LARVAL DYNAMICS OF THE DUNGENESS CRAB, *CANCER MAGISTER*, OFF THE CENTRAL OREGON COAST, 1970-71

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ABSTRACT

The larval dynamics of the economically important Dungeness crab, *Cancer magister*, were investigated from plankton samples collected bimonthly during 1970 and 1971 along a trackline near Newport, Oreg. Larvae appeared at maximum densities (8,000/1,000 m^3) within 15 miles of the coast in late January 1970 and remained in the plankton until late May for an approximate larval period of 130 days. The bulk of the larval population was retained in the nearshore area by the strong alongshore and onshore components of the surface currents and to some extent by the behavior of larvae in determining their position in the water column. During the 1971 season, larvae appeared initially at about the same time and densities, but a mass mortality may have occurred in the early zoeal stages coinciding with the unusually severe weather in February and March. A significant difference between the 1970 and 1971 larval populations was suggested by analysis of covariance using sea surface temperature and salinity as environmental variables. However, the effect of the low temperature and salinity values that occurred during the winter of 1971 were not clearly indicated by multiple regression analyses of laboratory experimental data to be the prime factors directly affecting larval survival. Neither did a gut-fullness study of planktonic larvae substantially explain the 1971 larval mortality. Therein various hypotheses are explored in view of the present knowledge of processes affecting larval survival and recommendations are suggested for further research.

It is well known that many species of economically important marine resources fluctuate greatly in number and location. These fluctuations may be explained in part by changes occurring in the larval populations. That the larval stage is the most critical period for the majority of marine animals was originally emphasized by Hjort (1914, 1926) for fish larvae and by Thorson (1946) for marine invertebrate larvae. Survival through this period is usually considered the major factor in determining the strength of the year class. The causes or extent of larval mortality, however, are still relatively unknown.

Bimonthly plankton samples were collected from 1969 through 1971 along a transect off the central Oregon continental shelf to document the species of crab larvae present, their seasonality and abundance, and their onshore-offshore distribution in relation to seasonal changes in oceanographic conditions (Lough 1975b). A major effort was made to assess the larval population of the Dungeness crab, *Cancer magister* Dana, as it supports one of the most important fisheries in the Pacific Northwest.

Cancer magister occurs along the Pacific coast from Unalaska to lower California and ranges from mean low water to 50 fathoms (91 m) (Schmitt 1921). Although it prefers sandy or sandy-mud bottoms of the nearshore area, specimens have been found on all bottom types within estuaries and on the continental slope. Adult females generally reach maturity by their second or third year and may produce three or four broods during a life-span (MacKay 1942; Cleaver 1949; Butler 1960). Egg-carrying females are found in Oregon waters from October to March with essentially one brood produced per year (Waldron 1958). Field observations (Waldron 1958) and laboratory rearings by Poole (1966) and Reed (1969) indicate that larvae hatch off northern California and Oregon from January through March and are present in the nearshore waters through July for a total estimated larval life of 128 to 158 days. *Cancer magister* passes through five zoeal stages and one megalops during its larval development before settling out of the water and metamorphosing to the benthic juvenile.

HYDROGRAPHIC FEATURES OF STUDY AREA

The surface waters along the U.S. west coast are dominated by the California Current; a slow,

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broad, and shallow current flowing equatorward (Wooster and Reid 1963). The nearshore currents vary seasonally and are dependent upon wind direction and strength. During the fall and winter months when the winds are predominantly from the southwest, a subsurface countercurrent flowing northward along the coast develops into the Davidson Current. Drift bottle studies by Wyatt et al. (1972), Burt and Wyatt (1964), and Schwartzlose (1964) indicate that the Davidson Current first develops along the Oregon-Washington coast in September reaching maximum speeds between 0.5 and 2 knots within 20 miles of the coast during the month of November.

The major change in the surface currents from northward to southward occurs in March and April (Wyatt et al. 1972). The phenomenon of coastal upwelling occurs when the northwesterly winds intensify and sometimes persist from May to September. As the surface waters are transported offshore and to the southwest, cold, high salinity waters from below a permanent pycnocline (60-100 m) are brought to the surface (Smith et al. 1966). This zone of active upwelling occurs within 20 miles of the coast but its effects can be observed to the edge of the slope.

The area within 5 miles of the coast has not been studied in much detail but is believed to be dominated by mixing processes (Mooers 1970). The surface currents are generally well correlated with the wind direction, but tidal currents predominate when the wind is reduced. A very strong alongshore current with an onshore component is indicated within 3-5 miles of the coast (Keene 1971; Wyatt et al. 1972; Holton and Elliot 1973).

The dominant processes modifying surface water properties off the Oregon coast during the winter are rainfall and river runoff; while during the summer, the major processes are upwelling in conjunction with heating and mixing with the Columbia River plume water (Pattullo and Denner 1965). Surface temperatures and salinities taken on early life history cruises from June 1969 through August 1971 at stations NH01-NH10 are presented in Figures 1 and 2. Temperatures range annually from about 7° to 17°C and are highest from May through October, peaking in September. More variability is evident during the summer due to surface heating interrupted by local upwelling of near 7°C bottom water. Surface salinity values are generally low during the winter and high in the summer reflecting seasonal precipitation and upwelling, respectively. The annual range of salinity is from about 25 to 35‰. Low salinity values at stations NH03 and NH05 from November through April are probably associated with the Yaquina Bay plume which flows north along the coast during the winter (Kulm and Byrne 1966).

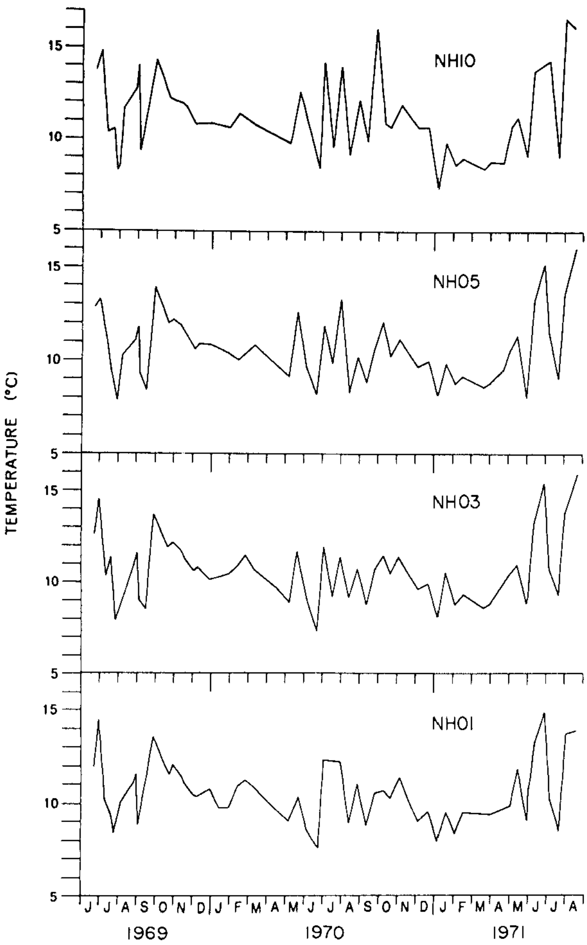

FIGURE 1.—Surface temperature (°C) at stations NH01, NH03, NH05, and NH10 from June 1969 through August 1971.

METHODS

Sampling Program and Gear

This study was conducted primarily on a trackline off Newport, Oreg. (lat. 44°39.1'N) across the continental shelf and slope. The 12 sampling stations are designated on the Newport Hydrographic line (NH) in Table 1, which correspond in distance to nautical miles from the

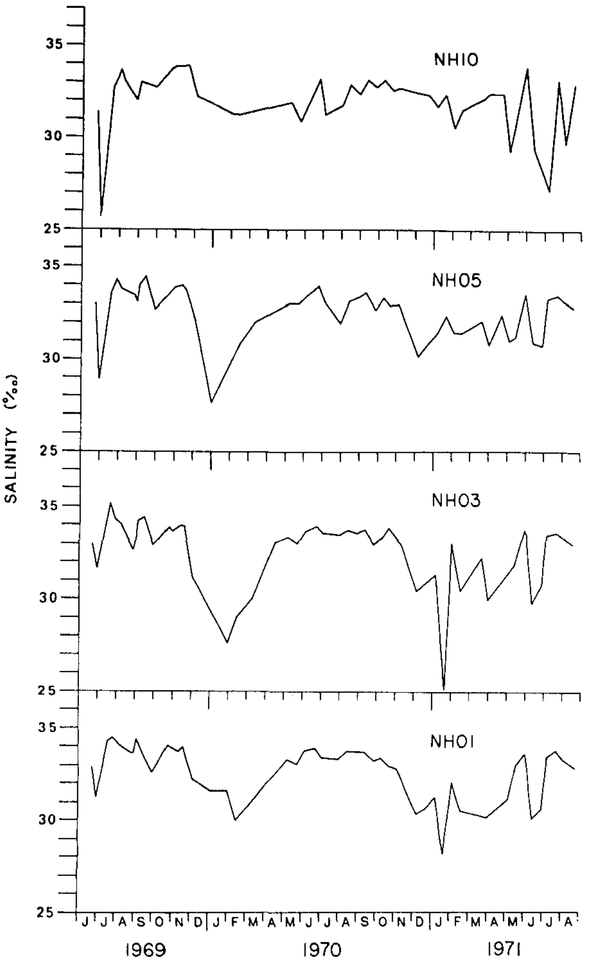

FIGURE 2.—Surface salinity (‰) at stations NH01, NH03, NH05, and NH10 from June 1969 through August 1971.

TABLE 1. — Location of plankton sampling stations and bottom depths along the Newport Hydrographic line (NH) off Newport, Oreg.

Station (Lat. 44°39.1'N)	Long.	Depth (m)
NH01	124°05.4'W	20
NH03	124°08.6'W	46
NH05	124°10.7'W	59
NH10	124°17.7'W	85
NH15	124°24.7'W	95
NH20	124°31.7'W	142
NH25	124°38.7'W	330
NH30	124°45.7'W	220
NH35	124°52.7'W	340
NH40	124°59.7'W	1,060
NH50	125°13.7'W	1,300
NH60	125°27.7'W	2,850

coast. Plankton samples initially were collected at the four inshore stations (NH01-NH10) constituting the main series of samples from June 1969 through August 1971. The sampling program was extended offshore to NH60 by 5- or 10-mile intervals beginning with the 3 February 1971 cruise.

A high-speed bongo net sampler (Posgay et al. 1968) with a 0.2-m mouth diameter was used exclusively from 22 June 1969 through 20 October 1970. The two cylinder-cone nets, 1.8 m in length, were constructed of 0.233- and 0.571-mm nylon mesh and had an effective straining surface (pore size area) to mouth area ratio of ca. 10 to 1. A 30-pound lead ball or a 15-pound V-fin depressor was attached to the sampler line.

Starting with the 4 November 1970 cruise, a 0.7-m diameter bongo net sampler was used in conjunction with the 0.2-m sampler to strain a greater volume of water and to reduce avoidance by the larger larvae. The 0.7-m bongo nets had a net length of 5.1 m, were constructed of 0.571-mm nylon mesh, and had an effective straining area ratio of ca. 8 to 1. Both samplers were equipped with TSK[2] flowmeters mounted on brackets 18 cm from the rim of the inside frame. A multiplane kite-otter wire depressor (ca. 80 pounds), modified after Colton (1959), was used with the dual bongo net array to produce a wire angle ratio of 2 to 1. The sampling objective was to make a high speed, oblique, plankton tow, sampling the water column in equal stepped intervals from 150 m depth, or in shallower areas from bottom to surface. Wire was let out and retrieved at 50-75 m/min while the vessel was underway at 2-3 knots. Most of the samples represent daylight (0600-1800) tows ranging in duration from 10 to 25 min. The longer tows were generally made on stations beyond 5 miles. Plankton samples were immediately preserved in 5-10% Formalin and later buffered with sodium borate.

A bathythermograph (BT) cast was made at each station near bottom or to 150 m depth. Surface bucket temperatures also were taken at each station to calibrate the BT readings. Salinity samples were collected on the surface and near bottom or to 150 m depth by a Nansen bottle cast and analyzed by an inductive salinometer. Salinity, temperature, and depth (STD) data from a real-time printout computer were available for several cruises.

The Nekton Cruise of 11-12 April 1970 at station NH45 was included in this study as it is one of the few cruises that sampled the offshore

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[2] Tsurumi-Seiki Kosakusho. Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

plankton during 1970. The objective of this cruise was to identify those organisms associated with sound scattering layers in the upper 150 m of seawater and, if possible, to follow their day-night migration patterns. Six successive integrated tows of approximately 45 min each were taken to a depth of 150 m (total time: 1852-2355). A standard 6-foot (1.8-m) Isaacs-Kidd mid-water trawl (IKMT) with a 2.9 m^2 mouth opening [1½-inch (3.8-cm) mesh with a ¼-inch (0.6-cm) linear nylon liner] was used for this series. The second series of eight samples alternately sampled from surface to 150 m and from 150 m to surface with an eight-bar electronic multiple plankton sampler (EMPS) attached to the IKMT (Pearcy and Mesecar 1970) (total time: 0134-0514). The cylinder-cone nets were approximately 2.9 m in length with a mouth diameter of 0.4 m and made of 0.571-mm nylon mesh. Another series also used the EMPS to sample eight discrete layers from the surface to 330 m depth covering three bands of scatters (total time: 0640-1113). Scattering layers were located using 12 and 38.5 kHz echo sounders. One automated STD cast was made.

Processing of Plankton Samples

Samples from both mesh sizes of the 0.2-m bongo nets were processed for the nearshore area, stations NH01-NH10. Only one side of the 0.7-m bongo net sampler was processed to examine the offshore area, NH15-NH60. Generally, the entire sample was sorted, however, many required subsampling using an 8-cm diameter plankton splitter (Longhurst and Seiburt 1967). Approximately 22% of the 0.2-m bongo net samples and 39% of the 0.7-m bongo net samples required subsampling. Those samples which required splitting were usually from stations NH01 and NH03.

All crab larvae were removed from the samples and positive identification of *C. magister* larvae was made from the descriptions given by Poole (1966) and from preserved specimens reared by Thomas F. Gaumer, Fish Commission of Oregon, Marine Laboratory, Newport, Oreg. Catches of larvae were first converted by computer to number per 1,000 m^3 of seawater and ordered in a format. Graphs of stage density against time were plotted for the 0.2-m bongo net samples, 0.571-mm mesh, with the aid of a CalComp plotter using the Oregon State University CDC3300 computer.

SAMPLING VARIABILITY

The detailed analyses of the various methods by which sampling variability affected the estimates of larval crab abundance are given by Lough (1975b). Variability estimates and sampler comparisons were made in this study on other species of crab larvae than *C. magister* for the most part, as limited ship time and weather played an important role in determining the objectives and priorities of the sampling program. Analysis of variance techniques were used to estimate the variance of a single observation in the manner of Winsor and Clarke (1940). Confidence limits for a single observation of either sampler usually exceeded the 50-200% range reported by Winsor and Clarke due to the relatively low densities of crab larvae sampled during replicate tows. A range of an order of magnitude was considered necessary to distinguish a real difference between any two observations. There was no significant difference between the total number and kinds of crab larvae caught by the two sides of the different sized samplers. The 0.7-m bongo net sampler gave smaller confidence limits for larval crab catches and was much superior in establishing significant differences between stations than the 0.2-m bongo net sampler.

Most of the nearshore samples (NH01-NH10) were taken during daylight hours; only 8.6% of the 0.2-m bongo net samples were taken at night between 1800 and 0600 h. More (26.7%) of the 0.7-m bongo net samples sorted beyond NH10 were collected at night. Most larvae were caught more abundantly in night tows than day tows for both sized samplers. Day-night differences in larval abundance were greater for the 0.2-m sampler than the 0.7-m sampler. There was a nearly equal distribution in the number of kinds of crab larvae caught between day and night samples using the 0.7-m sampler; however, using the 0.2-m sampler, significantly more kinds of larvae were caught at night.

The results of the Nekton Cruise showed that the larvae of *C. magister* occur in relatively low densities offshore as far as station NH45 during early April 1970. They are most likely to occur in the surface waters above 120 m, the depth of the thermo- and halocline and are probably associated with the first sound scattering layer at 25 to 90 m depth. A Mann-Whitney two sample rank test (Tate and Clelland 1957) retained the null hypothesis that there was no significant difference between the number of *C. magister* megalopae, or the total number of larvae caught in the first two series of tows. In the second series of samples more larvae were caught towing from surface to 150 m than from 150 m to surface and the total number of larvae decreased with time (0134-0514) for both alternate types of tows. The coefficients of variation (standard deviation/mean) for the total number of larvae were about the same for the first two series of tows (1.25 and 1.31, respectively) indicating a somewhat patchy distribution of the larvae in the upper 150 m of water at night. Very few larvae were caught during the third series of tows.

RESULTS

Distribution and Abundance of *Cancer magister* Larvae

Two larval seasons were encompassed by the sampling program (Figure 3). Zoea 1 larvae made their first substantial appearance during the first season on 29 January 1970 at stations NH03, NH05, and NH10 with maximum densities ranging from 1,000 to 3,000/1,000 m^3. The subsequent zoeal stages were found most abundantly at stations NH05 and NH10. Few zoea 4 and no zoea 5 stages were found at any of the four inshore stations. In general, the number of larvae captured decreased from zoea 1 through 5. However, large numbers of megalopae were found at stations NH01, NH03, and NH05, suggesting a general inshore transport of larvae during this season. Maximum densities of the magalopae ranged from 1,000 to 8,000/1,000 m^3, densities comparable to those of the zoea 1 stage found earlier in the year. Few megalopae appeared in the water column after 22 May 1970 and none after 16 July 1970. This indicates that the length of the larval period in the plankton is approximately 130 days (89-143 days). The summer upwelling conditions did not appear to have any effect on the larvae since the bulk of the megalopae had settled before the onset of intense upwelling.

The major appearance of zoea 1 larvae during the second season occurred at about the same time (18 January 1971) and stations (NH03, NH05, NH10), and at about the same densities (1,000-2,000/1,000 m^3). However, the density of the larvae appeared to decrease more rapidly at zoeal stages 2 and 3, and virtually no larvae of any stage were found after zoea 3. The 30 March 1971 cruise was the last sampling period which caught any significant number of larvae. Very few megalopae were found at any station throughout the summer in day or night samples.

Cancer magister was the most abundant crab larvae caught at station NH45, 11-12 April 1970 (Nekton Cruise). Its megalopae had the highest densities of any larval stage with 19/1,000 m^3, followed by zoea 5 at 12/1,000 m^3. Fewer zoea 4 and 3 were present. Scattered occurrences of all larval stages were present the following year, 1971, to 60 miles offshore in the 0.7-m bongo net samples. Megalopae and zoea 3-5 predominated offshore with densities usually much less than 200/1,000 m^3, suggesting that these larvae had originated nearshore and subsequently drifted offshore. Larvae present at stations NH35 to NH60 are under the influence of the Columbia River plume as indicated by the warmer temperatures and lower salinities measured at these stations during the sampling period.

All observations indicate a dramatic difference in the abundance of megalopae between the 2 yr. Sampling was much more intensive during the 1971 season from the standpoint of day-night replicate tows using both size samplers in the inshore and offshore areas when the megalopae were sparse.

Climate and Hydrography 1970-1971

The winter of 1971 along the Oregon coast was generally more severe than that of 1970. Climatological records (U.S. Environmental Data Service 1970,1971) for Newport and other ports of Oregon show monthly mean air temperatures for February and March 1971 to be substantially lower than the same months during 1970. Also, total precipitation generally was greater during the winter of 1971 but showed considerable variability along the coast. Ocean surface temperatures correspondingly were much colder during this period in 1971 than 1970. Gonor et al. (1970) and Gonor and Elvin (1971)[3] reported Agate Beach, Oreg. mean surf temperatures and Wyatt and Gilbert (1971, 1972) reported monthly mean surface temperatures for various ports along the Oregon coast to be as much as several degrees lower during the later winter of 1971 than 1970.

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[3] Gonor, J. J., and D. W. Elvin. 1971. Inshore sea surface temperature and salinity conditions at Agate Beach, and Yaquina Head, Oregon in 1971. Unpubl. data. School Oceanogr. Oreg. State Univ.

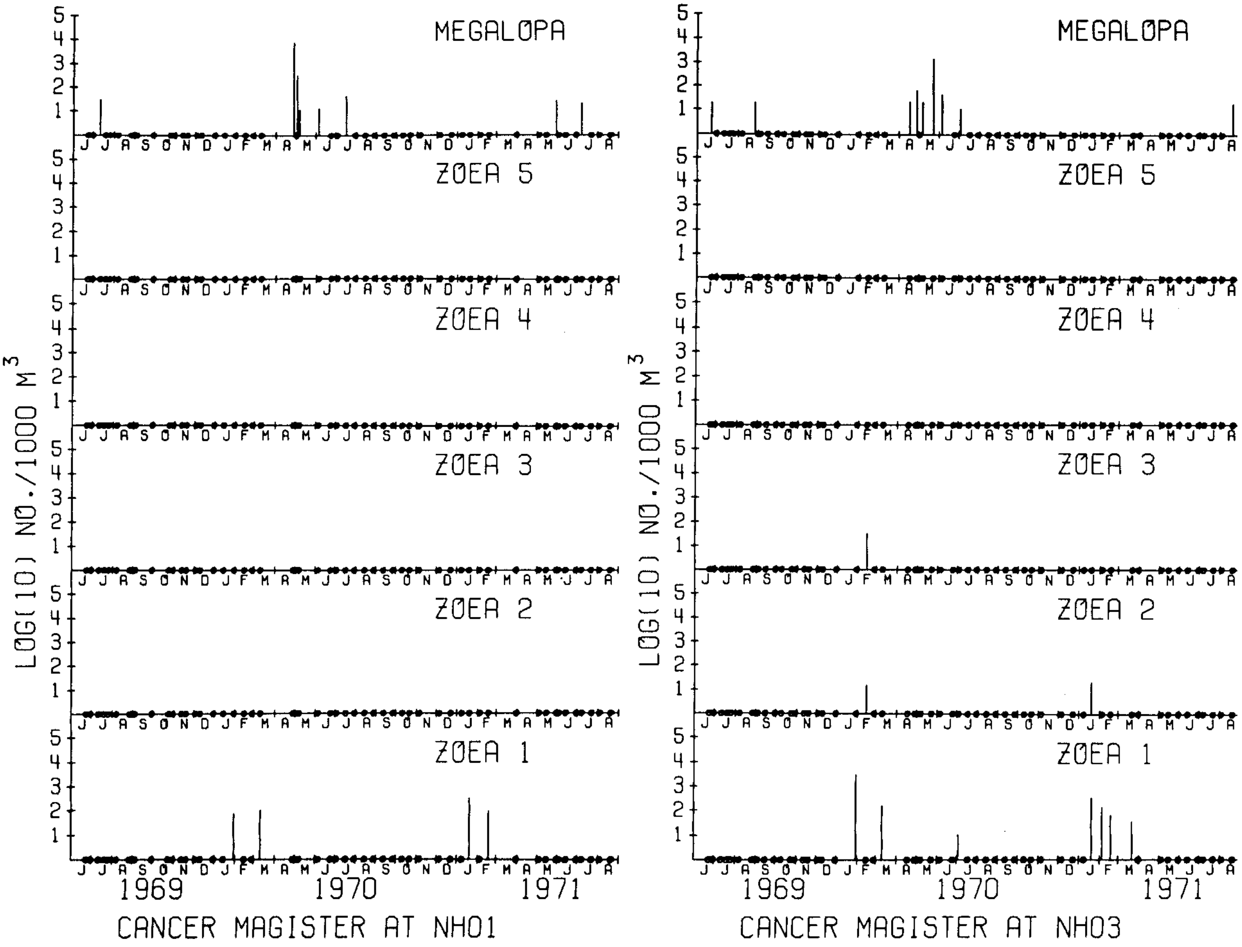
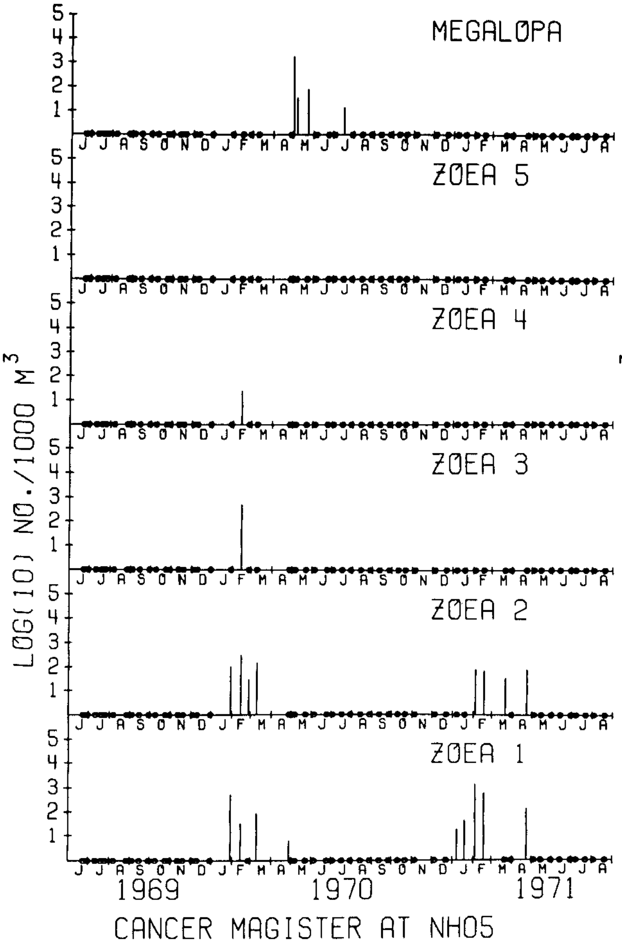
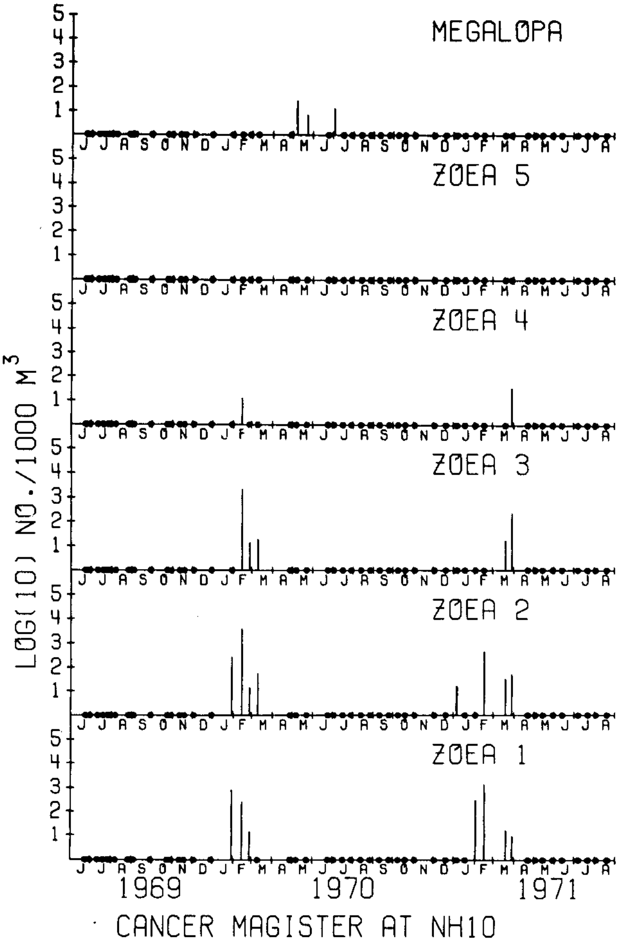


FIGURE 3.—Density of *Cancer magister* larvae at stations NH01, NH03, NH05, and NH10 from June 1969 through August 1971, collected with the 0.2-m bongo net sampler, 0.571-mm mesh.

Salinity values showed considerable variability among stations and months such that a generalized trend could not be observed between the two seasons. The anomalous winter of 1971 was further substantiated by Bakun's (1973) indices of coastal upwelling intensity for selected locations along the west coast of North America based on offshore Ekman surface wind transport from monthly mean surface atmospheric pressure data. Positive values indicate periods of coastal upwelling whereas negative values indicate downwelling. January and February of 1970 at lat. 45°N, long. 125°W show significantly greater negative indices (−98 and −71, respectively) than the same period in 1971 (−32 and −16, respectively). High negative values are indicative of strong downwelling along the coast which Bakun stated would accelerate the southward flow. In either case, more offshore surface water would be transported onshore. During the March transition period, the 1970 index was normal (+1); however during 1971 an anomalously high negative index (−49) occurred. This indicates that downwelling and subsequent transport of surface waters was more intense during March of 1971 than 1970. Downwelling also was more intense during March 1971 than in the previous 2 mo of that year. Drift bottle data compiled by Wyatt et al. (1971) reported a 14.7% return for bottles released off Newport from 25 February to 3 March 1970. By contrast, a 28.6% return occurred during 6-9 March 1971. The average percent return of drift bottles on all stations west of Newport, 1961-71, during both February and





March was 18% (Wyatt et al. 1972). High percentages of returns near 30% were observed only during February and March 1961, 1962, 1963, and 1967.

April 1970 showed a high positive index value (+25) indicative of upwelling processes, whereas downwelling was still in process during the same month in 1971 (−2). However, by May 1971 the upwelling intensity was twice the magnitude of that in 1970 (+66 and +33, respectively). In all regards the year 1971 can be considered the most anomalous whereas 1970 can be considered the least anomalous of the sampling period and the most typical over a 20-yr span. Kukla and Kukla (1974) reported large-scale global anomalies in weather patterns developing early in 1971. Snow cover in the northern hemisphere increased dramatically for the months of February, March, April, and September 1971.

Larval Population Analyses Between 1970 and 1971

Despite the rather restricted data set, a rigorous statistical analysis is attempted at this point to explore the relative importance of some environmental variables associated with the *C. magister* larval populations. An attempt is made to examine potential causative factors underlying the difference in larval abundance between 1970 and 1971 seasons. A basic assumption in the analysis is that the larval data collected in a single sampling transect are representative of a much larger homogeneous area. Patches of larvae may be quite localized so that differences in larval abundance from year to year may be due to dispersal and not mortality caused by an environmental variable per se. However, the distribution of adult breeding populations are confined to shallow waters less than 50 m depth and appear fairly uniform along the Oregon coast based on commercial landings of legal-sized adults (Waldron 1958). This implies that the distribution of larvae along the entire Oregon nearshore area would be relatively homogeneous from year to year. Wind induced turbulence and mixing would tend to increase the homogeneity of the larval population despite any initial patchiness.

If we assume that the total number of *C. magister* larvae combined over the four inshore stations (NH01, NH03, NH05, NH10) is representative of the total population on a local basis, then the question may be asked whether there is a significant difference in the population means between the 2 yr, 1970 and 1971, and can a difference be explained using the concomitant observations of time, temperature, and salinity?

An analysis of multiple covariance was used to test this hypothesis on two sets of data for *C. magister* larvae. The first set of data compares the sampling period from 29 January 1970 to 29 July 1970 with that of 18 January 1971 to 21 July 1971. This period includes, for these 2 yr, the first major larval release through the time at which no megalopae were present in the water column. Larval density estimates from both sizes of mesh of the 0.2-m bongo net sampler were used in the analyses. Surface temperatures and salinities comprised the only complete data set for the two larval seasons and the average values of the four inshore stations were used for each sampling period. Nevertheless, sea surface temperatures and salinities are representative of nearshore subsurface conditions during the winter period from November through March-April as extensive wind mixing occurs in the shallow areas producing isothermal conditions (Renfro et al. 1971). During the spring and summer, a weak thermocline of less than 2°C exists in the nearshore area (<20 m). Larval and environmental data used in the analyses are given in Appendix Table 1.

The mathematical model used for the initial analysis was of the form:

$$Y = b + b_0(y) + b_1(t) + b_2(T) + b_3(S) + b_4(T^2) + b_5(S^2) + b_6(T \times S)$$

where, $Y = \log_{10}(X + 1)$ number of larvae per 4,000 m^3 of water, b = a mean effect, y = a year effect, t = a time effect (days elapsed since 1 January), T = linear effect of sea surface temperature (°C), S = linear effect of sea surface salinity (‰), T^2 = quadratic effect of temperature, S^2 = quadratic effect of salinity, and $T \times S$ = interaction effect between temperature and salinity.

The b's in the model were estimated from a general linear hypothesis testing computer program contained in the Oregon State University Statistical Program Library. Various hypotheses can be specified by the user to test the importance of the individual parameters in the model.

A summary of the analysis on the initial run is given in Table 2. A highly significant difference (1% level) was found between y means after being adjusted for all the covariates in the model. However, only t was found to be highly significant in explaining the yearly difference. That is, the appearance of larvae in the plankton was of shorter duration in 1971 than in 1970. Subsequently, a new model was generated using only t as a covariate:

$$Y = b + b_0(y) + b_1(t).$$

The importance of t was again found to be highly significant in explaining the difference between y population means of *C. magister* larvae (Table 3).

TABLE 2. — A comparison of the total number of *Cancer magister* larvae for 1970 and 1971 (January through July) by analysis of multiple covariance (full model).

Source of variation	Degrees of freedom	Sum of squares	Mean square	*F*-level
t	1	12.983	12.983	15.079**
T	1	1.323	1.323	1.537
S	1	0.120	0.120	0.140
T^2	1	0.513	0.513	0.594
S^2	1	0.296	0.296	0.344
$T \times S$	1	1.303	1.303	1.513
y (adjusted)	1	9.074	9.074	10.538**
Residual	44	37.887	0.861	

**$F_{.99(1,44)} = 7.12$

Fitted model: $Y = -11.313 + 0.470(y) - 0.018(t) - 5.076(T) + 2.576(S) + 0.043(T^2) - 0.060(S^2) + 0.127(T \times S)$.

		Mean of covariates					
Year	Mean Y	t	T	S	T^2	S^2	$T \times S$
1970	2.19518	124.21	10.36	32.23	109.05	1,040.49	333.13
1971	1.57263	109.38	10.01	31.71	102.74	1,007.00	316.70

TABLE 3. — A comparison of the total number of *Cancer magister* larvae for 1970 and 1971 (January through July) by analysis of multiple covariance (reduced model).

Source of variation	Degrees of freedom	Sum of squares	Mean square	*F*-level
t	1	45.149	45.149	52.336**
y (adjusted) .	1	9.448	9.448	11.218**
Residual	49	42.271	0.863	

**$F_{.99(1,49)} = 7.17$

Fitted model: $Y = 3.856 + 4.366(y) - 0.017(t)$.

The second data set compares the sampling period 29 January-2 May 1970 with 18 January-14 May 1971. The period selected compares the larval period prior to summer upwelling, eliminating the erratic surface temperature and salinity fluctuations. Most of the *C. magister* larvae are megalopae by early May.

The same full model was used in the initial run for the second data set and is presented in Table 4. There was a significant difference (5% level) between *y* means after being adjusted for all the covariates in the model. The covariates, *t*, *T*, and $T \times S$ were all significant.

TABLE 4. — A comparison of the total number of *Cancer magister* larvae for 1970 and 1971 (January to May) by analysis of multiple covariance (full model).

Source of variation	Degrees of freedom	Sum of squares	Mean square	*F*-level
t	1	6.807	6.807	7.073*
T	1	5.277	5.277	5.483*
S	1	0.156	0.156	0.162
T^2	1	0.018	0.018	0.019
S^2	1	0.012	0.012	0.012
$T \times S$	1	5.183	5.183	5.385*
y (adjusted)	1	6.260	6.260	6.504*
Residual	26	25.023	0.962	

$^*F_{.95(1,26)} = 4.22$

Fitted model: $Y = 180.944 + 0.712(y) - 0.024(t) - 20.294(T) - 4.907(S) - 0.037(T^2) - 0.022(S^2) + 0.656(T \times S)$.

		Mean of covariates					
Year	Mean Y	t	T	S	T^2	S^2	$T \times S$
1970	2.80494	90.56	10.35	31.76	107.91	1,010.36	328.08
1971	2.09844	80.13	9.59	31.28	92.82	979.08	299.81

The initial model was reduced to the following form:

$$Y = b + b_0(y) + b_1(t) + b^2(T) + b_3(S) + b_4(T \times S)$$

which greatly increased the significance of the parameters in the final model (Table 5). A highly significant difference (1% level) was found between *y* means after being adjusted for all the covariates. In explaining the difference between *y* means of *C. magister* larvae, the covariate *t* was most significant (1% level) followed by *T* and *S*, and $T \times S$ at the 5% level.

The foregoing analyses support the contention that there was a significant difference between the *C. magister* larval populations of 1970 and 1971. Fewer larvae appeared in 1971 and they appeared in the plankton for a shorter period of time suggesting widespread larval mortality. This apparent larval mortality was associated by these analyses with the colder surface temperatures and lower salinities that occurred during the winter of 1971. The direct effects of temperature and salinity on larval survival will be explored in the next section.

TABLE 5.—A comparison of the total number of *Cancer magister* larvae for 1970 and 1971 (January to May) by analysis of multiple covariance (reduced model).

Source of variation	Degrees of freedom	Sum of squares	Mean square	*F*-level
t	1	7.629	7.629	8.530**
T	1	5.859	5.859	6.551*
S	1	5.230	5.230	5.845*
$T \times S$	1	5.774	5.774	6.456*
y (adjusted)	1	8.650	8.650	9.672**
Residual	28	25.043	0.894	

$^*F_{.95(1,28)} = 4.20$; $^{**}F_{.99(1,28)} = 7.64$

Fitted model: $Y = 201.891 + 0.705(y) - 0.023(t) - 20.547(T) - 6.148(S) + 0.641(T \times S)$.

Temperature-Salinity Tolerance of Laboratory-Reared Larvae

A laboratory study by Reed (1969) determined the effects of temperature and salinity on the larval survival of *C. magister*. However, it was necessary to assess more thoroughly the effects of these factors on survival during development and to extrapolate from Reed's data in order to derive better estimates of larval survival at the low temperatures that occurred during the 1971 season. The response surface technique used in the analysis of his data is not only valuable in its predictive role, but also visually represents any change in response at various stages of development. Details of this response surface technique and its application to the study of marine ecology are discussed by Alderdice (1972).

A multiple regression analysis was applied to Reed's (1969) survival data of *C. magister* after 20, 30, 40, and 50 days of culture at experimental conditions. The mathematical model used in the analysis was of the form:

$$Y = b_0 + b_1(S) + b_2(T) + b_3(S^2) + b_4(T^2) + b_5(S \times T)$$

where, Y = percentage survival, b_0 = a constant, S = linear effect of salinity, T = linear effect of temperature, S^2 = quadratic effect of salinity, T^2 = quadratic effect of temperature, and $S \times T$ = interaction effect between salinity and temperature.

The *b*'s in the model were estimated by a stepwise multiple regression computer program. Further details of the regression analysis are given by Lough (1975a). The calculated regression coefficients from a particular equation are fitted by computer to a full quadratic equation in temperature and salinity in order to print a contour diagram of the response surface. Temperature and salinity scales on all plots were set to range beyond the experimental conditions in order to facilitate response comparison and to allow the overall form of the surface to be visualized. Contours extrapolated beyond the experimental data lie outside the dotted lines.

A summary of the multiple regression analyses on survival after the various periods of rearing and the response surfaces are given in Table 6 and Figure 4. The analyses indicated that after 20 days of rearing under the experimental conditions S and S^2 were the two most important variables in the model. T and $S \times T$ were of lesser importance but still contributed significantly to the model. Analyses of the later rearing periods of *C. magister* emphasized the effect of temperature and showed the decreasing importance of both S and S^2 and $S \times T$. This trend is more evident when one compares the response surface plots from 20 through 50 days of rearing. After 20 days of rearing, the response surface contours are nearly circular, with a slight tilt to the main axis, indicating a small interaction effect. The axis of the contours tilts progressively towards the temperature axis until, at 50 days of rearing, the contour axis is almost perpendicular to the temperature axis. Also, the survival contours progressively constrict about the temperature axis with time showing the narrowing of the temperature range tolerated by the larvae. Maximum survival (80% contour) at 20 days is predicted to occur between 6.5° and 17.5°C and 21.5 and 35.0‰, while at 50 days, maximum survival is predicted to occur between 9.0° and 15.0°C and above 28.5‰. The area of maximum survival (80% contour) shifts somewhat during the 20- to 50-day period from an initial low salinity-wide temperature range to a high salinity-low temperature tolerance. However, when the 20- and 50-day survival polynomials were tested by an analysis of covariance (Ostle 1963:205), they were not found significantly different in their response (Table 7). In summary, salinity appears to exert an immediate effect on *C. magister* larval survival, while the effect of temperature becomes increasingly important with time.

Survival at a given temperature, salinity, and time can now be estimated using the fitted equations. All of the fitted equations for the four time

TABLE 6. — Multiple regression analyses of *Cancer magister* larval survival in 20 temperature and salinity combinations.

Regression step number	Variable	R^2	F-value	Degrees of freedom	Significance level	Coefficients	t-value	Significance level
				20 days				
1	S	0.505	18.378	(1,18)	1%	29.4369	4.069	1%
2	S^2	0.591	3.723	(2,17)	5%	−0.4720	3.040	1%
3	T^2	0.659	3.030	(3,16)	N.S.	−0.7068	4.635	1%
4	T	0.834	15.819	(4,15)	1%	23.4636	4.559	1%
5	$S \times T$	0.865	3.272	(5,14)	5%	−0.2277	1.809	N.S.[1]
	Constant					−457.6092		
				30 days				
1	S	0.417	12.878	(1,18)	1%	18.3726	2.026	N.S.
2	T^2	0.529	4.044	(2,17)	5%	−0.6903	3.611	1%
3	T	0.702	9.290	(3,16)	1%	23.0272	3.569	1%
4	$S \times T$	0.744	2.443	(4,15)	N.S.	−0.2503	1.586	N.S.
5	S^2	0.768	1.446	(5,14)	N.S.	−0.2340	1.202	N.S.
	Constant					−335.2887		
				40 days				
1	S	0.416	12.830	(1,18)	1%	14.3243	1.602	N.S.
2	T^2	0.491	2.511	(2,17)	N.S.	−0.8113	4.305	1%
3	T	0.744	15.824	(3,16)	1%	25.5095	4.011	1%
4	$S \times T$	0.768	1.509	(4,15)	N.S.	−0.1892	1.217	N.S.
5	S^2	0.779	0.713	(5,14)	N.S.	−0.1620	0.844	N.S.
	Constant					−313.8493		
				50 days				
1	S	0.373	10.717	(1,18)	1%	13.4195	1.687	N.S.
2	T^2	0.432	1.756	(2,17)	N.S.	−0.8265	4.931	1%
3	T	0.757	21.339	(3,16)	1%	25.7928	4.559	1%
4	$S \times T$	0.778	1.451	(4,15)	N.S.	−0.1662	1.201	N.S.
5	S^2	0.791	0.901	(5,14)	N.S.	−0.1620	0.949	N.S.
	Constant					−305.2337		

[1] N.S. = Not significant.

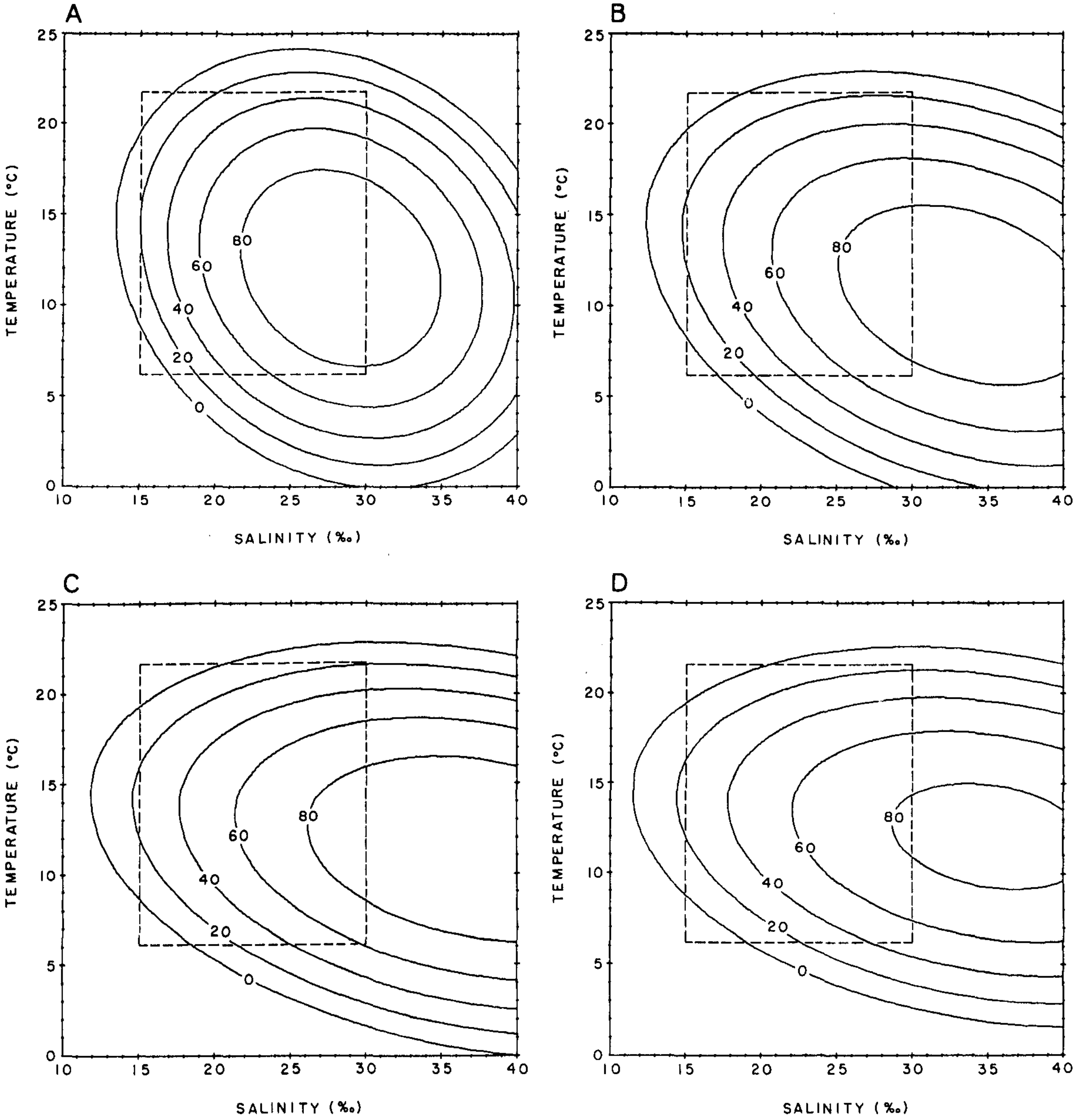


FIGURE 4. — Response surface estimation of percent survival of *Cancer magister* larvae after (A) 20 days, (B) 30 days, (C) 40 days, and (D) 50 days of development at 20 different temperature and salinity combinations.

periods explained a significant 77-87% of the variance in the data. The lowest surface temperature and salinity reported for any sampled station during the 1971 season was 7.4°C and 25.17‰. After 20 days at this combination, 76.8% survival is predicted; after 50 days, 44.6% survival. The monthly mean surface temperature and salinity compiled at the Oregon State University Marine Science Center dock, Newport, is reported by Wyatt and Gilbert (1972) for March 1971 to be 8.81°C and 30.12‰. Survival of 92.3% is predicted at this temperature and salinity combination after 20 days, and 71.0% survival after 50 days. The direct effect of these temperatures and salinities found off the central Oregon coast on the survival of *C. magister* larvae would appear to

TABLE 7. — An analysis of covariance between the 20- and 50-day survival polynomials of *Cancer magister* larvae. Null hypothesis: no significant difference between 20- and 50-day survival polynomials.

Source of variation	df	Sum of squares	Mean square	*F*-value
Polynomial 1: 20-day survival	14	4,217.780		
Polynomial 2: 50-day survival	14	5,096.684		
Total: Polynomial 1 and 2	28	9,314.464	332.659	
Polynomial 3: Combined 20- and 50-day survival	34	13,287.052		
Difference: Polynomial 3 and total	6	3,972.588	662.098	[1]1.99

[1]Not significant, $F_{.95(6,25)} = 2.44$.

be minimal. Forty-five percent survival would still occur, even after an unrealistic period of 50 days at nonconservative temperatures and salinities.

Gut-Fullness Analysis of Planktonic Larvae

The physical appearance of *C. magister* larvae was examined for clues to the difference in the larval populations between the two seasons, 1970 and 1971. Whatever happened to the larvae occurred early in their development during the months of February and March 1971, as a marked decrease in the total larval population was observed by the second zoeal stage. Those larvae examined from the 1971 season appeared more flaccid with a soft exoskeleton, had less eye pigmentation, and were more transparent compared to the larvae caught during the 1970 season. However, these features of appearance could not be readily quantified. Further examination indicated a possible difference on a population basis in the amount of food in their guts among stages, stations, and years. Differences in larval gut-fullness may indicate good versus poor food availability, or possibly a dying larval population weakened by some factor in their environment other than food.

Food and/or feces in the guts could readily be seen through the body wall up to the fourth or fifth zoeal stage and a close estimation of the percentage fullness could be made by noting the proportion of gut segments filled with food. The larval body can be divided into eight equal segments; the thorax constituting twice the length of an abdominal segment. The food or feces was considered to be of the same approximate diameter and could be estimated to within 3% of the total gut length. A sample size of 30 larvae was necessary before any significant difference could be considered.

The 0.2-m bongo net samples were used to compare the 1970 and 1971 larval seasons at stations NH01, NH03, NH05, and NH10. Samples were combined with both meshes of the 0.2-m bongo nets. Only whole larvae were used and usually the entire sample was analyzed. Specimens from the 0.7-m bongo net samples were used to compare inshore-offshore larval gut-fullness between the 12 stations, NH01 through NH60, for the 1971 season.

Zoea 1 larvae from the 1970 season showed maximum mean percentage gut-fullness at stations NH03 and NH10 compared to those from NH01 and NH05 (Table 8). A general decrease in gut-fullness was observed with increasing stage of development. Surprisingly, all zoeal stages of larvae caught during the 1971 season showed an increase in gut-fullness over those of the 1970 season. The notable exception occurred for zoea 1 larvae at station NH03, where the 1971 gut-fullness is significantly lower than that for the 1970 season.

The onshore-offshore comparison showed that the greatest gut-fullness for any larval stage oc-

TABLE 8. — A comparison of *Cancer magister* larval gut-fullness[1] between 1970 and 1971 at four Newport Hydrographic line (NH) stations.[2]

Stage	Year	NH01	NH03	NH05	NH10
Zoea 1	1970	13.19 ± 2.74(4)	31.23** ± 0.06(126)	19.64 ± 0.12(65)	29.53 ± 0.07(106)
	1971	14.26 ± 0.34(19)	9.86 ± 0.10(78)	24.10** ± 0.03(241)	36.13** ± 0.04(187)
Zoea 2	1970		7.56 ± 1.97(5)	15.57 ± 0.10(72)	12.94 ± 0.02(269)
	1971		25.00 ± (1)	23.29** ± 0.24(38)	30.39** ± 0.11(87)
Zoea 3	1970		10.49 ± 10.49(2)	23.76 ± 0.09(81)	14.02 ± 0.02(212)
	1971			18.75 ± (1)	20.20** ± 0.09(51)
Zoea 4	1970			9.40 ± 3.36(4)	15.99 ± 1.19(6)
	1971				19.50 ± 1.61(7)
Zoea 5	1970				
	1971				

[1]Gut-fullness is expressed as a reconverted $\arcsin\sqrt{\text{percentage}}$ transformed mean followed by its standard error and the number of observations in parentheses.

[2]The station samples in this table represent the combined specimens from both mesh sizes of the 0.2-m bongo net sampler.

**1% level significant difference between yearly means based on a two-sample *t*-test.

TABLE 9. — A comparison of *Cancer magister* larval gut-fullness[1] between 12 Newport Hydrographic line (NH) stations for 1971.[2]

Station	Zoea 1	Zoea 2	Zoea 3	Zoea 4	Zoea 5
NH01	8.51* ± 1.33(9)				
NH03	10.51** ± 0.06(82)	0.79 ± 0.79(2)	0.0 ± (1)		
NH05	27.89** ± 0.05(134)	17.57** ± 1.09(14)			
NH10	26.51** ± 0.07(137)	29.79** ± 0.07(109)	45.77* ± 0.71(12)		
NH15	23.50** ± 0.07(76)	35.11** ± 0.33(36)	60.77** ± 2.27(8)		
NH20	34.43** ± 0.12(72)	23.69** ± 0.13(69)	20.99 ± 0.12(5)	25.00 ± (1)	43.75 ± (1)
NH25	6.26** ± 0.25(33)	6.41 ± 0.48(20)	3.01 ± 3.01(3)		
NH30	11.51 ± 0.07(56)	7.75 ± 0.39(9)	23.41 ± 0.52(4)		25.00 ± (1)
NH35		12.03 ± 0.99(3)	17.09 ± 0.16(5)	18.75 ± (1)	
NH40	53.14 ± 0.10(2)	0.0 ± (1)	6.70 ± 6.70(2)	6.25 ± (1)	13.92 ± 5.06(3)
NH50		6.25 ± (1)	0.0 ± 0.0 (2)	19.39 ± 19.39(2)	3.02 ± 1.74(8)
NH60	0.71 ± 0.71(3)	0.13 ± 0.13(10)	0.0 ± 0.0 (4)	0.0 ± 0.0(15)	0.0 ± 0.0 (3)

[1] Gut-fullness is expressed as a reconverted $\arcsin\sqrt{\text{percentage}}$ transformed mean followed by its standard error and the number of observations in parentheses.

[2] The station samples in this table are from the 0.7-m bongo net sampler exclusively.

*5% level significant difference between successive station means based on two-sample *t*-tests.

**1% level significant difference between successive station means based on two-sample *t*-tests.

curred between stations NH05 and NH20 (Table 9). Any zoeal stage caught within NH03 and farther offshore than NH20 showed a marked decrease in gut-fullness.

DISCUSSION

The initial appearance of *C. magister* larvae in the plankton off the central Oregon coast in late January and early February occurs at a time when sea surface temperatures are generally warming after the yearly mean low in January (Gonor et al. 1970). High densities of early stage zoea caught within 3-10 miles of shore are in agreement with the known distribution of the adults at this time. Relatively few occurrences of early stage larvae were found beyond 10 miles of shore during the sampling period as the northward flowing Davidson Current tends to retain the early developing larvae in the nearshore area. A very strong onshore component of the current has been observed within 5 miles of shore (Keene 1971; Wyatt et al. 1972; Holton and Elliot 1973). During the March and April transition period when the northward Davidson Current is replaced by currents flowing to the south and southwest, the larvae have developed to late stage zoea and megalopae. The bulk of the *C. magister* megalopae settle out of the water and metamorphose to juveniles by April and May before the onset of intense coastal upwelling in June and July, thus reducing the chance of being carried offshore by the resulting Ekman Current. During all seasons along the coast, larvae which occur increasingly closer to shore would be subject to decreasing current transport either alongshore or offshore.

1970 Season

It was observed during the 1970 larval season of *C. magister* that the late zoeal stages "disappeared" or were greatly reduced in numbers in the inshore sampling area, whereupon the megalopae reappeared after the proper time interval in densities comparable to those of the previously sampled zoea. Hypotheses to explain their disappearance and reappearance are as follows: 1) the late zoea were misidentified, 2) some stages are skipped in development, 3) the sampling interval missed those stages, 4) avoidance of the samplers increases with zoeal stages of development but decreases at megalopal stage, 5) the late zoeal larvae are carried offshore or alongshore but upon molting to the megalopal stages are transported onshore or back to their original release point, 6) the larvae were very dispersed at late zoeal development so that the volume of water filtered was not adequate, or 7) late stage zoea are resting on the bottom or below the depth sampled.

The late stages of *C. magister* larvae were not misidentified as they are morphologically distinct by this time and are nearly twice the size of any other local cancrid species. Apparently, the late larval stages of *C. magister* were not skipped in their development since zoea 4 and 5 stages were collected on the offshore stations in late March and early April. It is not believed that the late zoeal stages have greater swimming ability compared to the early zoea and megalopa which would permit them to avoid the samplers to a greater degree. On the contrary, personal observations of the late stage larvae in laboratory culture show them to be sluggish swimmers that spend considerable time resting on the bottom of the rearing vessel.

A species such as *C. magister*, which has a larval life of approximately 130 days, could conceivably be transported northward about 600 miles along the North Pacific coast as Wyatt et al. (1972) reported that the winter surface currents based on drift bottle studies have a mean speed of 0.2 knots, or a drift of 150 miles per month. The Ekman transport of surface waters due to wind stress decreases exponentially with depth due to frictional resistance, so that when the current has fallen to about one-twenty third that of the surface, this subsurface flow is negligible or reverse to that of the surface currents (Sverdrup et al. 1942). Recent studies indicate wind driven water motion extends to a depth of about 10 m (Bourke et al. 1971). If the larval population resides about 5m below the surface where the wind induced current is about one-quarter that of the surface, then the larvae would only be transported 150 miles in a linear distance. Larvae located in the water column below 5m depth, particularly the later zoeal stages, would experience relatively little transport in any direction. Holton and Elliot (1973) reported the greatest abundance and density of zooplankton containing crab larvae occurred at about 15m depth at nearshore stations off Newport during the daylight hours. Hypothetically, larvae released in January-February could be transported north along the coast in the surface currents and, after the transition period of currents in March, travel south a comparable distance in April and May. Or, taking into consideration the fact that the older stages may reside deeper into the water column, they could conceivably travel north in the surface currents as early zoea and travel south again as late larvae in a weak underlying countercurrent, but this seems unlikely. Huyer et al. (1975) reported the northward currents along the central Oregon coast essentially are constant with depth during the winter and southward at all depths in the spring but stronger at the surface. Larvae occurring within 3-5 miles of the coast probably are caught within a system of eddies and countercurrents characteristic of this zone, retarding large-scale dispersal in any direction. The mechanistic concepts of recruitment seem too contrived and unnecessary if stochastic processes are the general rule for species producing large numbers of expendable young. Most investigators would agree that the great majority of the pelagic larvae of marine invertebrates are lost to the population and that only a very small percentage of annual recruits are normally required to maintain a stable population for longer-lived adults. *Cancer magister* lives 4 or 5 yr so that a population unexploited by man would only require recruitment every other year or so. The fact that the adult populations are not retreating northward supports the view that at least some of the larvae are retained in the same general area as their point of origin.

The low densities of late stage larvae collected in the offshore area indicated that the small volume of water filtered on the inshore stations could account for their disappearance or reduced numbers.

Knowledge of their vertical location within the water column at different stages of development is important in understanding their spatial distribution and local abundance. However, a separate study of the larvae within the upper 150 m was not undertaken. Most crab larvae are photopositive to light in their early stages and migrate to the surface layers, whereas the late stages respond photonegatively and are found in the deeper layers near the bottom as they prepare to molt to juveniles (Thorson 1964). The larvae of *C. magister* appear to follow this same general pattern except that the early megalopal stage shows anomalous behavior as they have been observed to "swarm" near the sea surface along the coast (Cleaver 1949; Gaumer 1971; pers. obs.). Personal laboratory observations, as well as those by MacKay (1942) and others, substantiate the fact that the early zoea and megalopa of *C. magister* are generally photopositive in contrast to the late zoeal stages which are neutral or photonegative.

A scheme is proposed which would explain their distribution and abundance within 10 miles of the coast taking into account the differential behavioral response to light of the various larval stages. Newly hatched zoeal larvae are strongly photopositive and swim to the surface where current transport during the winter is generally onshore. They become progressively heavier and less photopositive with development until in the late zoeal stages they are neutral or responding negatively to light. As a consequence, the late zoeal stages reside in the deeper layers of water, possibly within a few meters of the bottom. They are now maximally dispersed in the nearshore area. Upon molting to the megalopic stage they are temporarily strongly photopositive to light and coupled with their increased powers of locomotion, they swarm to the surface again and are congregated by the prevailing currents usually in a band within 5 miles of the coast. If the late zoeal larvae do in fact reside near the sea bottom, the onshore drift current within 10-20 m of the bottom would prevent them from being transported offshore. Bottom flow in waters less than 40 m deep is towards the coast in the direction of wave travel throughout the year (Gross et al. 1969). The behavior of the larvae within the water column in relation to the hydrological features of the nearshore area under usual circumstances tends to restrict dispersal of the larvae to any great degree.

1971 Season

The sparseness of *C. magister* late zoeal larvae and megalopae during the 1971 season implies that a mass mortality occurred in the early zoeal stages. This apparent mortality was associated with sea surface temperature and salinity in analyses of covariance, but larval survival predicted through response surface methodology and gut-fullness analysis did not substantially explain their sparseness. The lack of highly supportive evidence leads to further speculation as to the causes of larval mortality in the plankton.

Hypothesis 1: Direct Effects of Temperature and Salinity

Sea surface temperature, and salinity to a lesser degree, were important environmental factors in explaining the difference in yearly larval population means of *C. magister* by analyses of multiple covariance. However, the statistical importance of these factors in determining larval abundance may be misleading. A wide temperature gradient during a larval season, i.e., a steep slope, could be statistically significant, but the range of temperatures may be well within the tolerance limits of an organism. In contrast, the salinity gradient during the same larval season is usually narrow resulting in a statistically nonsignificant slope, which may still occur outside the range tolerated by the larvae. Also, the erratic surface temperature and salinity fluctuations that occurred during the summer upwelling may cancel the effect of a significant gradient that occurred earlier in winter and spring.

Cancer magister larvae were reared by Reed (1969) under various temperature-salinity combinations and he concluded that these factors, as they normally occur off the Oregon coast, would not significantly affect survival. Response surface techniques, using Reed's data, predicted about 45% survival under the extreme temperatures and salinities that occurred during February and March 1971. The sea surface temperatures and salinities used in the analysis probably represent the most extreme long-term conditions that the larvae could have experienced in the field. Larvae several meters below the surface may be protected from the more extreme fluctuations of temperature and salinity, but some degree of exposure seems certain in view of the fact that extensive wind mixing occurs in shallow waters along the coast. The North Pacific is characterized by heavy precipitation during the fall and winter seasons resulting in considerable land drainage and river runoff along the nearshore area. Larvae along the coast, particularly near the mouths of bays and rivers, may lie in the low-salinity plume waters before sufficient mixing occurs. Harder (1968) reported that many planktonic organisms tend to accumulate near density interfaces that frequently occur in natural waters. Some species of copepods were observed under laboratory conditions to react to extremely small changes in density. Whether *C. magister* larvae have the ability to avoid these low-salinity surface waters that may be detrimental to them is not known. The early zoeal larvae would seem most vulnerable to low surface salinity as their behavioral response directs them to the surface and their swimming ability is slight compared to the megalops stage. Early larval ability to avoid low-salinity surface waters would have to be sufficient to overcome the increased storm-induced mixing during this season. The mortality rate of *C. magister* larvae reared in the laboratory under optimum conditions was constant and minimal throughout development (Reed 1969). Mortality increased greatly for larvae reared at 20‰ salinity; early zoeal larvae were killed within a short period in salinities less than 20‰. In addition, both the lower range of salinities and temperatures used in his experiments increased the duration of the larval instars where survival could be monitored for a sufficient time period.

It is difficult to evaluate the extent to which results from laboratory studies approach reality in order to understand how environmental variables may affect survival. Larvae reared at suboptimal conditions have been observed to survive for considerable periods of time, apparently unable to molt successfully. These same larvae eventually die, but laboratory experiments often are terminated before full mortality can be observed. Low salinity during the winter of 1971 may have been an important factor resulting in the demise of *C. magister* larvae that year. Subtle changes in the flux and composition of the internal ionic constituents can alter the molting process; larvae which appear normal in early development may mask deficiencies that express themselves later in development. Nevertheless, short-term exposure to extreme conditions may be just as detrimental as slightly suboptimal conditions over a long period of time (cf. Lough and Gonor 1973a, b). Although the nearshore surf salinities on a monthly average are in the range of tolerance by the larvae, daily measurements occasionally drop below 20‰ (Gonor et al. 1970). No larvae survived below 20‰ salinity in Reed's (1969) laboratory study.

The effect of low salinity in conjunction with wider than normal temperatures may play an important role in larval survival as indicated from the analyses. Low and high temperatures greatly accentuated the effects of marginally dilute salinities on *C. magister* larval survival. But again, the ecological significance of a synergistic effect has not been fully established in this study. More detailed, short-term studies of salinity-temperature variability and larval monitoring are needed in the nearshore area. Sastry and McCarthy (1973) observed distinct differences in temperature-salinity tolerances and metabolic responses of the larvae of two species of *Cancer* sympatrically distributed along the east coast of North America. Complete development for *C. irroratus* larvae occurred over a wide range of temperatures, whereas *C. borealis* larvae was restricted to a narrow range. The metabolic-temperature pattern of *C. irroratus* larvae indicated a progessive narrowing in temperature sensitivity. In contrast, the early stages of *C. borealis* initially were sensitive to warmer temperatures but in the later stages sensitivity shifted to colder temperatures. Hatching of the two *Cancer* species is separated in time so that the diverse metabolic responses observed are believed to be adaptations by larvae of the two species to the different temperature conditions encountered.

The combined effects of salinity and temperature have been studied under controlled laboratory conditions on other species of brachyuran larvae by Costlow et al. (1960, 1962, 1966), Costlow and Bookhout (1962), and Costlow (1967). Although the adults inhabit euryhaline waters, specific larval stages have been shown to require restricted ranges of salinity and temperature to varying degrees for complete development. In many cases, both temperature and salinity and the interaction of various combinations of the two environmental variables were observed to affect larval survival and retard development. Salinity generally has an immediate effect on survival while temperature appears to play a modifying role within the extremes of tolerance. Most of their work indicates that mortality was highest during the early zoeal stages and that the megalops stage was the least subject to environmental stress, although exceptions are reported. Recently, Costlow and Bookhout (1971) investigated the effects of cyclic temperatures compared to constant temperatures on the larvae of the estuarine mud crab, *Rhithropanopeus harrisii*. Duration of larval life and survival were about the same but survival was enhanced under cyclic temperatures at the higher end of the experimental range. Short-term fluctuations in temperature or other environmental variables throughout the water column have not been adequately monitored along the North Pacific coast. Their effect on *C. magister* larvae is not known and should be investigated.

Hypothesis 2: Food Quality and Quantity

May (1974) reviewed Hjort's (1914) critical period concept for fish larvae since Marr's (1956) evaluation and concluded from recent work that starvation may be an important cause of mortality, especially during the period immediately following the yolk sac stage. Although crab larvae do not have a strictly comparable yolk sac stage in their planktonic life, adequate food densities for efficient feeding may be of critical importance during a brief period following hatching. There is limited knowledge concerning the types of food organisms normally available and selected by *C. magister* larvae and concerning the densities of these food organisms sufficient for development. Most crab larvae are omnivorous, requiring substantial protein in their diet (Costlow and Sastry 1966; and others). Attempts to distinguish gut contents of field-caught *C. magister* larvae were unsuccessful in the present study. However, the specific kind of food organism encountered may not be as important as its size. The size of food organisms available for each larval stage must be within a restricted range in order for a larva to successfully capture and ingest. The progression of larval size with development would indicate that the different larval stages can utilize increasingly greater sizes of food organisms. Reed (1969) found in laboratory culture that the larvae of *C. magister* survived well feeding on *Artemia salina* (0.475-0.752 mm length) and *Balanus gladula* nauplii (0.370-0.420 mm length), but would only survive for a limited period on smaller size veliger larvae of *Mytilus edulis* (0.100-0.300 mm length?). He also reported that unfed *C. magister* zoea larvae would only survive for 14 days. This implies that under natural conditions larvae will not survive if a suitable food organism is delayed in its appearance by more than 2 wk, and that certain kinds of food organisms selected by the larvae are nutritionally inadequate for their long-term metabolic needs.

Chamberlain (1961, 1962) reared the larvae of two xanthid crabs, *Neopanope texana sayi* and *Rhithropanopeus harrisii*, on a variety of foods and found that development was retarded when larvae were fed on a mixture of nauplii and algae. Larvae fed algae alone would not molt and only lived 6-10 days in culture. Algae appeared to be nutritionally inadequate for successful development and restricts the intake of more suitable food by indiscriminate larval feeding. Costlow and Sastry (1966) suggested that high mortality of *Callinectes sapidus* larvae at the time of the third zoeal stage in nutritionally inadequate culture may be due to the initial availability of a large pool of free amino acids within the eggs through the first and second zoeal stages. They also pointed out that the variability in tolerance to suboptimal conditions may be related to the size of such a free amino acid pool.

Although the gut-fullness analysis in the present study did not provide insight into the difference in larval abundance between the 2 yr, it did suggest the existence of an optimum zone for adequate feeding between 3 and 20 miles offshore where suitable kinds and densities of food organisms occur. Zooplankton volumes along the Washington coast decrease to a minimum level during the winter and increase to maximum levels during the spring (Frolander 1962). During the winter, the volume of zooplankton and abundance of copepods were greater inshore than offshore as a consequence of the onshore transport of surface waters (Frolander 1962; Anderson 1964; Peterson 1972). Anomalous weather conditions such as occurred during the winter of 1971 may have been ultimately responsible for alterations in the usual types and availability of food organisms encountered during the first few weeks of larval feeding.

Hypothesis 3: Predators and Competitors

The importance of the combined or separate effects of predation and competition on larval populations is difficult to assess. Predation has generally been regarded as the major cause of larval mortality (Thorson 1946, 1950). Lebour (1919a, b, 1920, 1921, 1922, 1923) observed many species of young fish and medusae to prey upon crab larvae as well as most other small organisms in the plankton. Cannibalism is well known in laboratory culture. Knudsen (1960) observed in the laboratory that xanthid first stage zoea were eaten by older zoea and megalops as well as by copepods. Other predators known to feed on marine larvae, such as ctenophores, chaetognaths, euphausiids, and shrimps, appear seasonally in high densities along the North Pacific coast. Their effect on larval populations has not been fully ascertained. Peterson (1972) compared the ratios of copepod nauplii to total copepods off the Washington coast and found that more nauplii were hatched inshore than offshore throughout the year, but fewer developed to adults suggesting greater predation in the inshore area. Predation was reduced during the winter compared to other seasons within the inshore area. These findings might similarly apply to relative predation rates on *C. magister* larvae along the North Pacific coast.

Factors in the environment such as abnormally cold temperatures or lack of food that extend the pelagic life of the larval phase have been considered detrimental due to predation. It has been assumed that the longer the larvae remain in the plankton the more they will be preyed upon, although predation pressure upon their recruitment to the benthic habitat may be just as great, or greater (Thorson 1966). Larvae genetically feeble or weakened by some environmental factors may be more subject to predation so that under usual circumstances, the importance of predation may be secondary in mortality processes. The effect of predation on larval populations would not seem to be constant in the heterogeneous marine environment, but would more likely vary in intensity both temporally and spatially. Predation may only be a dominant factor in unusual years and/or on a small-scale basis.

Other members of the plankton community undoubtedly feed on the same food organisms as *C. magister* and competition may become an important factor when these food organisms become sparse. One potential competitor was tentatively identified as *C. oregonensis*. Its larvae are very abundant in the inshore area and cooccur with those of *C. magister*. Both species are morphologically similar and pass through the same number of larval stages, except that the larvae of *C. magister* become increasingly larger with development. There are studies showing the antagonistic effects of a mutually shared food resource. Brooks and Dodson (1965), in a study of two species of freshwater *Daphnia*, concluded that the larger species was more efficient in collecting both small and large particles and would competitively exclude the smaller species as long as size dependent predation was of low intensity. Conversely, Schoener (1969), in a theoretical study, concluded that large predators ate an equal or a greater range of food compared to the smaller ones as long as food was at some upper level. But, as food abundance was reduced, the optimal predator size shifted towards the smaller predator. Similar situations could conceivably occur and explain why *C. magister* larvae were less numerous in 1971. The interactions of hierarchies of predators and their prey involving temporal and spatial changes in densities and size frequencies can be exceedingly complex.

Hypothesis 4: Oceanic currents and multiple environmental effects

Planktonic organisms have limited means of locomotion and consequently are subject to the vagaries of oceanic currents. Changes in the strength or timing of these currents can be ultimately responsible for the success or failure of larval populations and their adult stocks (Coe 1956). The transport of entire larval stocks out of their normal environment can have catastrophic results for annual recruitment.

During the winter-spring larval period of *C. magister*, the major nearshore oceanographic feature is the northerly intrusion of the Davidson Current along the Oregon-Washington coast and its reversal in March-April. The strength and duration of the Davidson Current are critical factors in the initiation, development, and persistence of seasonally dominant plankton communities. Southern neritic zooplankton species appear abundant off the Oregon and Washington coasts during fall and winter and are believed to be carried by the northerly surface drift (Cross and Small 1967; Miller 1972; Frolander et al. 1973). Frolander (1962) observed widespread anomalous conditions off the Washington coast during February 1958, compared to the previous year. Lower plankton volumes and a change in plankton species were associated with an increase in the surface temperatures, a decrease in dissolved inorganic phosphate, and unusual weather during the anomalous February. These events were believed to be the result of southerly offshore waters moving into the coastal area to a larger extent that year.

Superimposed upon the nearshore currents with their characteristic water properties, a dominant modifying process results from precipitation and river runoff. A band of low salinity occurs all along the North Pacific coast. Little information is available on the effect of the heavy river runoff on the endemic plankton populations in the neritic zone, but some studies have been done concerning the effect of the Columbia River plume on the physical processes and biota over its range of influence (Anderson 1972). The Columbia River effluent flows north along the coast of Washington during the winter in response to the prevailing southwesterly winds (Barnes et al. 1972). Hobson (1966) and Anderson (1972) observed that chlorophyll and productivity at the surface of the plume and ambient waters were higher than nearby oceanic waters due to the increased stability of the water column providing an environment where phytoplankton could accumulate. The major influence of the Columbia River plume on phytoplankton development is believed to be in the timing of events. Phytoplankton populations can develop 3-5 wk earlier in the plume due to the increased stabilization. Heinrich (1962, 1968) stated that the seasonal cycle of phytoplankton communities are less balanced in the neritic zone and that the phytoplankton populations in this area can vary depending on the timing and differential growth of relative copepod species. Shifts in weather patterns create corresponding changes in nearshore currents resulting in the intrusion and displacement of endemic planktons. Nearshore modifying processes can change the character of these communities setting forth new interactions among the populations.

Anomalous hydrographic and meteorological conditions were observed along the Oregon coast during the winter of 1971 in the present study. Its effect on the plankton populations to date only have been investigated in relation to *C. magister* larvae. To what extent did the relaxation of onshore transport of surface waters during January and February with subsequent increased transport in March 1971, compared to the same period in 1970, affect the dynamics of the *C. magister* larval population? The circumstantial evidence suggests that heavy mortality of the larvae occurred in 1971. However, the difference in larval abundance for the 2 yr may not be real if the larvae were quite localized in their alongshore distribution and moved out of the study area. Sampling was not conducted in other areas for those years to fully answer this point. In addition, the late zoeal stages were undersampled both years leaving a gap in our knowledge of their true numbers, distribution, and condition. Assuming that a mass mortality of larvae did, in fact, occur in the study area, what are the most likely environmental mechanisms? Did the decreased onshore surface water transport in early winter of 1971 relative to 1970 allow more larvae to be carried offshore that year where food abundance was lower, etc.? Any larvae swept off the shelf area that survived would still probably be beyond successful recruitment to the adult nearshore population. Did the greater onshore transport of surface waters during late winter of 1971 move the bulk of the larval population closer to shore into a suboptimal environment too early in their development? What is the effect of the increased precipitation and river runoff during the winter of 1971 that reduced nearshore salinities? Was a phytoplankton bloom initiated earlier in the season and how did it affect populations of other planktonic organisms utilized as food for *C. magister* larvae? Chamberlain (1961) commented that, for crab larvae feeding indiscriminately on both algae and zooplankton, a phytoplankton bloom initially may retard zoeal development; however, following the increase of the herbivore population, more nutritionally adequate food is available and would accelerate larval development. Do the low-salinity Columbia River plume and other river effluents effectively act as barriers against northerly alongshore transport of larvae? The lower temperatures and salinities in 1971, particularly in the nearshore area, coupled with adverse biological pressures, i.e., increased predation, may have had a synergistic effect on larval mortality. Many alternatives are open in marine ecosystems where stochastic processes prevail producing innumerable permutations. The indirect effect of physical variables on larval food organisms and predator-prey relations can be extremely complex and important. Subtle changes in these relations may have an accumulative effect on a larval population already in a stressed condition and near the point at which recovery diminishes.

Answers to these questions remain conjectural and may only be sought through further comprehensive and detailed studies. However, in conclusion, there is no substantial evidence from this study that the colder winter of 1971 caused a delay in the initial appearance and developmental schedule throughout the larval period of *C. magister*. The generally poor appearance of the early zoeal larvae collected during the 1971 season suggests that whatever factor(s) responsible for the apparent mortality appeared to have an immediate effect on these stages. The first few zoeal stages may be the critical period in the early life history of *C. magister* where the greatest mortality occurs ultimately determining future year class strength.

RECOMMENDATIONS FOR FUTURE RESEARCH

Studies to date have provided a broad overview of knowledge concerning the initial timing, abundance, and dispersal of *C. magister* larvae in relation to major oceanographic events off the central Oregon coast. First approximation estimates of length of larval life, mortality, and feeding have been achieved, but we are still lacking detailed insight into the dynamics of the larvae-plankton-environment matrix. This study points out our limited knowledge and understanding of the physical and biological mechanisms affecting the dispersal and subsequent survival of *C. magister* larvae. An understanding of these processes is necessary for an understanding of the stability and long-term productive potential of the Dungeness crab as a fishery resource in the Pacific Northwest. By studying processes controlling the dispersal and survival of the larvae, we may be able to gain insight into stock-recruitment relations and be able to predict the effects of long-term environmental changes. Some specific recommendations for further work are listed below.

1. A minimum of three surveys should be conducted between late January and early June to monitor initial hatching, production, rate of development, and dispersal of the larvae. It is imperative that survey coverage be extended along the Oregon coast to observe patchiness and alongshore dispersal. A grid of stations to within 30 miles of the coast from at least Cape Blanco, Oreg. to Cape Flattery, Wash. is recommended. A sufficient time series of data is required to adequately assess yearly changes in the larval populations in order to gain insight into mortality processes. Also, a long-term series is needed as a background of knowledge upon which more specialized short-term studies can be based. Six or seven years of plankton sampling seems to be a minimum time series for establishing trends, although 10-15 yr are required to substantiate significant differences.
2. Intensive close-order grid sampling on a short-term basis, following a fairly well-defined and homogeneous "patch" of larvae, should be conducted to assess in more detail mortality and feeding in good and poor areas.
3. This study emphasizes the need for more detailed oceanographic studies in the nearshore environment and how they affect the population dynamics of organisms living in this zone. In conjunction with larval surveys, circulation studies should be expanded during the winter and spring along the Oregon coast to improve the basis for predicting and evaluating dispersal, primary productivity, etc. A continuous program of temperature, salinity, and current measurements are needed of the nearshore currents during the larval period from January through June and particularly the timing and extent of the March-April transition of the Davidson Current.
4. Short-term exposure of the larvae to environmental variables such as low salinity in combination with varying temperature, food density, etc. and subsequent transfer to optimum conditions for long-term observations in the laboratory are needed to properly evaluate the effects of these factors.
5. Detailed descriptions of the three-dimensional composition of the associated plankton communities are needed in terms of the dominant species, size categories, and diurnal variability. Investigations into the contagious distribution of these organisms, mechanisms of initiation and destruction, are central to understanding prey-predator interaction and attempts to model these phenomena.
6. Fine-mesh (0.165 and 0.053 mm) sampling with the 0.2-m bongo nets should be used concurrently with the 0.7-m bongo nets to examine and answer the questions of food composition and availability utilized by early *C. magister* larvae. In particular, the invertebrate component for both coarse- and fine-mesh samples should be analyzed initially between contrasting years or areas of larval abundance. The use of plankton pumps may be more amenable in this case as fine-mesh nets clog rapidly.
7. The vertical distribution and diurnal movements of *C. magister* larvae throughout its pelagic life is especially important in regard to sampling variability, dispersal, and feeding, and should be studied. Do most of the older zoeal larvae, in fact, reside within a few meters of the bottom in the shallow inshore area?
8. Laboratory studies should be undertaken to analyze the phototactic behavior of the larvae at various stages of development to gain a better understanding of their diurnal movements as may be modified by temperature, hunger state, presence of prey and predators, etc.
9. A new approach is needed in the analysis of larval gut contents. Biochemical techniques of gut material may be used to identify food organisms utilized by the larvae. Energy budgets should be constructed to determine minimum food requirements of the various larval stages. Condition factors indicative of the physiological well-being of larvae may be used to evaluate good versus poor areas and years of feeding.
10. Potential predators that cooccur with *C. magister* larvae should be identified and ingestion rates determined from field and laboratory experiments in order to estimate

their effect on the larval population. Transitional experiments should be carried out in the field to further assess the reality of laboratory studies.

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LITERATURE CITED

ALDERDICE, D. F.
 1972. Factor combinations. Responses of marine poikilotherms to environmental factors acting in concert. *In* O. Kinne (editor), Marine ecology, Vol. 1, Part 3, p. 1659-1722. Wiley-Interscience, Lond.

ANDERSON, G. C.
 1964. The seasonal and geographic distribution of primary productivity off the Washington and Oregon coasts. Limnol. Oceanogr. 9:284-302.
 1972. Aspects of marine phytoplankton studies near the Columbia River, with special reference to a subsurface chlorophyll maximum. *In* A. T. Pruter and D. L. Alverson (editors), The Columbia River estuary and adjacent ocean waters, p. 219-264. Univ. Wash. Press, Seattle.

BAKUN, A.
 1973. Coastal upwelling indices, west coast of North America, 1946-71. U.S. Dep. Commer., NOAA Tech. Rep. NMFS SSRF-671, 103 p.

BARNES, C. A., A. C. DUXBURY, AND B. A. MORSE.
 1972. Circulation and selected properties of the Columbia River effluent at sea. *In* A. T. Pruter and D. L. Alverson (editors), The Columbia River estuary and adjacent ocean waters, p. 41-80. Univ. Wash. Press, Seattle.

BOURKE, R. H., B. GLENNE, AND B. W. ADAMS.
 1971. The nearshore physical oceanographic environment of the Pacific Northwest coast. Dep. Oceanogr. Oreg. State Univ., Ref. 71-45, 120 p.

BROOKS, J. L., AND S. I. DODSON.
 1965. Predation, body size, and composition of plankton. Science (Wash., D.C.) 150:28-35.

BURT, W. V., AND B. WYATT.
 1964. Drift bottle observations of the Davidson Current off Oregon. *In* K. Yoshida (editor), Studies on oceanography, p. 156-165. Univ. Tokyo Press, Tokyo.

BUTLER, T. H.
 1960. Maturity and breeding of the Pacific edible crab, *Cancer magister* Dana. J. Fish. Res. Board Can. 17:641-646.

CHAMBERLAIN, N. A.
 1961. Studies on the larval development of Neopanope texana sayi (Smith) and other crabs of the family Xanthidae (Brachyura). Chesapeake Bay Inst., John Hopkins Univ., Tech. Rep. 22:1-35.
 1962. Ecological studies of the larval development of *Rhithropanopeus harrisii* (Xanthidae, Brachyura). Chesapeake Bay Inst., John Hopkins Univ., Tech. Rep. 28:1-47.

CLEAVER, F. C.
 1949. Preliminary results of the coastal crab (Cancer magister) investigation. Wash. Dep. Fish., Biol. Rep. 49A:47-82.

COE, W. R.
 1956. Fluctuations in populations of littoral marine invertebrates. J. Mar. Res. 15:212-232.

COLTON, J. B., JR.
 1959. The multiplane kite-otter as a depressor for high-speed plankton samplers. J. Cons. 25:29-35.

COSTLOW, J. D., JR.
 1967. The effect of salinity and temperature on survival and metamorphosis of megalops of the blue crab *Callinectes sapidus*. Helgoländer wiss. Meeresunters. 15:84-97.

COSTLOW, J. D., JR., AND C. G. BOOKHOUT.
 1962. The larval development of *Hepatus epheliticus* (L.) under laboratory conditions. J. Elisha Mitchell Sci. Soc. 78:113-125.
 1971. The effect of cyclic temperatures on larval development in the mud-crab *Rhithropanopeus harrisii*. *In* D. J. Crisp (editor), Fourth European Marine Biology Symposium, p. 211-220. Cambridge Univ. Press., Lond.

COSTLOW, J. D., JR., C. G. BOOKHOUT, AND R. MONROE.
 1960. The effect of salinity and temperature on larval development of Sesarma cinereum (Bosc) reared in the laboratory. Biol. Bull. (Woods Hole) 118:183-202.
 1962. Salinity-temperature effects on the larval development of the crab Panopeus herbstii Milne-Edwards, reared in the laboratory. Physiol. Zoöl. 35:79-93.
 1966. Studies on the larval development of the crab, *Rhithropanopeus harrisii* (Gould). I. The effect of salinity and temperature on larval development. Physiol. Zoöl. 39:81-100.

COSTLOW, J. D., JR., AND A. N. SASTRY.
 1966. Free animo acids in developing stages of two crabs, *Callinectes sapidus* Rathbun and *Rhithropanopeus harrisii* (Gould). Acta Embryol. Morphol. Exp. 9:44-55.

CROSS, F. A., AND L. F. SMALL.
 1967. Copepod indicators of surface water movements off the Oregon coast. Limnol. Oceanogr. 12:60-72.

FROLANDER, H. F.
 1962. Quantitative estimations of temporal variations of zooplankton off the coast of Washington and British Columbia. J. Fish. Res. Board Can. 19:657-675.

FROLANDER, H. F., C. B. MILLER, M. J. FLYNN, S. C. MEYERS, AND S. T. ZIMMERMAN.
 1973. Seasonal cycles of abundance in zooplankton populations of Yaquina Bay, Oregon. Mar. Biol. (Berl.) 21:277-288.

GAUMER, T. F.
 1971. Controlled rearing of Dungeness crab larvae and the influence of environmental conditions on their survival. Commer. Fish. Res. Dev. Act Prog. Rep., Nov. 16, 1965 to June 30, 1971. Fish. Comm. Oreg., Closing Rep., 43 p.

GONOR, J. J., A. B. THUM, AND D. W. ELVIN.
 1970. Inshore sea surface temperature sand salinity conditions at Agate Beach, Yaquina Bay and Whale Cove, Oregon, in 1970. Data Rep. 45. Dep. Oceanogr. Oreg. State Univ., Ref. 70-44, 30 p.

GROSS, M. G., B.-A. MORSE, AND C. A. BARNES.
1969. Movement of near-bottom waters on the continental shelf off the northwestern United States. J. Geophys. Res. 74:7044-7047.

HARDER, W.
1968. Reactions of plankton organisms to water stratification. Limnol. Oceanogr. 13:156-168.

HEINRICH, A. K.
1962. The life histories of plankton animals and seasonal cycles of plankton communities in the oceans. J. Cons. 27:15-24.
1968. On seasonal phenomena in the plankton of the Northeastern Pacific. Okeanologiya 8:287-296.

HJORT, J.
1914. Fluctuations in the great fisheries of northern Europe viewed in the light of biological research. Rapp. P.-V. Réun. Cons. Perm. Int. Explor. Mer. 20:1-228.
1926. Fluctuations in the year classes of important food fishes. J. Cons. 1:5-38.

HOBSON, L. A.
1966. Some influences of the Columbia River effluent on marine phytoplankton during January 1961. Limnol. Oceanogr. 11:223-234.

HOLTON, R. L., AND W. P. ELLIOTT.
1973. The development of methods for studying physical and biological processes in the nearshore zone on the Pacific coast of the United States. Dep. Oceanogr. Oreg. State Univ., Ref. 73-3, 18 p.

HUYER, A., R. D. PILLSBURY, AND R. L. SMITH.
1975. Seasonal variation of the alongshore velocity field over the continental shelf off Oregon. Limnol. Oceanogr. 20:90-95.

KEENE, D. F.
1971. A physical oceanographic study of the nearshore zone at Newport, Oregon. M.S. Thesis, Oreg. State Univ., Corvallis, 91 p.

KNUDSEN, J. W.
1960. Reproduction, life history and larval ecology of the California Xanthidae, the pebble crabs. Pac. Sci. 14:3-17.

KUKLA, G. J., AND H. J. KUKLA.
1974. Increased surface albedo in the northern hemisphere. Science (Wash., D.C.) 183:709-714.

KULM, L. D., AND J. V. BYRNE.
1966. Sedimentary response to hydrography in an Oregon estuary. Mar. Geol. 4:85-118.

LEBOUR, M. V.
1919a. Feeding habits of some young fish. J. Mar. Biol. Assoc. U.K. 12:9-21.
1919b. The food of post-larval fish. No. II (1918). J. Mar. Biol. Assoc. U.K. 12:22-47.
1920. The food of young fish. No. III. (1919). J. Mar. Biol. Assoc. U.K. 12:261-324.
1921. The food of young clupeoids. J. Mar. Biol. Assoc. U.K. 12:458-467.
1922. The food of planktonic organisms. J. Mar. Biol. Assoc. U.K. 12:644-677.
1923. The food of plankton organisms. II. J. Mar. Biol. Assoc. U.K. 13:70-92.

LONGHURST, A. R., AND D. L. R. SEIBERT.
1967. Skill in the use of Folsom's plankton sample splitter. Limnol. Oceanogr. 12:334-335.

LOUGH, R. G.
1975a. A reevaluation of the combined effects of temperature and salinity on survival and growth of bivalve larvae using response surface techniques. Fish. Bull., U.S. 73:86-94.
1975b. Dynamics of crab larvae (Anomura, Brachyura) off the central Oregon coast, 1969-1971. Ph.D. Thesis, Oreg. State Univ., Corvallis, 299 p.

LOUGH, R. G., AND J. J. GONOR.
1973a. A response-surface approach to the combined effects of temperature and salinity on the larval development of *Adula californiensis* (Pelecypoda: Mytilidae). I. Survival and growth of three and fifteen-day old larvae. Mar. Biol. (Berl.) 22:241-250.
1973b. A response-surface approach to the combined effects of temperature and salinity on the larval development of *Adula californiensis* (Pelecypoda: Mytilidae). II. Long-term larval survival and growth in relation to respiration. Mar. Biol. (Berl.) 22:295-305.

MACKAY, D. C. G.
1942. The Pacific edible crab, Cancer magister. Fish. Res. Board Can., Bull. 62:1-32.

MARR, J. C.
1956. The "critical period" in the early life history of marine fishes. J. Cons. 21:160-170.

MAY, R. C.
1974. Larval mortality in marine fishes and the critical period concept. *In* J. H. S. Blaxter (editor), The early life history of fish, p. 3-19. Springer-Verlag, N.Y.

MILLER, C. B.
1972. Zooplankton indicators of the seasonal cycle of currents along the Oregon coast. Trans. Am. Microsc. Soc. 91:87.

MOOERS, C. N. K.
1970. The interaction of internal tide with the frontal zone of a coastal upwelling region. Ph.D. Thesis, Oreg. State Univ., Corvallis, 480 p.

OSTLE, B.
1963. Statistics in research. 2nd ed. Iowa State Univ. Press, Ames, 585 p.

PATTULO, J. G., AND W. DENNER.
1965. Processes affecting seawater characteristics along the Oregon coast. Limnol. Oceanogr. 10:443-450.

PEARCY, W. G., AND R. S. MESECAR.
1970. Scattering layers and vertical distribution of oceanic animals off Oregon. *In* G. Brooke Farquhar (editor), Proceedings of an international symposium of biological sound scattering in the ocean, p. 381-394. Maury Cent. Ocean Sci., Dep. Navy, Wash., D.C.

PETERSON, W. K.
1972. Distribution of pelagic copepoda off the coasts of Washington and Oregon during 1961 and 1962. *In* A. T. Pruter and D. L. Alverson (editors), The Columbia River estuary and adjacent ocean waters, p. 313-343. Univ. Wash. Press, Seattle.

POOLE, R. L.
1966. A description of laboratory-reared zoea of *Cancer magister* Dana, and megalopae taken under natural conditions (Decapoda, Brachyura). Crustaceana 11:83-97.

POSGAY, J. A., R. R. MARAK, AND R. C. HENNEMUTH.
1968. Development and tests of new zooplankton samplers. Int. Comm. Northwest Atl. Fish., Res. Doc. 68/85, ser. 2085, 23 p.

REED, P. H.
1969. Culture methods and effects of temperature and salinity on survival and growth of Dungeness crab

(*Cancer magister*) larvae in the laboratory. J. Fish. Res. Board Can. 26:389-397.

RENFRO, W. C., J. C. MCCAULEY, B. GLENNE, R. H. BOURKE, D. R. HANCOCK, AND S. W. HAGER.

1971. Oceanography of the nearshore coastal waters of the Pacific Northwest relating to possible pollution. Vol. I, II. Water Qual. Off., Environ. Prot. Agency, Grant No. 16070 EOK.

SASTRY, A. N., AND J. F. MCCARTHY.

1973. Diversity in metabolic adaptation of pelagic larval stages of two sympatric species of brachyuran crabs. Neth. J. Sea Res. 7:434-446.

SCHMITT, W. L.

1921. The marine decapod crustacea of California. Univ. Calif. Publ. Zool. 23:1-470.

SCHOENER, T. W.

1969. Models of optimum size for solitary predators. Am. Nat. 103:277-313.

SCHWARTZLOSE, R. A.

1964. Nearshore currents of western United States, Baja, California, as measured by drift bottles. Calif. Coop. Oceanic Fish. Invest., Prog. Rep. 1 July 1960 - June 1962, p. 15-22.

SMITH, R. L., J. G. PATTULLO, AND R. K. LANE.

1966. An investigation of the early stage of upwelling along the Oregon coast. J. Geophys. Res. 71:1135-1140.

SVERDRUP, H. U., M. W. JOHNSON, AND R. H. FLEMING.

1942. The oceans their physics, chemistry, and general biology. Prentice-Hall, N.Y., 1087 p.

TATE, M. W., AND R. C. CLELLAND.

1957. Nonparametric and shortcut statistics in the social, biological, and medical sciences. Interstate Printers and Publishers, Inc., Danville, Ill., 171 p.

THORSON, G.

1946. Reproduction and larval development of Danish marine bottom invertebrates, with special reference to the planktonic larvae in the sound (Oresund). Medd. Komm. Dan. Fisk.-og. Havunders. Ser. Plankton. 4(1):1-523.

1950. Reproductive and larval ecology of marine bottom invertebrates. Biol. Rev. (Camb.) 25:1-45.

1964. Light as an ecological factor in the dispersal and settlement of larvae of marine bottom invertebrates. Ophelia 1:167-208.

1966. Some factors influencing the recruitment and establishment of marine benthic communities. Neth. J. Sea Res. 3:267-293.

U.S. ENVIRONMENTAL DATA SERVICE.

1970. Climatological data, Oregon. Environ. Sci. Serv. Admin., Dep. Commer. 76.

1971. Climatological data, Oregon. Environ. Sci. Serv. Admin., Dep. Commer. 77.

WALDRON, K. D.

1958. The fishery and biology of the Dungeness crab (*Cancer magister* Dana) in Oregon waters. Fish. Comm. Oreg., Contrib. 24, 43 p.

WINSOR, C. P., AND G. L. CLARKE.

1940. A statistical study of variation in the catch of plankton nets. J. Mar. Res. 3:1-34.

WOOSTER, W. S., AND J. L. REID, JR.

1963. Eastern boundary currents. *In* M. N. Hill (editor), The sea, Vol. 2, p. 253-280. John Wiley & Sons, Inc., Lond.

WYATT, B., AND W. GILBERT.

1971. Surface temperature and salinity observations at Pacific Northwest shore stations during 1970. Data Rep. 47. Dep. Oceanogr. Oreg. State Univ., Ref. 71-8, 19 p.

1972. Surface temperature and salinity observations at Pacific Northwest shore stations during 1971. Data Rep. 51. Dep. Oceanogr. Oreg. State Univ., Ref. 72-2, 15 p.

WYATT, B., D. A. BARSTOW, W. E. GILBERT, AND J. L. WASHBURN.

1971. Drift bottle recoveries and releases off the Oregon coast 1961 through 1970. Data Rep. 50. Dep. Oceanogr. Oreg. State Univ., Ref. 71-36, 57 p.

WYATT, B., W. V. BURT, AND J. G. PATTULLO.

1972. Surface currents off Oregon as determined from drift bottle returns. J. Phys. Oceanogr. 2:286-293.

APPENDIX

TABLE 1. —*Cancer magister* larval abundance for 1970-71 seasons and associated environmental data used in analyses of multiple covariance.

Date	0.2 m-bongo net sampler mesh size (mm)	Larval abundance[1]	Surface temp. (°C)[2]	Surface salinity (‰)
1970:				
1/29	0.571	4,598	10.3	29.55
	0.233	2,607		
2/13	0.571	6,721	11.0	30.25
	0.233	13,276		
2/25	0.571	65	11.4	30.62
	0.233	152		
3/9	0.571	536	10.8	30.99
	0.233	381		
4/16	0.571	88	9.7	33.06
	0.233	0		
4/27	0.571	7,713	9.5	32.98
	0.233	5,267		
5/1	0.571	1,868	9.5	32.98
	0.233	1,847		
5/6	0.571	89	9.2	32.98
	0.233	39		
5/22	0.571	1,817	11.8	32.51
	0.233	1,697		
6/4	0.571	74	9.1	33.62
	0.233	32		
6/23	0.571	0	7.9	33.60
	0.233	26		
7/2	0.571	21	12.5	32.84
	0.233	38		
7/16	0.571	56	9.6	32.73
	0.233	28		
7/29	0.571	0	12.7	32.63
	0.233	0		
1971:				
1/18	0.571	736	9.9	29.50
	0.233	1,007		
2/3	0.571	1,762	8.6	31.80
	0.233	1,930		
2/16	0.571	2,539	9.3	31.00
	0.233	3,408		
3/20	0.571	205	8.5	32.16
	0.233	21		
3/30	0.571	305	8.9	30.81
	0.233	316		
4/22	0.571	390	9.6	32.45
	0.233	999		
5/03	0.571	0	10.4	30.74
	0.233	0		
5/14	0.571	0	11.5	31.76
	0.233	0		
5/29	0.571	26	8.8	33.69
	0.233	25		
6/2	0.571	0	10.1	33.52
	0.233	0		
6/12	0.571	0	13.4	30.04
6/28	0.571	0	15.1	30.75
7/6	0.571	20	11.7	31.83
7/21	0.571	0	9.0	33.53

[1] Number of larvae per 4,000 m^3. Larvae summed over four inshore stations: NH01, NH03, NH05, NH10.

[2] Averaged values over four inshore stations.