the molt between Stage I and II ($\bar{x}_{\text{T. L.}}$ = 23%, $\bar{x}_{\text{C. L.}}$ = 26%). The mean growth
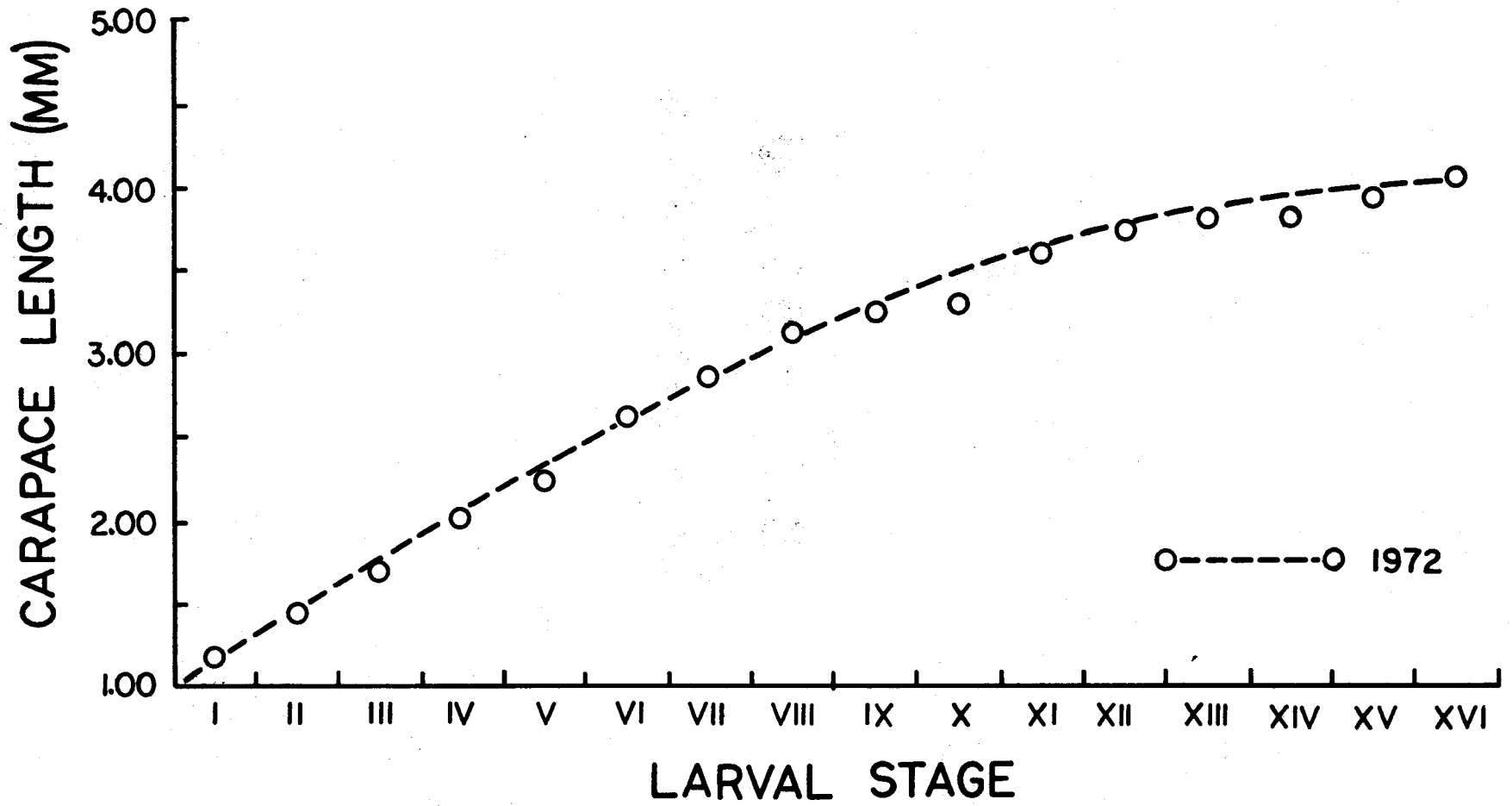
Figure 25. Relationship between carapace length and larval stage from measurement of 1972 field samples.

Table XIII. Regression equations for carapace length/
larval stage relationship from 1971 and
1972 field samples.

Carapace length (1971)

$$\text{C. L.}_{\text{I-XVI}} = 1.2497 + 0.19756 \text{ (zoeal stage)}$$

$$r = 0.9728 \qquad r^2 = 0.9464$$

$$\text{C. L.}^2_{\text{I-XVI}} = 0.1495 + 1.0842 \text{ (zoeal stage)}$$

$$r = 0.9746 \qquad r^2 = 0.9498$$

Carapace length (1972)

$$\text{C. L.}_{\text{I-XVI}} = 1.2405 + 0.19612 \text{ (zoeal stage)}$$

$$r = 0.9767 \qquad r^2 = 0.9539$$

$$\text{C. L.}^2_{\text{I-XVI}} = 0.1732 + 1.0750 \text{ (zoeal stage)}$$

$$r = 0.9920 \qquad r^2 = 0.9841$$

Table XIV. Growth increment (L_z/L_{z+1}) at five experimental temperatures. Increment calculated for total length (tip of rostrum to tip of telson) and carapace length (rear edge of orbit to posteriormost edge of carapace). Measurement based on five animals at each stage and temperature except where number is contained in parentheses.

Stage	Total length							Carapace length						
	5°C	8°C	11°C	14°C	17°C	n	$\bar{x}$	5°C	8°C	11°C	14°C	17°C	n	$\bar{x}$
II	1.18	1.27	1.29	1.25	1.16	25	1.23	1.20	1.41	1.30	1.25	1.13	25	1.26
III	1.03	1.18	1.11	1.12	1.09 (4)	24	1.11	1.10	1.09	1.19	1.16	1.20 (4)	24	1.15
IV	1.15	1.09	1.18	1.19	-	20	1.15	1.12	1.22	1.16	1.20	-	20	1.18
V	1.04 (3)	1.04	1.05	1.06	-	18	1.05	1.05 (3)	0.97	1.05	1.08	-	18	1.04
VI	-	1.12	1.10	1.13	-	15	1.12	-	1.16	1.13	1.16	-	15	1.15
VII	-	1.12 (3)	1.10	1.05	-	13	1.09	-	1.17 (3)	1.03	1.06	-	13	1.09
VIII	-	-	1.14	1.10	-	10	1.12	-	-	1.08	1.00	-	10	1.04
IX	-	-	1.08 (3)	1.01 (2)	-	5	1.04	-	-	1.07 (3)	1.07 (2)	-	5	1.07
n	4	6	8	8	2		28	4	6	8	8	2		28
$\bar{x}$	1.10	1.14	1.13	1.11	1.13		1.12	1.12	1.17	1.13	1.12	1.16		1.14

increments at each temperature were relatively constant (range: total length, 1.10-1.14; carapace length, 1.12-1.17). There was no evidence of a trend in the growth increment with respect to larval stage. Overall mean growth increment per molt was 1.12 based on total length and 1.14 based on carapace length.

Field Estimate. Estimates of larval growth increments from field samples are shown in Figure 26. The growth increment was not constant through the 16 larval stages. A general but variable decreasing trend in larval growth increment was seen in both years as larval age increased. The highest percent increase in carapace length occurred in the molt from Stage I to Stage II (26%, 1971; 22%, 1972). In 1971 larvae in Stage VII and younger increased in length by increments of greater than 10% per molt (26-12%). A transition occurred at Stage VII dropping a 6% carapace length increase at that stage. Carapace length increased in increments below 10% per molt (9-3%) through the remainder of the larval stages.

The general pattern was similar in 1972. A transition such as that observed between Stages VII and VIII in 1971 also occurred in 1972 but was between Stages VI and VII. Stage VI and younger stages increased carapace length in increments above 10% (22-13%) while larval Stages VII and older increased carapace length in increments of 10% or less (10-0%).
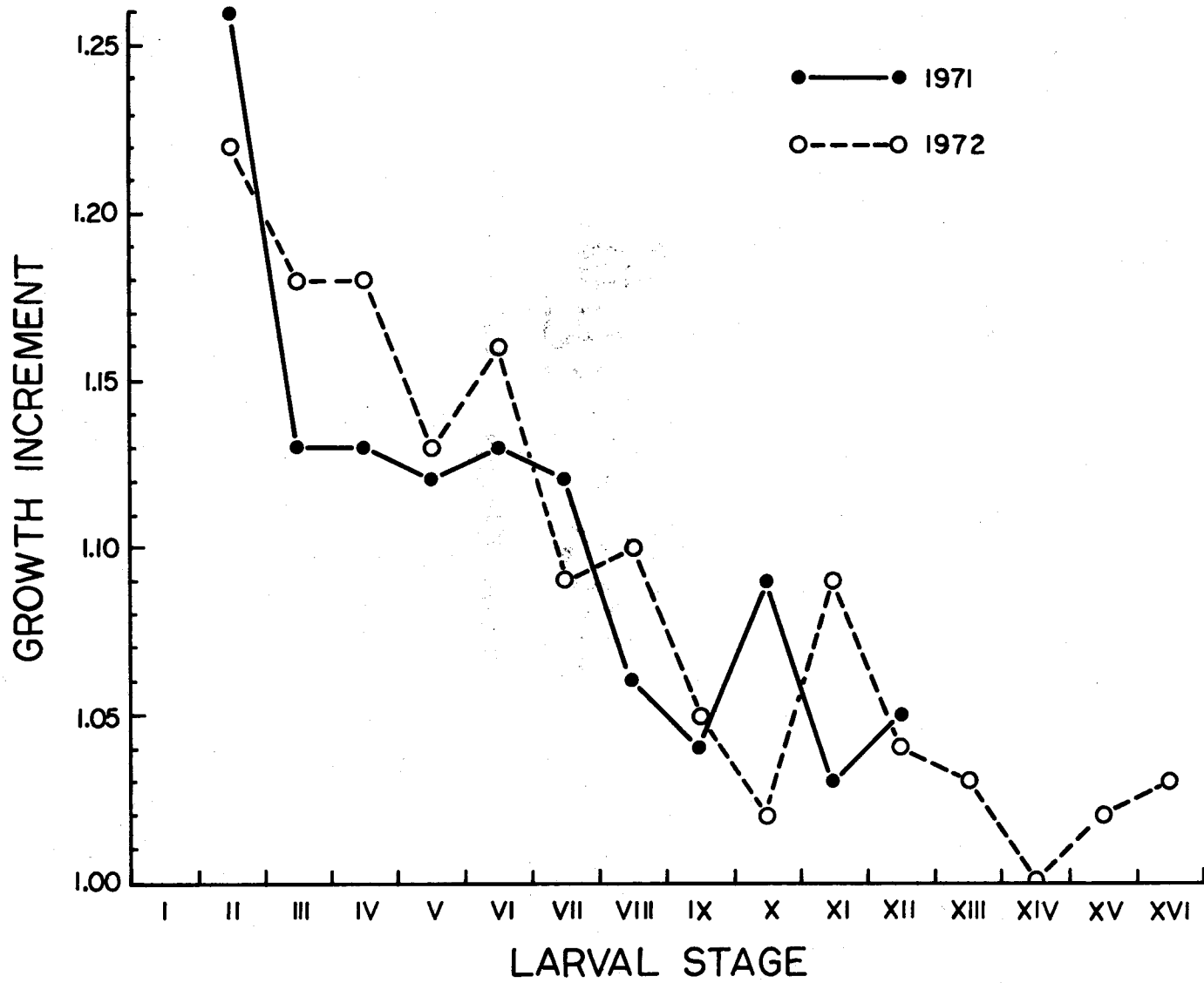
Figure 26.   Growth increments based on carapace length for 1971 and 1972, versus larval stage.

The subtle transition in the magnitude of growth increment is not striking in itself. However, the molts at which it occurred corresponded to the transition in growth rates seen in laboratory reared larvae at 11 and 14°C. This also corresponded to the observed change in feeding habits seen in the laboratory animals at about the same time. The fact that this transition in growth increment was not seen in the laboratory reared larvae may be due to the relatively small number ($\leq$ 5) of larvae measured at each stage and temperature. However, the existence and character of a transition must be left for further study.

The mean growth increment from field estimates was 11.1 per molt in 1971 and 1.09 in 1972.

Fowler (1909) formalized the discrete size increments in crustacean growth first noted by Brooks (1886) into 'Brooks' Law, ' stating that during early growth each stage increases in size, at each molt, by a fixed percentage of its length. He called the proportionate increase in size the growth factor. Gurney (1942) applied the growth factor concept to accounts published to that time and concluded that in decapod larvae the average growth factor was about 1.26, with considerable variation. Furthermore, he believed that if the growth factor exceeded 1.5 between any two stages there was probably an error in identification and two species were involved. Rice (1968), in his review of larval growth increments, found that the mean was 1.22

(range 0.93-2.70) for all decapods based on published length measurements, and that within the macrurans the mean was 1.19 (range 0.93-2.25). He commented on the striking range of values, and believed it was due, in part, to errors of various types (identification, measurement, allometric growth, etc.).

In the present study growth increment data were collected for both laboratory reared and field collected larvae. There was no apparent effect of temperature on growth increment. The growth increment data, with respect to stage of development, in laboratory reared larvae are very limited because of low numbers of larvae available for measurement and are, therefore, inconclusive. Large numbers of larvae for almost all stages were obtained and measured from plankton samples. Distinctive trends in growth increment were evident. In both 1971 and 1972 there was a variable but steady decrease in the magnitude of the growth increment with later stages of development. In both years a shift in growth increment was noticed in the mid larval stages (Stage VII - VIII in 1971 and VI - VII in 1972). A similar transition in growth increment was noted by Kurata (1955) in the post-larvae of P. kessleri between the eighth and ninth instar. His calculation of the mean growth increment before the shift was 1.15 and after the shift 1.11.

The only other accounts of larval growth of P. jordani are incomplete attempts to rear P. jordani in the laboratory (Modin and

Cox, 1967; Lee, 1969). Calculations of growth increment based on extrapolations of measurement data in those studies show general agreement with the growth increment data presented here.

Larval Survival

Estimates of Larval Survival from Field Sampling--1971 and 1972

In this study a rather simplified technique was used to estimate differences in larval survival between the larval seasons of 1971 and 1972. Mortality was estimated from the decreasing abundance at successive stages of larval development. This method of estimating survival required that the reproduction of the population be relatively synchronous and that only one generation is produced per year (Fager, 1973; Mullin and Brooks, 1970). In both years larvae of early stages were in the water column for one to two weeks before and after the peak of hatching. However, the main pulse of hatching did occur within a relatively limited period and therefore, the reproduction of P. jordani along the central Oregon coast is believed to be synchronous.

A numerical model of survival through stages of development and time was developed to gain insight into the effect of sampling frequency on the estimation of abundance to each developmental stage and, therefore, survival rate. The model imposed an intermolt

period of six days over the entire length of the developmental period

and an instantaneous daily mortality rate (i) of 0.077799. This

mortality was constant over all stages and also held constant within

the molt cycle. The mortality rate was incorporated into a simple

exponential decay formula to estimate survival rate over time

$(N_t = N_o e^{-it})$. Two hatching frequency distributions were used; one

was the standard normal distribution with one million individuals

released over 20 days, while the other was a severely peaked distribu-

tion, in which 850,000 of the one million individuals were released

over five days around the median. It was felt the latter configuration

more accurately reflects the hatching of P. jordani larvae in the field.

At selected sampling intervals stage abundance was estimated

by summing all sampled individuals, within each developmental

stage, over the entire developmental period. These abundance esti-

mates are compared with "actual" abundance graphically in Figure 27.

The heavy center line represents the "actual" survival rate, which

could only be estimated by daily sampling. As would be expected,

sampling more than once within an intermolt period (every four days)

tended to overestimate survival to each larval stage. Sampling every

nine days (1.5 times the intermolt period) consistently underestimated

larval numbers and, therefore, survival. Larval abundance estimates

with a severely peaked configuration of larval release resulted in an

oscillating estimate of larval survival. The magnitude of the
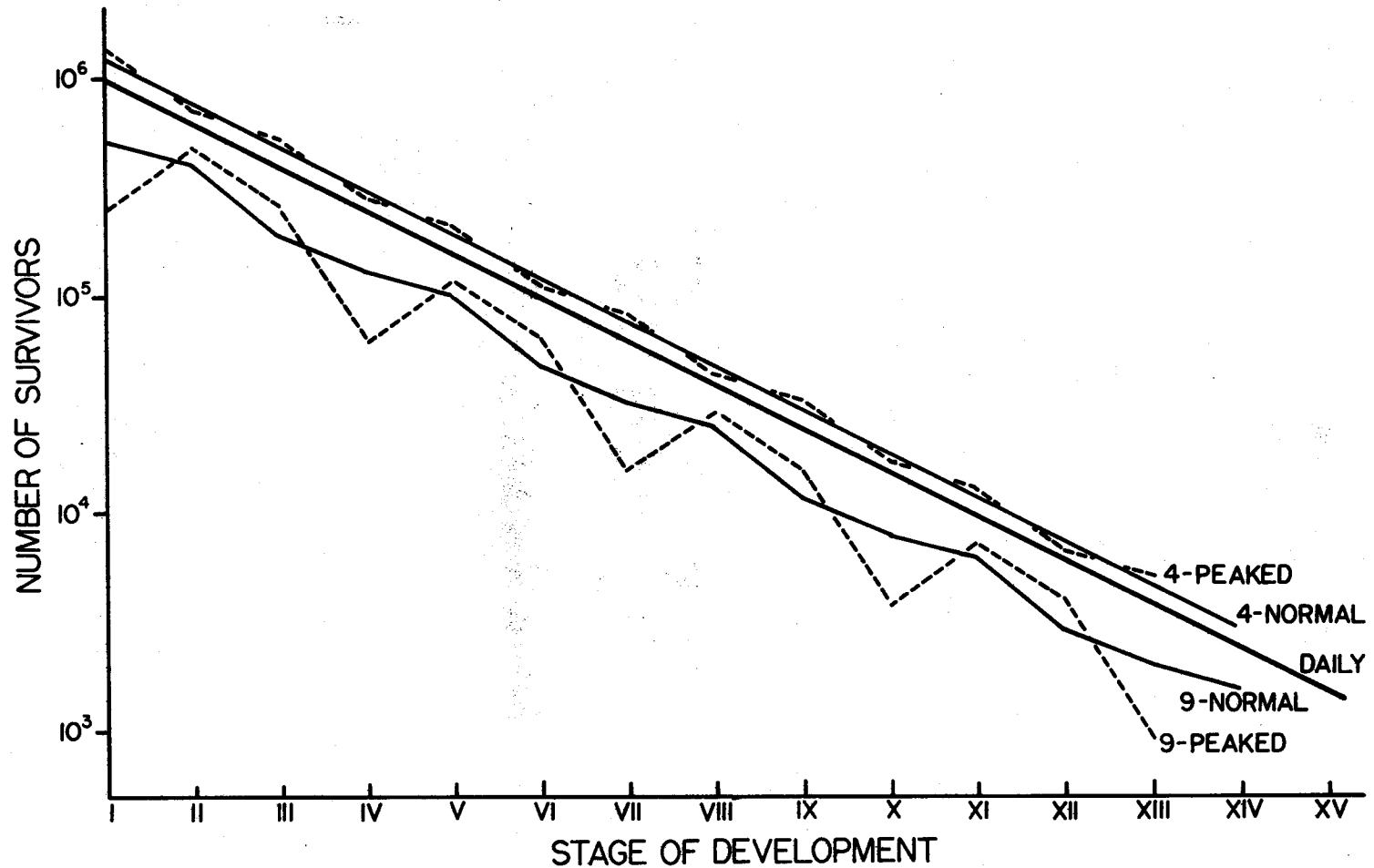
Figure 27. A graphic representation of the effect of sampling interval, and larval hatching distribution on estimates of larval abundance and survival rate. Heavy line indicates "actual" survival rate; 4 - normal, sampling standard normal distribution of larvae every four days; 9 - normal, sampling every 9 days; 4 - peaked, sampling peaked distribution of larvae every 4 days; 9 - peaked, sampling the peaked distribution every 9 days.

oscillation was related to the degree the sampling frequency and the molting frequency were in phase. In all cases, however, whether the number of larvae were over- or underestimated at any particular stage due to the relationship between the sampling and molting frequency, the survival rate based on estimates of abundance paralleled the "actual" rate.

Table XV summarizes the time between cruises, the estimated surface temperatures for each intercruise period (taken from Figure 15), and an estimated intermolt period for the larvae based on the larval rearing experiments (Table XI). The shortest period between two cruises over the two-year sampling period was eight days (22-30 May 1972) while the average was 14.5 days. Surface temperature for the larval period was seldom below $8^{\circ}C$ (intermolt period for $8^{\circ}C$ = 8.08 days) and was $10^{\circ}C$ between 22 and 30 May 1972 for which the estimated intermolt period was 7.0 days. The mean ratio of interval between cruises to intermolt period was 2.1, indicating that the survival estimation used in this study would underestimate survival to a certain extent because larvae could progress through more than two stages between some cruises.

In order to assess larval survival in the field, total abundance (no. /1000 m^2) of each larval stage over all cruises and stations was calculated. In each year the total number of Stage I's was taken to be 100% of the larval hatch and the number of each successive larval

Table XV. Summary of period between cruises (days), estimated temperature for the period (from Figure 15), intermolt period at the temperature (Table XI) and the ratio between inter-cruise period and intermolt period.

1971						1972				
Sampling date	Intercruise period	Temperature	Intermolt period	Ratio IC/IM		Sampling date	Intercruise period	Temperature	Intermolt period	Ratio IC/IM
1-II										
	13	9	7.3	1.8		4-III				
1-III							12	11	5.8	2.1
	19	9	7.3	2.6		16-III				
20-III							12	11	5.8	2.1
	10	8	8.1	1.2		28-III				
30-III							14	10	6.6	2.1
	23	9	7.3	3.2		11-IV				
22-IV							11	10	6.6	1.7
	12	10	7.0	1.7		22-IV				
4-V							30	10	7.0	4.3
	10	11	6.6	1.5		22-V				
14-V							8	10	7.0	1.1
	16	11	6.6	2.4		30-V				
1-VI							13	10	7.0	1.9
	11	12	6.4	1.7		12-VI				
12-VI							16	10	7.0	2.3
	16	14	6.3	2.5		28-VI				
28-VI										

Mean - 1971: 2.1

1972: 2.2

Overall: 2.1

stage found was expressed as a percent of the total number of Stage

I's. The sampling effort in each year was based on the total number

of cubic meters of water filtered. These volumes were so close

(1971 = 72,246.1 m^3; 1972 = 67,978.5 m^3; difference = 4,266.8 m^3)

that the difference was not considered to be a significant factor in

explaining the observed differences in survival between the years.

Figure 28 shows the results of these calculations. In 1971, 1653

Stage I's (140,040/1000 m^2) were used to estimate the larval hatch.

Only 26.9% survived to Stage II's and less than 1% survived past Stage

VII. Only one juvenile P. jordani (135/1000 m^2) was found in 1971

representing 0.09% of the larval hatch. The larval hatch in 1972 was

apparently much lower being represented by 530 Stage I larvae

(40,146/1000 m^2). Over 64% survived through Stage III, with numbers

and percentages decreasing gradually with age. During the 1972 larval

season five juveniles (426/1000 m^2) were caught in the water column,

representing 1.06% of the hatch. Though absolute numbers were very

low in both years, the percent surviving to juveniles in 1972 was an

order of magnitude greater than 1971 and therefore the difference was

probably significant.

Some of the variability in estimates of percent survival at

individual stages seen in Figure 16 is due to the relationship between

sampling frequency and molting frequency (mean intercruise period

of 14.5 days/mean intermolt period of 6.8 days = 2.1) and its effect

on abundance estimates at those larval stages.
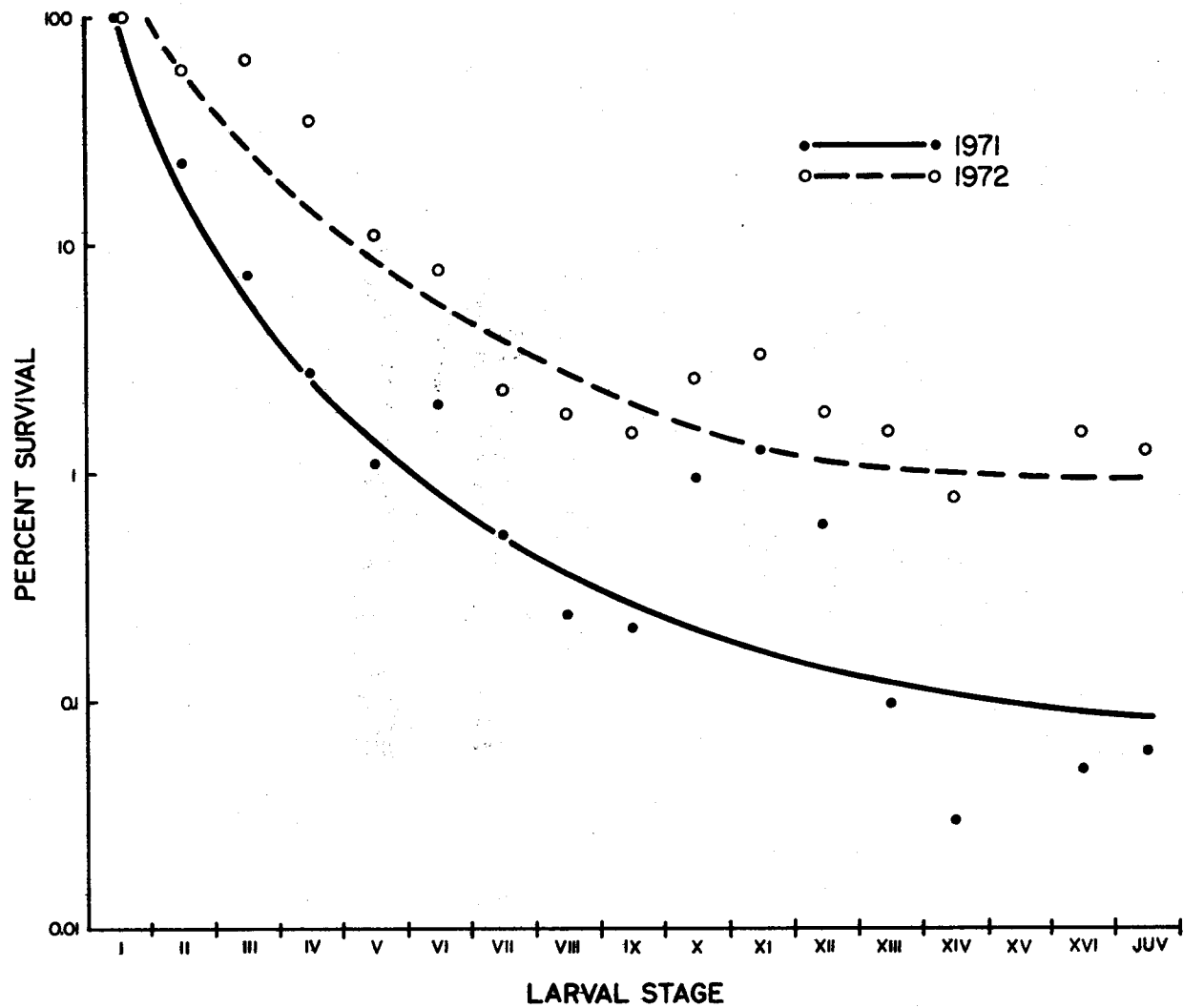
Figure 28. Larval survival (percent), based on total numbers at each stage caught in the plankton.

Estimates of Larval Survival from
Commercial Landings

Long range trends in P. jordani larval survival were sought from

Oregon fishery statistics in order to put into perspective the apparent

differences in larval survival seen in 1971 and 1972. Jack Robinson

(Fish Commission of Oregon) provided data on numbers of ova and

numbers of age I shrimp. Numbers of ova were estimated from

adjusted biomass estimates of numbers of females from samples of

commercial landings in April along with an established length/

fecundity relationship (Robinson, 1971). Numbers of age I shrimp

were estimated from commercial landings 1.5 years later in Novem-

ber when they were fully recruited to the commercial gear. Figure

29 shows the fluctuations in number of ova produced and number of

age I shrimp estimated from the commercial catch by year class from

1961 to 1973. The instantaneous rate of total mortality from these

commercial landings was calculated (i, Table XVI) (Ricker, 1958).

An effort to separate mortality during the planktonic larval

stage from the total mortality estimated above required an estimate

of juvenile mortality of P. jordani developed by Gotshall (1969, 1972).

Gotshall has shown that Pacific hake (Merluccius productus) prey with-

out respect to age on P. jordani. Hake stomach content analysis,

therefore, provides a means of sampling very early juvenile shrimp

before they are recruited to the commercial or survey gear.
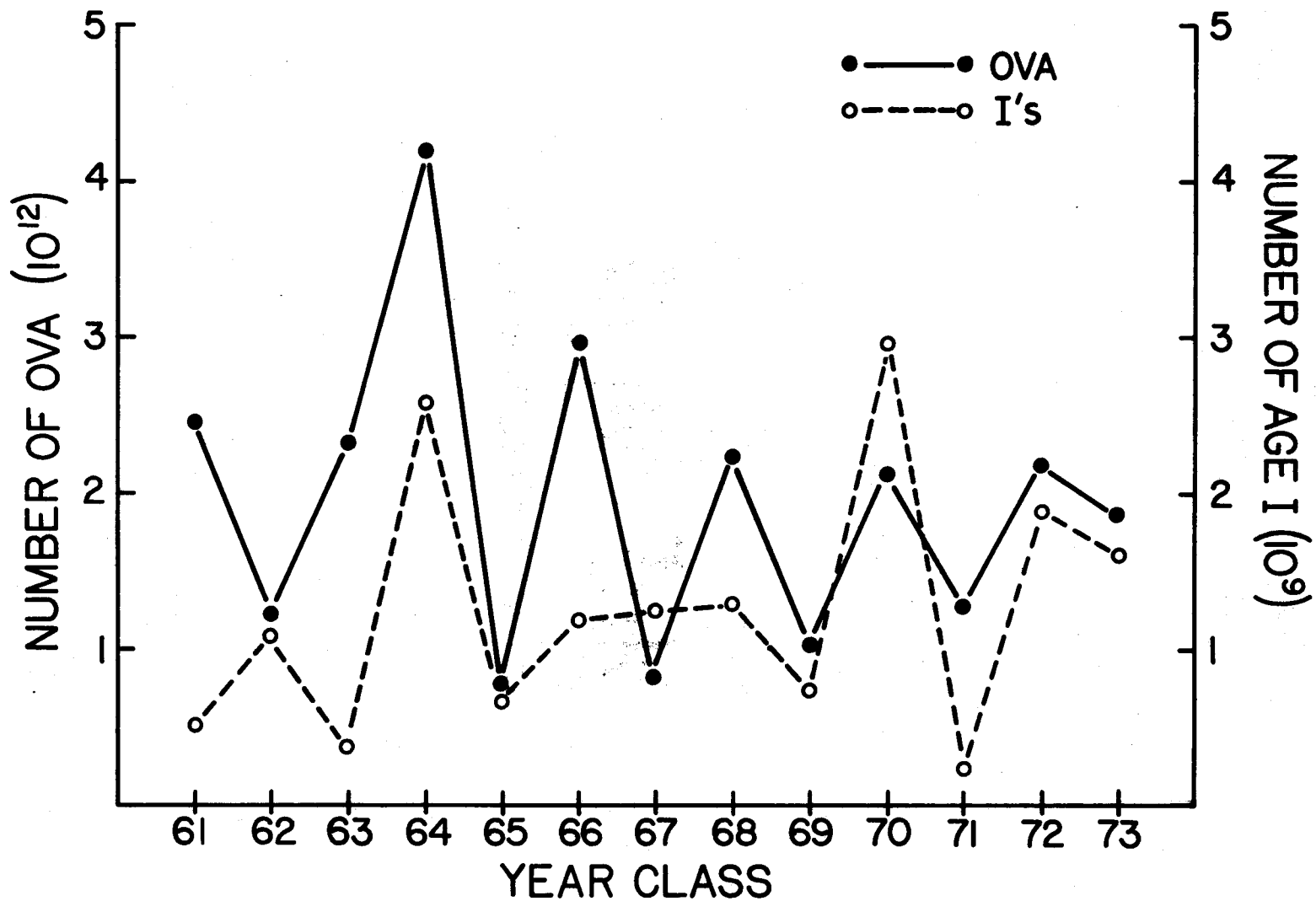
Figure 29. Number of ova spawned and number of age I shrimp recruited to the commercial fishery 1.5 years later, by year class (Robinson, unpublished data).

Table XVI. Estimates of larval survival (e^{-it}) from fishery data supplied by Jack Robinson, Fish Commission of Oregon, and from field estimates of larval abundance.

FOOTNOTES:

a/ $i = -\ln(N_t/N_o)/t$ where $t = 1.5$ years, the interval from hatching to recruitment to the commercial gear

b/ $i_{juv.}$ = calculation for first year instantaneous mortality after recruitment to the bottom, from stomach analysis of hake, Merluccius productus, by Gotshall (1969, 1972)

c/ i_{larval} = instantaneous larval mortality as a proportion of the total instantaneous mortality (i) with instantaneous juvenile mortality ($i_{juv.}$) held constant:

$$i_{larval} = \frac{1.5(i) - 1.083(i_{juv.})}{0.417}$$

d/ $t = 0.417$, estimated time of larval period in plankton

e/ $t = 0.417$, period between calculation of N_o and N_t in 1971

f/ $t = 0.375$, period between calculation of N_o and N_t in 1972

Table XVI.

Year	$N_o \times 10^{12}$	$N_t \times 10^9$	$N_t/N_o \times 10^4$	$-\ln N_t/N_o$	i [a]	$i_{juv.}$ [b]	i_{larval} [c]	e^{-it} [d]	$e^{-it} \times 10^4$
1961	2.45	0.50	2.04	8.50	5.66	1.50	16.49	1.03×10^{-3}	10.3
1962	1.25	1.10	8.80	7.04	4.69	1.50	12.98	4.46×10^{-3}	44.6
1963	2.30	0.33	1.52	8.79	5.86	1.50	17.20	7.67×10^{-4}	7.7
1964	4.20	2.60	6.19	7.39	4.93	1.50	13.83	3.13×10^{-3}	31.3
1965	0.75	0.75	10.00	6.91	4.61	1.50	12.68	5.05×10^{-3}	50.5
1966	2.95	1.20	4.07	7.81	5.20	1.50	14.84	2.05×10^{-3}	20.5
1967	0.80	1.25	15.62	6.46	4.31	1.50	11.61	7.90×10^{-3}	79.0
1968	2.25	1.30	5.78	7.46	4.91	1.50	13.99	2.93×10^{-3}	29.3
1969	1.00	0.75	7.50	7.20	4.80	1.50	13.37	3.79×10^{-3}	37.9
1970	2.15	3.00	13.95	6.58	4.38	1.50	11.88	7.06×10^{-3}	70.6
1971	1.75	0.25	1.43	8.85	5.90	1.50	17.35	7.21×10^{-4}	7.2
1972	2.20	1.95	8.86	7.03	4.69	1.50	12.97	4.48×10^{-3}	44.8
1973	1.85	1.66	8.97	7.02	4.68	1.50	12.93	4.55×10^{-3}	45.5
Mean:								3.69×10^{-3}	

Estimation of larval survival, from larval abundance (no. /1000 m^2)

Year	$N_o \times 10^{12}$	$N_t \times 10^9$	$N_t/N_o \times 10^4$	$-\ln N_t/N_o$	i [a]	$i_{juv.}$ [b]	i_{larval} [c]	e^{-it} [d]	$e^{-it} \times 10^4$
1971	140,040	135	9.64	6.94 [e]			16.64	5.93×10^{-4}	5.9
1972	40,146	426	106.28	4.54 [f]			12.12	6.38×10^{-3}	63.8

See preceding page for explanation of footnotes.

Gotshall has estimated an instantaneous mortality rate during this initial period using hake as a biological sampler ($i_{juv.}$, Table XVI).

A proportional analysis of instantaneous mortality within the 18 months from hatching to commercial recruitment yielded the instantaneous total mortality attributed to the larval phase:

$$i = \frac{0.417(i_{larval}) + 1.083(i_{juv.})}{1.5}$$

where:

$$i = \ln(N_t/N_0)/t, \text{ with } t = 1.5 \text{ years}$$

$i_{juv.}$ = calculation for the first year mortality after recruitment to the bottom from hake stomach content analysis (Gotshall, 1969, 1972)

i_{larval} = instantaneous rate of total larval mortality

Solving for i_{larval}:

$$i_{larval} = \frac{1.5(i) - 1.083(i_{juv.})}{0.417}$$

These values are shown in Table XVI for the 13-year period, 1961-1973, along with an instantaneous larval mortality calculated from number of larvae collected in the plankton in 1971 and 1972.

The expected overall larval survival (e^{-it}) was calculated for all 13 years, along with survival based on larval numbers in the plankton samples of 1971 and 1972 (Table XVI). Calculations based on the plankton samples were similar to those from the fishery, indicating that 1971 was a very poor year for larval survival while 1972 was near average.

Factors Affecting Larval Survival

From the earlier analysis of the effect of wind patterns and degree of upwelling on larval distribution and abundance, it was felt that Bakun's upwelling index (1973 and pers. comm.) was the best general indicator of hydrographic conditions for correlative purposes. Monthly, bimonthly and quarterly indices were calculated and regressed against the expected overall larval survival ($e^{-it} \times 10^4$). Table XVII shows the regression coefficients and R^2 values for the regression equations for the various time periods tested. The degree of upwelling in July was the most highly correlated single month ($R = 0.5992$) while the average for the three-month period, June, July, August, gave the highest overall correlation ($R = 0.7501$, $F = 14.15**$ with 1, 11 d. f.). The equation, $e^{-it} \times 10^4 = -8.429 + 7.33$ (upwelling index), accounted for 56.3% of the variability in larval survival. Figure 30 shows the general positive relationship between high upwelling index with high larval survival. Though not an outstanding correlation, the value does give some insight into what factors may be limiting larval survival and therefore affecting year class strength in the P. jordani fishery.

Surface seawater temperatures in 1971 and 1972 (Figure 15) were different in several respects. The regression analysis draws attention to differences in the months June, July and August. It is

Table XVII. Summary of regression coefficients, R, and R^2 values from the regression analysis of monthly, bi-monthly and quarterly upwelling indices (from Bakun, 1973, pers. comm., and original) and estimated larval survival, $e^{-i} \times 10^{-4}$ for the 14-year period, 1960-1973.

Time period	R	R^2
Months		
January	0.0313	0.0010
February	0.3241	0.1050
March	0.5495	0.3020
April	0.0469	0.0022
May	0.2824	0.0797
June	0.5842	0.3413
July	0.5992	0.3590
August	0.4510	0.2034
September	0.1193	0.0142
October	-0.2069	0.0428
November	0.0220	0.0005
December	-0.0146	0.0002
Bi-monthly		
June-July	0.6731	0.4531
Quarters		
First	0.3221	0.1037
Second	0.5279	0.2787
Third	0.6923	0.4793
Fourth	-0.0970	0.0094
March-May	0.4970	0.2470
May-July	0.6249	0.3905
June-August	0.7501	0.5627
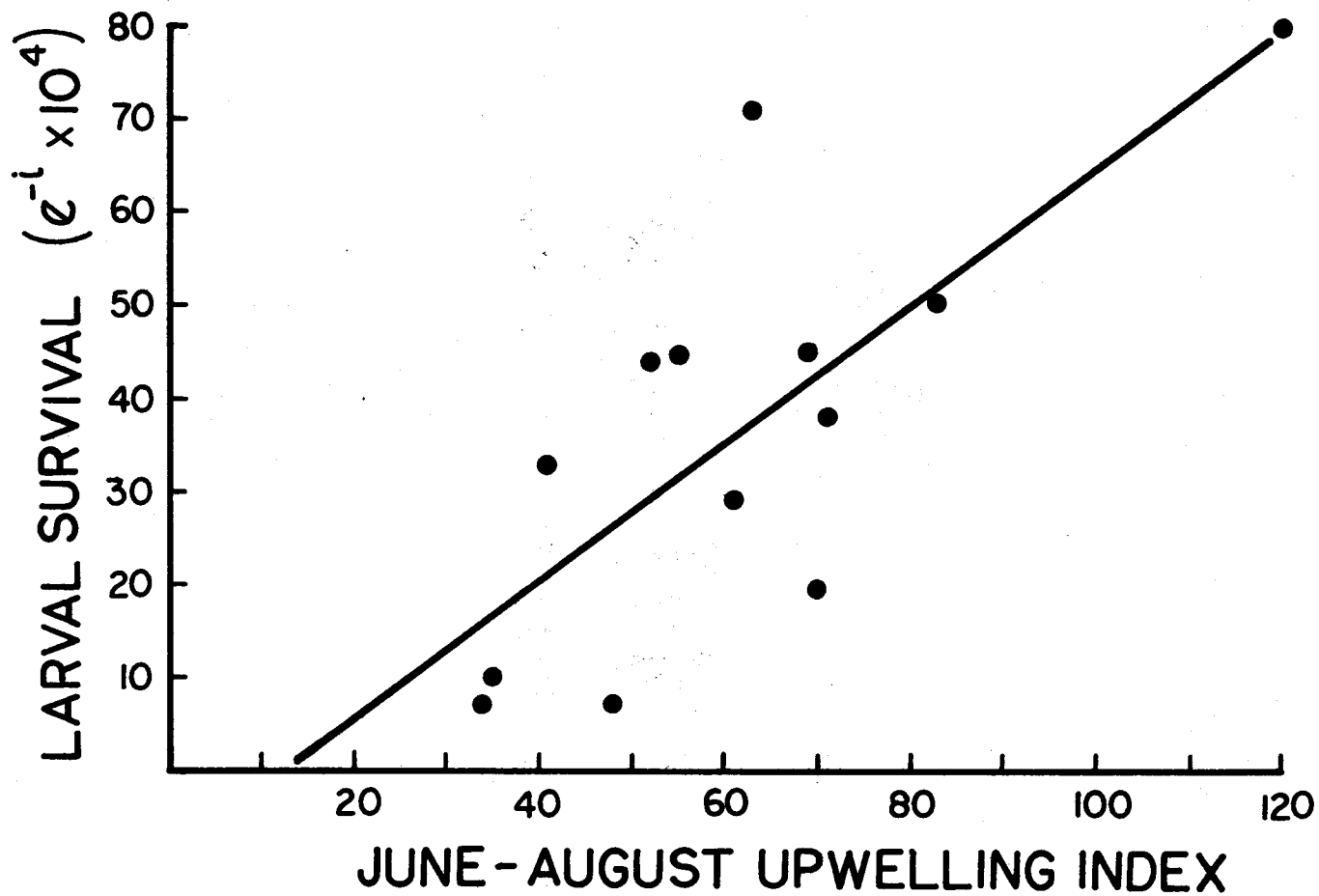
Figure 30. Scatter diagram with fitted regression line for the relationship between average upwelling in June, July and August, 1960-1973 and larval survival ($e^{-i} \times 10^4$), 1961-1973.

apparent that in the later months of larval development temperatures were several degrees higher in the nearshore stations in 1971 than in 1972. Evaluation of the laboratory rearing experiments showed that $11-12^\circ C$ was optimal and survival decreased rapidly above that range. In 1971, when upwelling was weak, surface temperatures were between $14-15^\circ C$ at NH 10-25 where the majority of the larvae were located late in the larval season. In 1972 late larvae were abundant at NH 15. Temperatures were held at a near optimal range (between $11-12^\circ C$) by increased upwelling. The temperature data gathered on the Early Life History cruises do not offer very high resolution of temperature trends. However, the indications of upwelling strength from both the progressive vector diagram analysis and the upwelling indices calculated by Bakun are in agreement with the evidence that high average upwelling levels in the early summer months enhance larval survival. It is reasonable to suppose that upwelling acts to keep temperatures down to near optimal levels, whereas weak upwelling is accompanied by elevated surface temperatures ($>14^\circ C$) which have been shown in the laboratory to be limiting.

The importance of upwelling in enhancing the productivity of certain nearshore oceanic regions of the world is well documented (Ryther, 1969; Ryther and Menzel, 1965; Steeman-Neilsen and Jensen, 1957). Year-to-year fluctuations in the strength of seasonal winds, upwelling and surface advection in the northeast Pacific are known

Hubbard and Pearcy, 1971; Peterson and Miller, in press; Wickett,

1967). However, until a means of quantifying these phenomena was

developed by Bakun (1973) it was difficult to actually correlate strength

of upwelling with fluctuations in productivity at any level. By use of

Bakun's index, Peterson (1973) has shown fluctuations in upwelling are

correlated with the landings of Cancer magister in Oregon 1.5 years

thereafter. He hypothesized a link between upwelling, food availa-

bility and molting of older year classes to a harvestable size.

The object of this study was not to develop a predictive tool to

forecast shrimp landings, but to determine what environmental factors

were affecting larval survival and therefore to some degree affecting

the size of the incoming year class. This study uses a technique to

estimate fluctuations in larval survival using estimates from the

fishery. This approach is believed to be more sensitive than back

calculating several years from the commercial landings to the larval

period of the year class as was done by Winnor (1966) for the C.

magister fishery in California. He was able to find significant corre-

lations of presumed larval survival and hydrographic conditions,

mainly surface seawater temperatures. From these correlations he

surmised that low temperatures were indicative of current changes.

Therefore, advection was taken to be responsible for high larval

mortality by carrying larvae away from substrate suitable for larval

settlement. Winnor, however, knew nothing about the environmental requirements or distribution of larval C. magister under these varying conditions.

The usefulness of the technique used in the present study is somewhat limited by the estimation methods used. Bakun's upwelling index resolves upwelling conditions only in broad terms. The resolution gained from shorter term calculations, daily and weekly (Bakun, in prep.), should make it possible for the index to indicate critical periods and conditions of shorter duration that are masked in the present monthly indices. Furthermore, it is obvious that mortality of early juvenile shrimp on the bottom caused by limited food supplies, crowding, cannibalism, and predation by a number of fishes (Merluccius productus, Atheresthes stomias, Lyopsetta exilis, and others) fluctuates from year to year. The application of Gotshall's (1969, 1972) instantaneous mortality estimate to all years uniformly ignores all of this kind of variation. However, in spite of these limitations, the estimate of larval survival derived from this type of analysis was similar to estimates of larval survival derived from intensive plankton sampling.

In earlier studies (Hubbard and Pearcy, 1971; Wicken, 1967; Winnor, 1966) the advective nature of upwelling phenomena is stressed. This effect was seen in the distribution of P. jordani larvae. Larvae were generally held inshore during the periods of onshore surface flow

and were later moved offshore with the onset of upwelling in late spring and early summer. It is possible that the colder temperatures and, therefore, slower growth, along with the offshore advective transport caused by strong upwelling, was deleterious to P. jordani larvae. Therefore, high positive correlation between larval survival and upwelling in June, July and August was unexpected and would be hard to explain biologically without other knowledge of P. jordani larval biology. Laboratory rearing experiments showed optimal larval survival at temperatures of 11-12°C. Upwelling conditions help maintain these relatively low temperatures through the summer months. When upwelling is weak high water temperature results (Patullo et al., 1967). Temperatures above 14°C, seen in June of 1971 during weak upwelling conditions, were probably harmful and contributed to the low larval survival estimated that year. The advective properties of upwelling are also necessary to move larvae offshore in late spring. Without this advective transport, provided by strong upwelling, larvae would remain inshore in a habitat unsuitable for settlement.

This initial model is considered to be a good first approximation of the factors that limit larval distribution and abundance and, therefore, affect larval P. jordani survival. The regression coefficient, $R = 0.76$, between larval survival and June, July and August upwelling explained a significant amount ($F = 14.15$** with 1, 11 d.f.,

$R^2 = 0.5627$) of the variability in the fluctuations of larval survival for the years 1961 to 1973. Although there were several limitations, the technique shows promise in pointing out critical times and conditions, during the larval period, which play a part in establishing year class strength. No doubt higher resolution could be attained if a more complete series of estimates of first year mortality could be acquired using a predator, such as hake, as a biological sampler. This could help account for some of the unexplained variability in the present model caused by density dependent factors such as competition and predation on the bottom during the first year. With 10-15 years of routine sampling of commercial landings along with hake stomach content analysis, refinements in the correlation analysis of larval survival with hydrographic conditions could be made and thereby eliminate the need of costly and very time consuming field sampling of P. jordani larvae.

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APPENDIX

APPENDIX

The following larval descriptions are not meant to be detailed morphological accounts. Rather, they are intended to point out certain morphological features that were used to determine the stage of larvae sorted from plankton samples, as well as living larvae in the laboratory experiments. Morphological changes in the rostrum, telson, uropods and pleopods were best suited for this purpose. Appendix Table I summarizes the characteristics used to determine the zoeal stages of P. jordani.

STAGE I.   Large immobile eyes, rudimentary pereiopods, telson unsegmented from 6th abdominal segment (Appendix Figure I), absence of uropods at base of telson, no pleopods, no rostral spines, mean carapace length (C. L.) of 514 larvae collected from the plankton 1.18 mm.

STAGE II.   Eyes stalked, exopodites on the first two pairs of pereiopods, uropods seen enclosed in telson, small lateral spines in telson, no pleopods, no rostral spines, mean C. L. of 428 larvae 1.45 mm.

STAGE III. Uropods external, ventral pair simple about 1/3 length of telson (Appendix Figure 1), one small dorsal rostral spine, no pleopods, mean C. L. of 362 larvae 1.70 mm.

STAGE IV.   Dorsal and ventral pairs of uropods almost equal in length, about 2/3 length of telson, two small dorsal rostral spines, very small pleopod buds (Appendix Table I), mean C. L. of 225 larvae 1.98 mm.

STAGE V.   Uropods almost length of telson, telson narrowing at terminal end with 10 terminal spines, three dorsal rostral spines, pleopod buds slightly longer, mean C. L. of 127 larvae 2.24 mm.

STAGE VI. Uropods reach full development, dorsal slightly longer than ventral, ventral uropod equal to telson in length, 8 rostral spines (Appendix Figure 2), pleopod buds biramous, mean C. L. of 128 larvae 2.58 mm.

STAGE VII. Tip of telson nearly square with 10 terminal spines, 9 rostral spines on dorsal surface, pleopods enlarge only slightly, mean C. L. of 83 larvae 2.83 mm.

STAGE VIII. Little change in telson, 10 rostral spines, pleopods enlarge with no setation, mean C. L. of 52 larvae 3.09 mm.

STAGE IX. Little change in telson, 10 dorsal rostral spines, pleopods lengthen with no setation, mean C. L. of 38 larvae 3.20 mm.

STAGE X. Four lateral spines on telson extend up 2/3 of length, 10 dorsal rostral spines, first evidence of setae on pleopods, mean C. L. of 78 larvae 3.32 mm.

STAGE XI. Two middle spines on terminal margin of telson longer than those in preceding stages and longer than adjoining 3 pairs, 6 lateral spines on telson, 6 indentations (spine precursors) appear on ventral side of rostrum (Appendix Figure 2), 13 dorsal spines, pleopods larger and are more robust, setation on pleopods sparse, mean C. L. of 77 larvae 3.57 mm.

STAGE XII. Telson more pointed at terminal margin that previous stages with 8 terminal spines (4 large, 4 small), 14 rostral spines dorsally, 6 indentations ventrally, well developed setae on functional pleopods, expodites on pereiopods still functional, mean C. L. of 69 larvae 3.72 mm.

STAGE XIII. Little change in telson, 15 rostral spines on dorsal surface, 6 indentations ventral, pleopods longer, expodites on pereiopods still robust and functional, mean C. L. of 20 larvae 3.84 mm.

STAGE XIV. Little change in telson, 15 dorsal rostral spines, 6 ventral rostral spines, pleopods enlarged, mean C. L. of 10 larvae 3.84 mm.

STAGE XV. Six spines on terminal margin of telson (4 large, 2 small), 15 dorsal rostral spines, 7 ventral spines on rostrum, pleopods enlarge, exopodites not functional but still prominent, mean C. L. of 5 larvae 3.92 mm.

STAGE XVI. Telson as in juvenile with four large terminal spines, 16 dorsal and 8 ventral rostral spines (Appendix Figure 2), only very small buds of the exopodites still present, mean C. L. of 23 larvae 4.00 mm.

JUVENILE. Very similar to stage XVI with respect to telson and rostral spination, remnants of exopodites completely gone, C. L. greater than 4.20 mm.

Appendix Table II summarizes the species of pandalid shrimps for which there are published larval descriptions, and the stages described for each species. The larval descriptions of P. jordani by Modin and Cox (1967) and Lee (1969) are in general agreement with the present account, as far as they go. Lee's account was admittedly incomplete, while Modin and Cox state that the eleventh zoeal stage described was the last zoeal stage and was followed by the first juvenile instar. They did not describe this first juvenile instar or state the differences between it and the preceding larval stage.

In the present study, 16 zoeal stages were found, both in laboratory reared and field collected larvae. The additional larval stages (XII-XVI) differ from one another morphologically by small differences in the degree and arrangement of rostral and telson spination.

The gradual increase in the natatory function of pleopods, along with the concomitant gradual decrease in size and function of

the exopodites makes the definition of a distinct post-zoeal or pre-juvenile (megalopal) stage impractical according to the definition of this stage given by Williamson (1969). Whether or not the fifteenth and sixteenth zoeal stages should be considered megalopal stages because of their reduced exopodites is largely a semantic argument.

Though the morphological transition between the last zoeal stages and the first juvenile stage was very gradual a distinct difference in the day/night vertical distribution and habitat selection was revealed in the field sampling, in that during daylight juveniles are primarily bottom dwelling while late zoeae are not.

Of interest is the large number of instars of P. jordani larval development compared with the number of larval stages reported for other pandalids (see Appendix Table II). The first zoeal stage of P. jordani is morphologically less well developed than that of other pandalid species. An extreme example can be seen in the difference in the degree of development between Stage I zoeae of P. jordani and those of P. kessleri. Upon hatching, Pandalus kessleri has a chelate second pereiopod, well developed third through fifth pereiopods, a well developed rostrum and antennae and, most notably, biramous setous pleopods on the first five abdominal segments (Kurata, 1958). A similar state of development is not reached by P. jordani until Stage X or XI. Further comparison between the two species shows that P. jordani spawns many more eggs than P. kessleri (2000-3000

vs. ca. 200 respectively); the total length of the first zoea of P. jordani is 4.87 mm while P. kessleri is 8.1 mm (excluding the rostrum); the number of larval stages is very different, 16 for P. jordani and only 4 for P. kessleri; and at 11°C it takes larvae of P. jordani 95 days to complete the planktonic phase and only about 28 days for P. kessleri (extrapolations from data presented in Kurata, 1958). These extreme differences, one of the few comparisons that can be made from the literature, show very different reproductive strategies by these two congeners. These different strategies, expressed in the degree of development and length of the larval period may be related to the seasonality of reproduction and its relationship to hydrographic regimes and to food availability for adults and larvae.

Appendix Table I. Summary of <u>Pandalus jordani</u> larval characters:
telson spination; rostral spination and pleopod
length, used for larval staging.

Stage	Telson spines (one side)		Rostral spines		Pleopod length 5th
	terminal	lateral	dorsal	ventral	(mm)
I	7	0	0	0	0
II	7	1	0	0	0
III	7	1	1	0	0
IV	6	2	2	0	0.3
V	5	3	3	0	0.5
VI	5	3	8	0	0.8
VII	5	3	9	0	1.3
VIII	5	3	10	0	1.8
IX	5	4	10	0	2.2
X	5	4	11	0	2.1^a
XI	5	6	13	$0 (6)^b$	4.8^c
XII	4	8	14	0 (6)	5.0^d
XIII	4	9	15	0 (6)	5.5
XIV	4	9	15	6	6.5
XV	3	9	15	7	7.0
XVI	2	9+	16	8	7.0
Juv.[e]	2	9+	16	8	7.0

[a] First minimal pleopod setation

[b] Number in parentheses indicates number of small indentations that
are precursors to spines

[c] Setation still sparse, base of pleopod more robust, not functional

[d] More and longer setae, pleopod functional

[e] Setation similar to larval Stage XVI, but exopodites of pereiopods
are completely gone as is the supra-orbital spine

Appendix Table II.   Summary of the published larval descriptions for
                     the family Pandalidae.

Species	Larval stages described	Investigator
Dichelopandalus bonneri	I - VI	Pike & Williamson (1964)
Pandalina brevirostris	I - VII	Pike & Williamson (1964)
Pandalopsis dispar	I - III, V	Berkeley (1930)
Pandalus bonneri	I, III - V	Lebour (1939)
P. borealis	I - VI	Berkeley (1930)
P. danae	I - VI	Berkeley (1930)
P. goniurus	I - VII	Makarov (1967)
P. hypsinotus	I	Berkeley (1930)
P. jordani	I - XI I - VIII[a]	Modin & Cox (1967) Lee (1969)
P. montagui	I - VI	Pike & Williamson (1964)
P. platyceros	I, II, IV, VI I - VI	Berkeley (1930) Price & Chew (1972)
P. stenolepis	I - VI	Needler (1938)
P. propinquus	I - VII	Pike & Williamson (1964)
Parapandalus richardii	I - VIII	Lebour (1939)

[a]No larvae surviving in the laboratory rearing experiment after the
eighth stage.
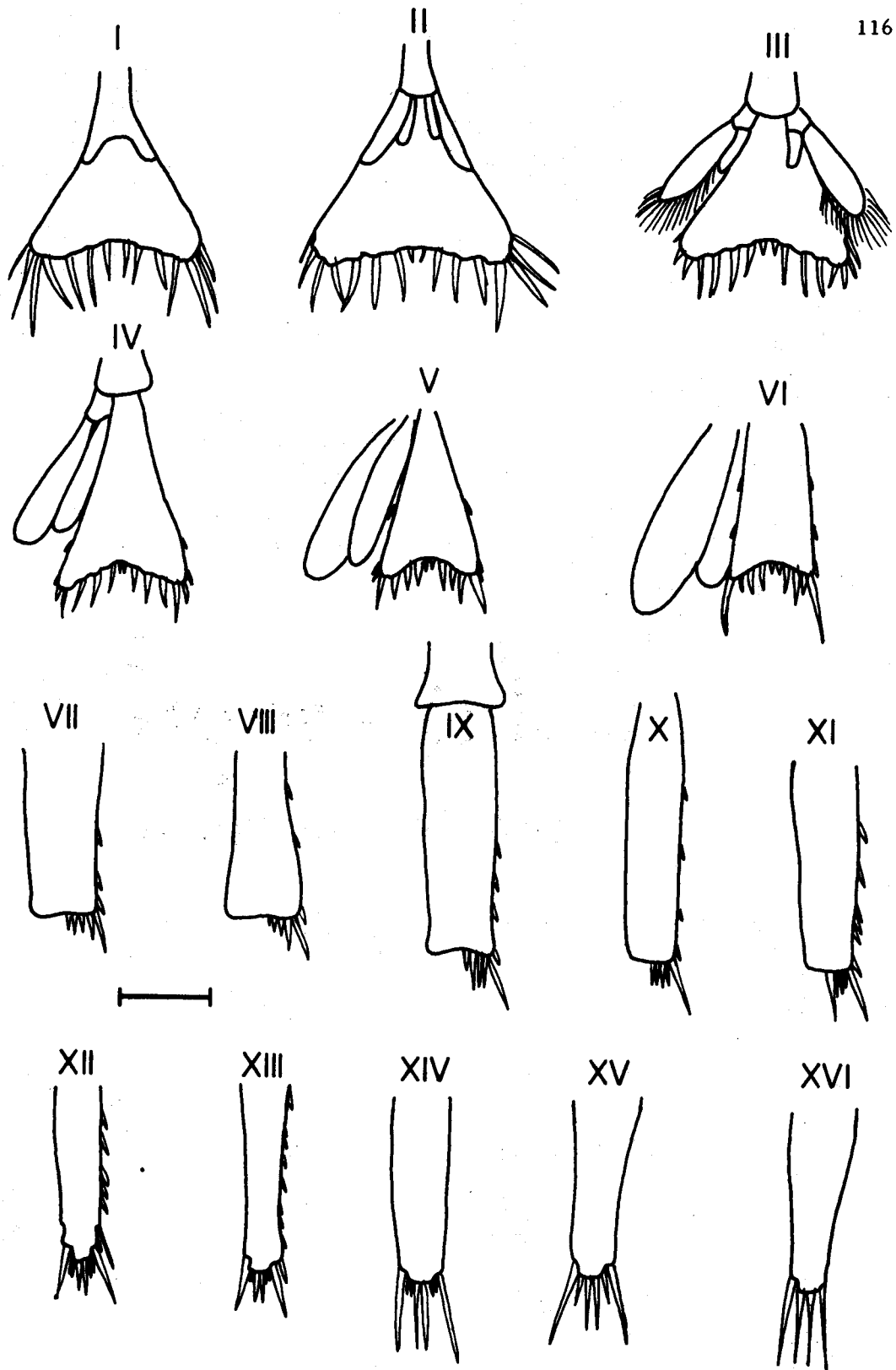
Appendix Figure 1. Spination of telson and degree of development of uropods of the 16 larval stages of Pandalus jordani. Scale = 1 mm.

STAGE VI

| I MM |

STAGE XI

STAGE XVI
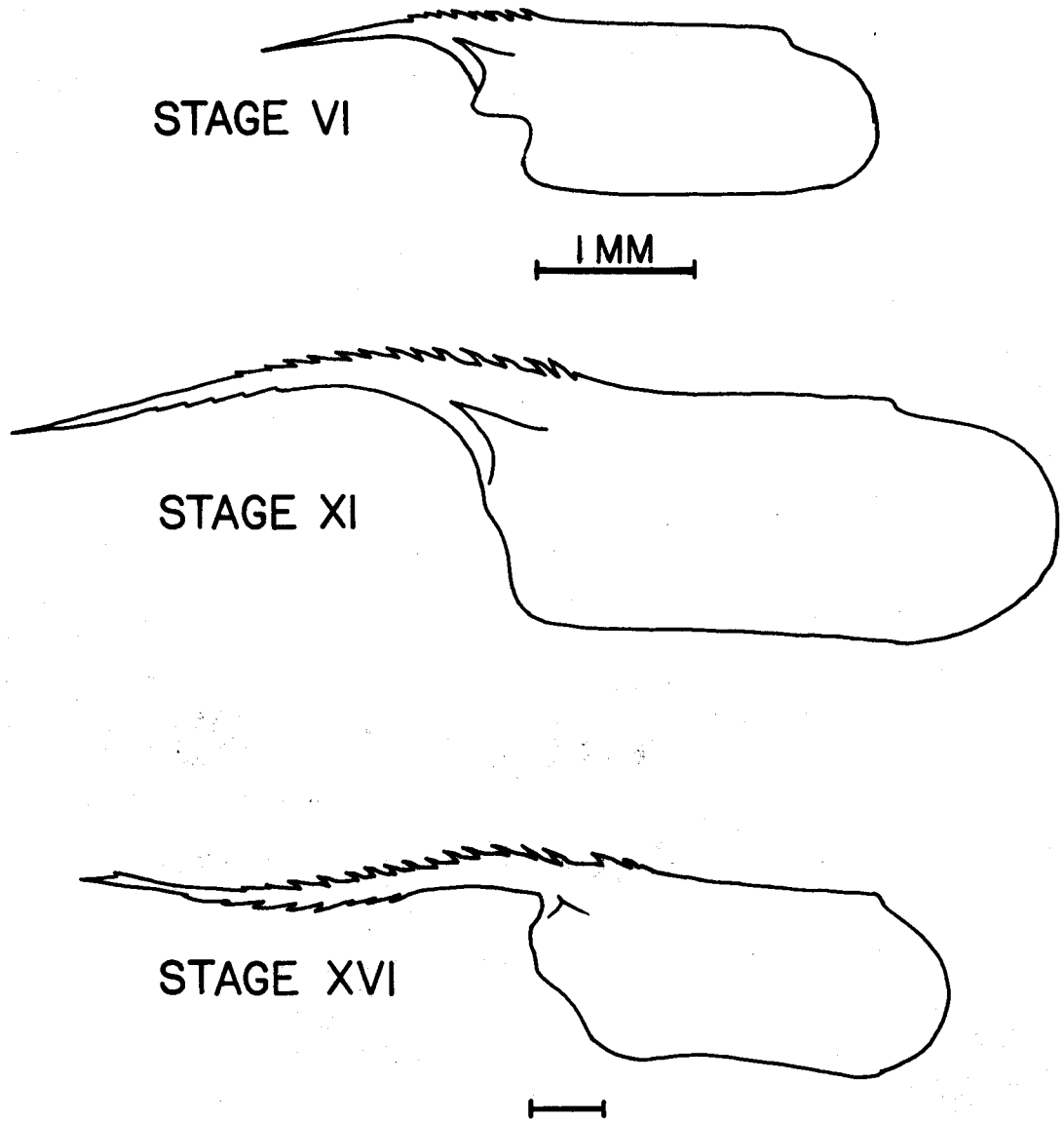
Appendi Figure 2. Rostral development and spination of Stage VI, XI and XVI larvae of _Pandalus jordani_. Scale = 1 mm.