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Title: LIFE HISTORY AND ECOLOGY OF CALANUS MARSHALLAE Frost IN THE OREGON UPWELLING ZONE

Abstract Approved: Redacted for privacy
Charles B. Miller

The life history and ecology of the neritic copepod Calanus marshallae was studied in order to learn (1) how the population is retained in the Oregon coastal upwelling zone and (2) what factors control population size.

Calanus marshallae is the largest dominant member of the coastal zooplankton. It occurs between February and September. There are no pronounced fluctuations in abundance. At least three generations are seen during the eight month growing season. The population probably passes the other months in diapause.

During the summer upwelling season, water flows offshore above 20 m and onshore below 20 m over most of the continental shelf. Offshore flow from the nearshore zone (one to three miles from shore) is shallower. Water circulation patterns and animal behavior retain individuals within the upwelling zone. The six naupliar (N) stages develop at depths of 10 to 20 m in the nearshore zone where offshore

transport is minimal. Each of the five immature copepodite (C) stages are found at progressively farther distances from shore within the upper 20 m. These individuals are moved seaward at the same rates at which the water flows. C4 and C5 undergo diel vertical migration on some nights which minimizes their offshore transport. Females live deeper in the water column than the C4 and C5 stages so are returned nearshore where eggs are laid.

Alongshore transport of individuals may be balanced over an annual period. During the summer generations, an adult is transported about 250 miles south from that point where its development began as an egg. Two generations are seen during the upwelling season so total transport south could be 500 miles. Individuals may be returned northward during winter diapause, but during the February-April generation, northward transport could be 500 miles if water flow were 15 cm sec^{-1}.

Three basic life history parameters were studied: development, reproduction and mortality. Nearly all aspects showed K-selected traits. Development in the laboratory followed a sigmoid model. Development from egg to N3 took only 3.5 days. C5 to C6 took 33% of the total 65 day developmental period. Adults live at least 70 days in the laboratory. Development in the field could be studied because cohorts were seen. Field animals developed at the same rate as laboratory animals implying that food resources in the field are not limiting. Individuals from N4 to C5 grow exponentially at a rate of 0.18 µg μg^{-1} day^{-1}.

Calanus marshallae is iteroparous. Females lay a clutch of 30 yolky eggs every 30 hours on the average. Reproductive effort is low:

7% of a female's body weight is laid as eggs each day. Egg laying rates did not differ between season or between different sized females. Egg production was strongly affected by food concentration. Starved females produced no eggs. Egg production increased linearly with increasing abundance of the diatom Thalassiosira fluviatilis to 3500 cells ml^{-1} (450 µg carbon $liter^{-1}$), above which egg laying rates did not increase. Maximum ingestion rates also occurred at 3500 cells ml^{-1}. Because of egg cannibalism, maximum egg laying rates could occur at food levels as low as 2000 cells ml^{-1}. Egg laying rates in the field were the same as laboratory rates again suggesting that food is not limiting in the field.

Egg, N1 and N2 mortalities are extremely high in the field. Only 10% of all eggs laid each day survive to N3. Females live less than one week in the field. As a result, net reproductive rates are low, only 5.1 female offspring produced per female.

In conclusion, even though Calanus marshallae individuals have the necessary behavioral traits which prevent them from being advected out of the upwelling zone, the population does not increase in numbers. Food is not limiting. The problem is that mortality is high on both eggs and females. It is suggested that the C. marshallae population is controlled by predators rather than food limitation or physical processes.

Life History and Ecology of *Calanus marshallae* Frost in the Oregon Upwelling Zone

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LIFE HISTORY AND ECOLOGY OF *CALANUS MARSHALLAE* Frost IN THE OREGON UPWELLING ZONE

CHAPTER I. INTRODUCTION

GENERAL REMARKS. Coastal upwelling systems support great standing stocks of commercially important fishes. These stocks exist because of a combination of physical and biological oceanographic circumstances. Under the influence of the earth's rotation, winds blowing equatorward drive surface waters equatorward and offshore. This offshore transport within the upper layers of the water column is balanced by onshore and upward movement of deep water. These deep waters are rich in plant nutrients. Mixing of nutrient-rich deep water into the surface layers allows phytoplankton blooms to continue for many months. Therefore high standing crops of phytoplankton are maintained throughout an upwelling season. These plants in turn support large stocks of zooplankton, clupeid fishes and their predators.

The details of the ways in which herbivorous zooplankton become abundant in upwelling zones interests me. The mechanisms are not as simplistic as outlined above however. Biological and physical processes are most important but it is possible that they act in opposition to each other. Since phytoplankton are abundant, herbivores should reproduce and grow at their maximum rates, thereby increasing in numbers. On the other hand, the upper layers of the water column where phyto- and zooplankton are most abundant are advected offshore and away from the main upwelling center. The plankton could be rapidly

transported out of the system and lost. This process would decrease plankton numbers. Clearly, there is a problem here.

Peterson, Miller and Hutchinson (1979) showed that off Oregon, the main concentration of zooplankton during the upwelling season is found within 20 km of shore and the upper 5 to 20 m of the water column. Upwelling is most intense within 15 km of shore. Extraordinary zooplankton abundances (20 to 80 individuals per liter) and dry weight biomass (50 to 200 mg per cubic meter) occur here. One or a combination of only four calanoid copepod species constitute most of the biomass: Pseudocalanus sp., Acartia longiremis (Lilljeborg), Acartia clausii Giesbrecht, and Calanus marshallae Frost. Through various behavioral responses, each of these dominant species has a different mechanism by which its population avoids being swept out of the upwelling zone. Some populations complete their entire life cycle within 10 km of shore where offshore surface transport is minimal. Others develop farther offshore but return to lay their eggs close to shore. For all species, it was hypothesized that populations are retained in the upwelling zone because reproduction and naupliar development occur in locations which minimize seaward advective losses.

In this dissertation, I show how one herbivorous copepod, Calanus marshallae, is retained in an upwelling zone. Data on the distribution of all life cycle stages within the system are incorporated with data on developmental, growth and reproduction rates, into a description of the life history of this copepod in the Oregon upwelling zone.

THE HYPOTHESIS. The spatial distribution of eggs, larvae,

juveniles, and adults of Calanus marshallae off Oregon was fairly well known from previous data sets. It was clear that there was a zonal gradient in population age structure. Older stages lived offshore at least 20 km from the beach. Females somehow were returned shoreward where they laid their eggs within five km from shore. The younger stages developed and grew in the very nearshore zone, within 2 km from the beach. Through some mechanism, individuals were moved both seaward and shorward during development from egg to adult. It remained to discover the mechanism.

An hypothesis that could explain the landward transport of adults and subsequent seaward transfer of developing juveniles was given by Peterson, Miller and Hutchinson (1979). We suggested that the distributional patterns were a direct result of the upwelling circulation patterns, coupled with diel vertical migration of the older life history stages.

The hypothesis advanced, and illustrated in Figure 1, was as follows: Older copepodites and adults living offshore are transported landward with the deep onshore flow during active upwelling events. To accomplish this they must not perform any diel vertical migrations into surface waters. By remaining at depths greater than 20 m for at least a week, they would be brought into the nearshore zone with the newly upwelled water. Eggs laid here must be transported shoreward because the nauplii, which hatch approximately 40 h after the eggs are laid, are found loser to shore than the eggs. Shoreward transfer of both eggs and nauplii can occur during relaxation of upwelling when surface flow is onshore. It would also occur during active upwelling if the

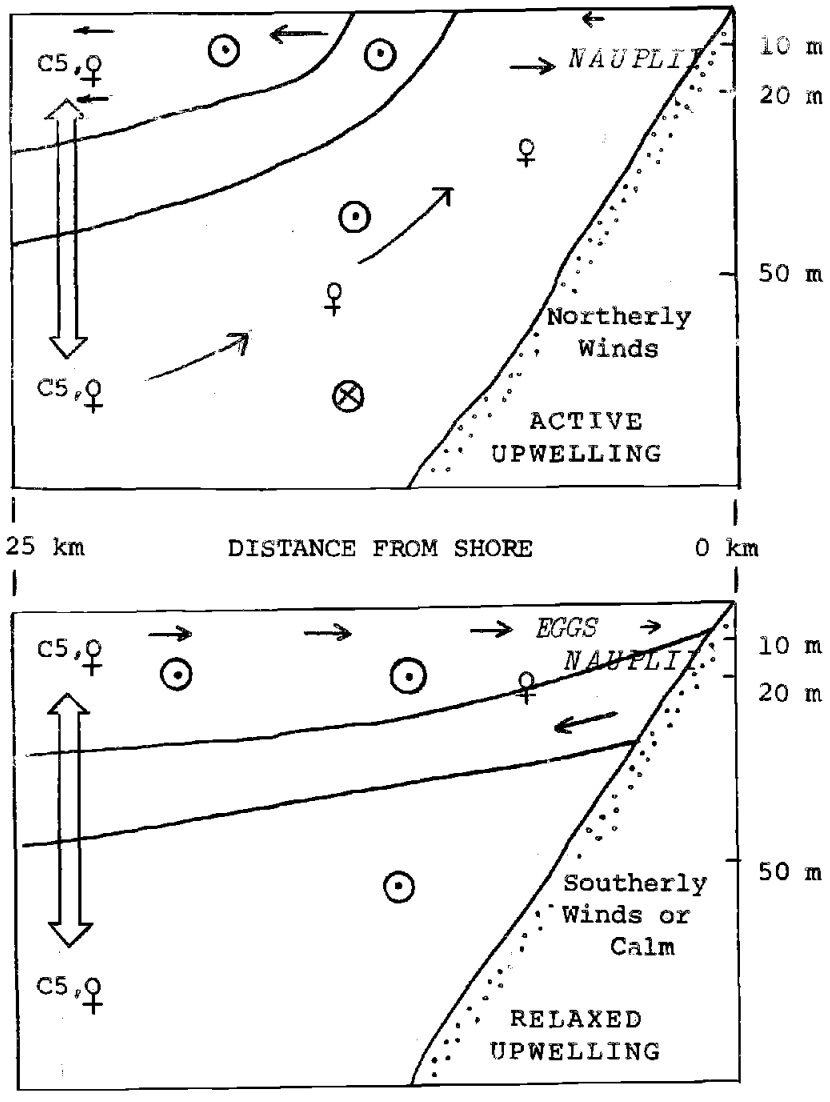


Figure 1. A cross section of the central Oregon coast looking north, illustrating the hypothesized mechanism by which the Calanus marshallae population is retained in the Oregon upwelling zone. During active upwelling, adults are brought into the nearshore zone where egg laying takes place. Eggs are transported landward. Nauplii develop close to shore. Older copepodites develop at progressive distances seaward. During relaxed upwelling, eggs are laid at maximum rates. Nauplii are shifted seaward and older copepodites returned landward. Diel vertical migration of older copepodites on some nights minimizes offshore and southward advective losses from the population.

flow diverging from the frontal region has a landward component at and below 10 m. Seaward transfer of early copepodite stages can occur if they occupy the seaward-moving surface layers. This seaward transfer may also be initiated during relaxation of upwelling. During such times, Calanus nauplii and early copepodite stages would be mixed seaward because they remain at depths of 10 to 20 m. Farther transport away from the coast would be achieved by older stages because they perform diel vertical migrations on some nights. Residence within the offshore moving surface layer during some fraction of each 24 h day, alternating with residence at depth, could result in a net transfer seaward.

EVALUATING THE HYPOTHESIS. The hypothesis outlines a complex set of events. I think it is a good hypothesis because it explains how the Calanus marshallae population can be retained in the Oregon upwelling system regardless of the state of the upwelling process. The most important facets of the hypothesis are that reproductive individuals are not washed out of the system and that reproduction has a high probability of success whether upwelling is in an active or relaxed state.

To evaluate this hypothesis, two general approaches were taken. First, better field data were needed. In 1977, an extensive sampling program was undertaken. High resolution vertical profiles of Calanus marshallae abundances were obtained at closely spaced stations. Sampling was done weekly during July-August 1977 at stations within 10 miles from shore.

The objectives of this sampling program were as follows:

1. To determine the distribution of all life history stages of Calanus marshallae during the development of the summer generation.
2. To test the generality of the distribution scheme known for the central Oregon coast by sampling along transects off northern Oregon, along the Washington State coast and off Vancouver Island, Canada.
3. To learn whether the Calanus marshallae population is continuous between Washington and Oregon coastal waters despite possible disruption by the Columbia River.

The second approach taken involved laboratory studies on living animals. The life history of Calanus marshallae was investigated from laboratory measurements of development, growth, reproduction and mortality rates. These data were gathered in order to facilitate a dynamic description of how the population could be successful living in an upwelling zone. The laboratory rates are compared to field data to help decide whether the population is growing and reproducing at its maximum potential in the field.

The laboratory program had two general objectives:

1. In order to understand the time scales involved in the seaward transfer of developing copepodites and shoreward transfer of adults, I needed to know the rates of development of each life history stage. If

the age of each stage and the distance it has been transported from shore were both known, one could calculate the average daily offshore transfer rates.

2. In order to understand why eggs are usually laid only at stations 5 km from shore, I needed to acquire a basic knowledge of reproductive biology. Laboratory measurements of egg laying rates at various food concentrations and different temperatures were made. Egg hatching times and egg sinking rates were measured in order to understand why eggs were abundant only at certain depths.

The significance of this work is that it is the first comprehensive study of the distribution of a copepod species in an upwelling system. Binet and Suisse (1975) and Binet (1977) are the only other workers who have proposed mechanisms by which zooplankton are retained in upwelling zones, based on field sampling. My study is the first to explore the coupling between those biological and physical processes which act to control zooplankton abundance. This study will contribute to our general understanding of productivity in upwelling systems because it shows both how individual copepods grow and reproduce and how their behavior keeps them from being advected out of the system.

CHAPTER II. SYSTEMATICS

Five Calanus species occur off Oregon: C. marshallae, C. pacificus, C. plumchrus, C. cristatus, and C. tenuicornis. All are easily separated except the first two, which are easily confused. They were not separated by myself in earlier publications. Peterson and Miller (1977) do not list C. pacificus as occurring off Oregon, but it does appear in a species list shown in Pearcy, Lorz and Peterson (1979). I have since rechecked many of the past samples for which I was responsible and have satisfied myself that even though Calanus pacificus does occur off Oregon, it is not usually a conspicuous member of the continental shelf zooplankton. It was abundant in the nearshore zone in June, November and December 1969, and March through May 1978. It can always be taken in the open ocean beyond the continental shelf off Oregon. Calanus marshallae is generally the dominant Calanus species nearshore.

Calanus marshallae and C. pacificus are distinguishable in the later copepodite stages IV, V and VI (adult) by the shape of the head in lateral view (Figure 2). Calanus marshallae has a more rounded head shape. A so called "frontal gland," as described by Frost (1974), is clearly visible in C. marshallae. The younger copepodites can be differentiated if one has a trained eye, but the differences between the two species are subtle so are not easy to describe. The best criteria for distinguishing the two is probably total length. Calanus pacificus is almost always the shorter of the two species. Total length of the adult female is a fair driterion for differentiating between adults, but some classification errors will result from size overlap. Total length of the adults is compared in Table 1.

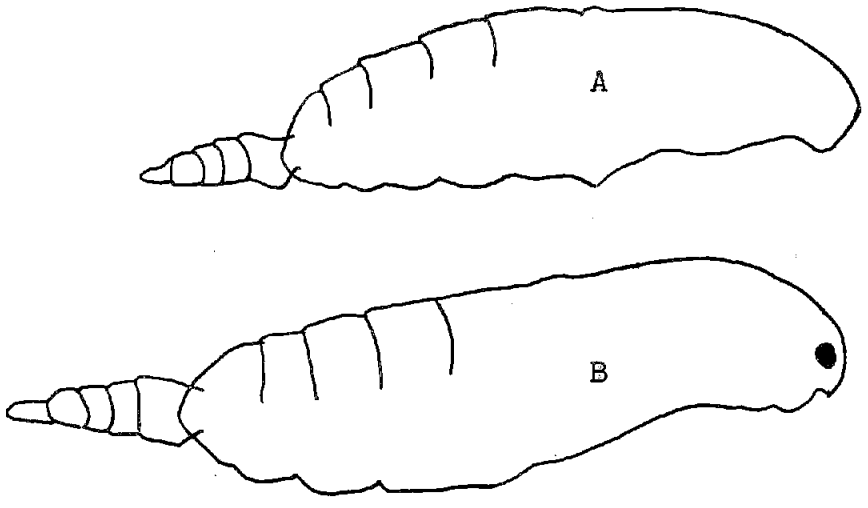


Figure 2. Body shape in lateral view of female Calanus pacificus (A) and Calanus marshallae (B). The head shape of C. pacificus is more pointed whereas that of C. marshallae is more rounded. The dark circle near the anterior end of C. marshallae represents the frontal gland described by Frost (1974).

Table 1. A comparison of total body length of Calanus pacificus and Calanus marshallae females collected from the nearshore zone off the central Oregon coast. Calanus pacificus females are the smaller of the two species.

	Calanus pacificus			Calanus marshallae		
CLASS INTERVAL	FALL 1969	SUMMER 1977	SPRING 1978	SUMMER 1969	SUMMER 1973	SUMMER 1977
2.40 - 2.56 mm	0	0	0	0	0	0
2.60 - 2.76 mm	21	10	0	0	0	1
2.80 - 2.96 mm	41	12	0	0	2	1
3.00 - 3.16 mm	15	37	7	10	162	79
3.20 - 3.36 mm	2	20	12	98	647	400
3.40 - 3.56 mm	0	2	5	88	655	572
3.60 - 3.76 mm	0	0	0	29	182	213
3.80 - 3.96 mm	0	0	0	1	14	29
4.00 - 4.16 mm	0	0	0	0	0	2
number of observations	69	81	24	226	1662	1297

When alive, the two species are easily separated. Calanus pacificus has red pigment distributed along the distal 2/3 of the antennules and along the lateral margins of each thoracic segment. Calanus marshallae has no pigment except for some red coloration along the distal 1/3 of the antennules and occasionally a few tiny, red-pigmented areas along the sternites of the thorax. The females can also be distinguished by the eggs that they lay. Calanus pacificus eggs have two membranes and are 160 to 170 µm in diameter. Calanus marshallae eggs have three membranes and are 220 µm in diameter. The eggs of C. pacificus are rose-tinted whereas those of C. marshallae have have no pigment. The naupliar stages of C. pacificus are pigmented when alive. The tips of all three pair of appendages are bright red. The nauplii of C. marshallae have only some red color within the body cavity. This is probably an oil droplet.

CHAPTER III. DISTRIBUTION AND ABUNDANCE

INTRODUCTION

Data showing where an organism lives and reproduces and under what conditions it is abundant allow static descriptions of its ecology and life history. This knowledge is fundamental to the formulation of testable hypotheses about the dynamic aspects of an organism's life history, such as rates of growth and reproduction. Good field data give an indication of how a population lives in a particular environment and may suggest what adaptations have evolved which help individuals to cope with their environment.

This chapter briefly describes the environment of Calanus marshallae. The seasonal cycle of total zooplankton abundance is compared to the seasonal cycle of Calanus marshallae abundance. The bulk of the chapter deals with ecological zonation. It is here that the data on distribution and abundance of Calanus marshallae life history stages are presented.

THE PHYSICAL ENVIRONMENT. The environment of Calanus marshallae is the epipelagic zone of the north Pacific Ocean, Bering and Beaufort Seas. It is found in coastal waters from the Beaufort Sea off northern Alaska south to at least the central Oregon coast. It is also known from the open ocean in the subarctic Pacific and the Puget Sound (Frost, 1974). The population discussed in this dissertation is abundant only in the neritic zone over the continental shelf within the upper 100 m of the water column. Abundances are greatest within the upper 20 m and within 20 km of shore.

Various aspects of the physical and biological environment of which Calanus marshallae is a part, have been published (Peterson and Miller, 1975, 1976, 1977; Peterson, Miller and Hutchinson, 1979, and references therein). Therefore, a detailed discussion is not given here. A brief summary follows. Winds along the Oregon coast are monsoonal. Southwesterly winds prevail during the winter rainy season from October through March, and northwesterly winds during the dry summer months of April or May through September. Circulation of shelf waters is influenced by the winds. Winter winds produce downwelling: warm offshore surface water is brought onshore. Northerly winds in summer cause coastal upwelling which is the opposite of downwelling: warm surface water is driven offshore and replaced by cool water from depth. The mean net water flow over the shelf is southward in summer and northward in winter. As a result of winter downwelling and summer upwelling, shelf waters change little in temperature during the year. In a usual year, temperatures are cooler in summer than winter. The annual range is 8 to 12°C, with occasional excursions to 15°C for brief periods during some summers and in the autumn. Since the temperature range is so small, it probably has very little influence on the physiological processes of Calanus marshallae.

THE BIOLOGICAL ENVIRONMENT. Calanus marshallae is an herbivorous copepod which feeds by filtering phytoplankton from the water. Phytoplankton are abundant within the upper 10-15 m of the water column from January through October. A subsurface maximum in phytoplankton abundance is sometimes seen during periods of extremely relaxed upwelling. The assemblage is always dominated by diatoms.

A modest winter bloom can be initiated by a sudden increase in solar radiation. Clear skies prevail for a one-two week period in January or February of most years. During this interval, the sea surface warms, the water column becomes weakly stratified and a phytoplankton bloom develops. The bloom ceases as soon as the usual 100% cloud cover returns to the region. Other blooms occur as additional periods of clear skies appear.

A large spring bloom begins in April or May. In a year of good upwelling, when favorable winds begin as early as April, this spring bloom will persist through October because plant nutrients are frequently replenished by the upwelling process. During poor upwelling years, that is, years in which significant upwelling does not begin until July, the spring bloom may last only a few weeks.

The Calanus marshallae population shares its environment with at least 100 other zooplankton taxa. It shares dominance with four other copepod species: Pseudocalanus sp., Acartia longiremis, A. clausii, and Centropages abdominalis. Predators include the ctenophore Pleurobrachia bachei, the chaetognath Sagitta elegans, and zooplanktivorous smelt such as the white-bait smelt Allosmerus elongatus and the surf smelt Hypomesus pretiosus.

METHODS

Three data sets are discussed in this dissertation. The first is a three-year time series of samples taken bi-weekly between 22 June 1969 and 5 August 1972. A pair of 20 cm diameter Bongo nets fitted with nets of 0.24 mm mesh were used. TSK flowmeters were mounted off-center in the net mouths. Stations were 1, 3, 5, and 10 miles from shore along the Newport Hydrographic (NH) transect line. It is located one mile north of Newport, Oregon, at 44°40' N latitude. See Peterson and Miller (1975, 1976) for additional details.

The other two data sets were taken to look at vertical distribution along transects. Samples were collected on 29 July and 14, 15 and 16 August 1973 from discrete depths with 12.7 cm Clarke-Bumpus samplers fitted with 0.12 mm mesh nets. Volumes filtered were estimated from calibrated flow meters mounted inside the net mouths. Samples were collected on 11 and 12 September 1973 using a model 10490 Jabsco impellor pump and a 50 m length of 2 in inside diameter suction hose.

The third data set is a more extensive series of vertically stratified samples. Water was pumped with a submersible sewage sump pump through 4 inch diameter collapsible discharge hose. Water was filtered on deck through 64 µm mesh nets. A transect at 45° N latitude (Sunflower line) was sampled on 8-9 July, 15-16 July, 21 July, 29 July, 3-4 August and 13 August 1977. One long cruise was taken between 21-29 July to sample transects off Tillamook Head, Oregon (22 July), the mouth of the Columbia River (23 July), Cape Shoalwater, Willapa Bay, Washington (24 July), Copalis Beach, Washington (25 July), Cape Flattery, Washington (26 July) and Nootka Sound, Vancouver Island, Canada (27 July).

Standard stations were 1, 3, 5, 7, and 10 miles from shore. Many transects included stations to 20 miles from shore if time permitted. Standard sampling depths were 1, 5, 10, 15, 20, 30, 50, 70, and 90 m, water depth and wire angle permitting. One station was sampled at night on many cruises.

The usual hydrographic observations were made. Water samples for salinity determination were taken at all depths and stations. Salinity was later measured in the shore laboratory with the aid of a Bissett-Berman Salinometer. Temperature was measured at sea from a bucket at the pump outflow. Density was calculated using standard formulas.

Phytoplankton biomass was measured by fluorometry, using a Turner Designs Fluorometer fitted with a flow-through cell. Water samples for plant pigment analyses were collected from most depths, filtered through 0.45 µm membrane filters, stored in a dessicator and frozen. This material was later processed ashore using standard techniques (Parson and Strickland, 1972).

In the laboratory, preserved zooplankton samples were poured into a graduated cylinder and allowed to settle for several hours. After reading the settled volume, water was added or decanted off to make a diluted volume of five times the settled volume. Aliquots for counting were taken with a 1 ml piston pipette. Animals were enumerated with the aid of a binocular dissecting microscope. Three aliquots were drawn from each sample. Taxa were counted in the first and successive aliquots until 50 animals were enumerated in each category. All taxa were counted but in this dissertation, I discuss only the Calanus marshallae enumeration data. Counts were multiplied by appropriate

factors to arrive at a number of individuals per cubic meter of water filtered.

RESULTS

ANNUAL CYCLE OF ZOOPLANKTON ABUNDANCE. The annual cycle of zooplankton species composition and abundance is known from the three-year time series of samples collected at stations 1, 3, 5, and 10 miles off Newport between June 1969 and August 1972. Results of this study are published (Peterson and Miller, 1975, 1976, 1977), and are only briefly summarized below.

Zooplankton species composition varies seasonally. Some species are found in coastal waters only during the summer upwelling season while others only occur during the winter. This alternation of species occurrence results from the annual cycle of nearshore circulation. During summer months when water flow is southward, species with northern affinities occur off Oregon. During winter when flow is northward and onshore, species from the south and offshore are brought into the coastal zone. A few other species are indigenous, occurring all year round.

The annual cycle of zooplankton abundance is shown in Figure 3. Abundances are high during the summer upwelling season, especially between June and September. Peak abundances tend to occur in July and August. Abundances are low during the winter monsoon period, from November through April. During both winter and summer, densities are highest at stations 1 and 3 miles from shore.

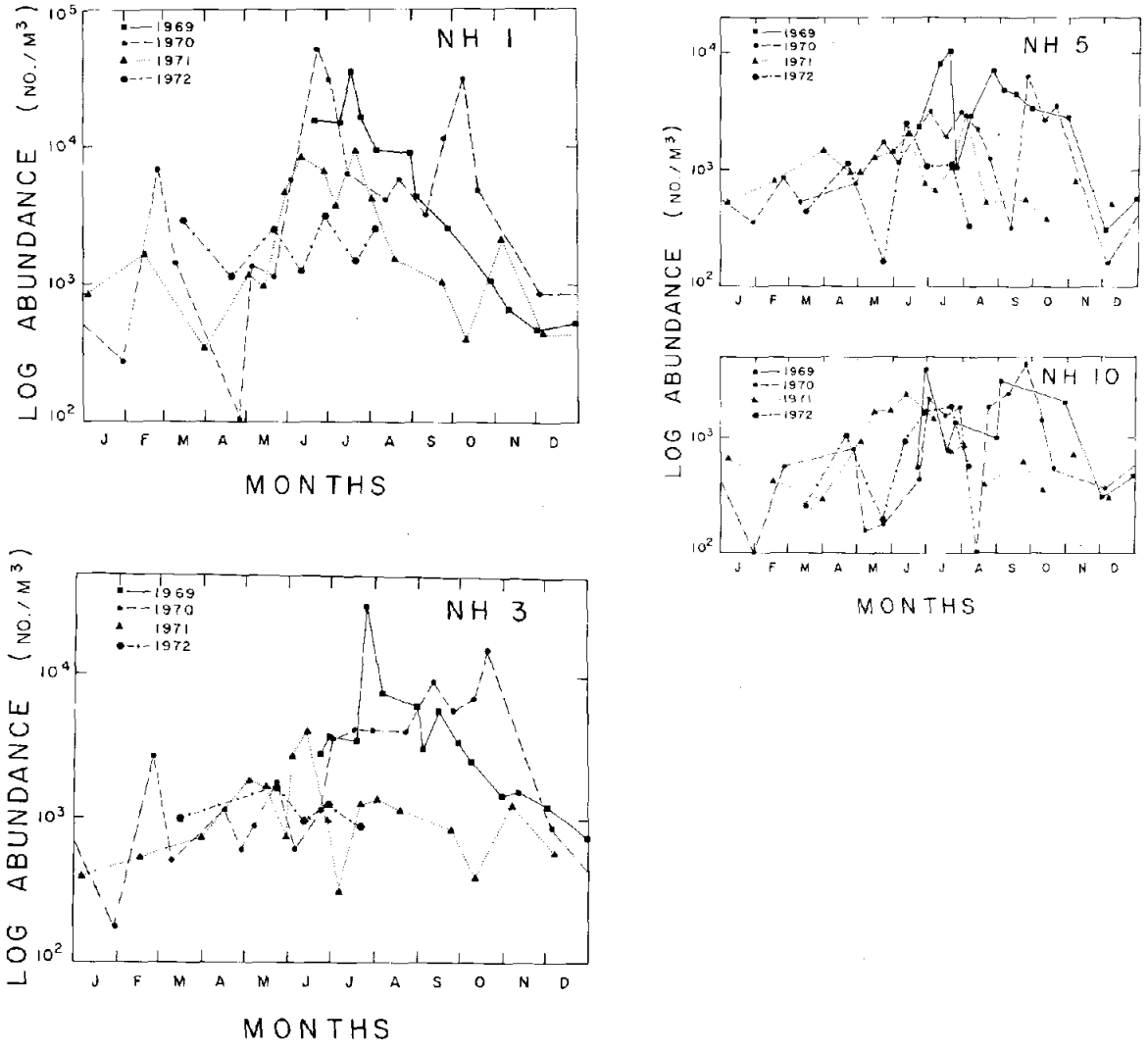


Figure 3. The annual cycle of total zooplankton abundance at stations 1,3,5, and 10 miles off Newport, Oregon during the indicated years. Abundances peak in late-summer of all years.

It is safe to conclude that herbivorous zooplankton are abundant over the continental shelf during the upwelling season because phytoplankton are abundant. The autumn decline is coincident with a drop in phytoplankton abundance. As the winter monsoon begins, intense cyclonic storms lash the coast, the entire water column over the shelf becomes well mixed and solar radiation is at a minimum. These are unfavorable conditions for rapid phytoplankton growth.

The pronounced seasonal period of the abundance cycle comes from increases and decreases in biomass of six indigenous copepod species. These are, in decreasing order of mean rank of abundance in the summer samples: Pseudocalanus sp., Acartia longiremis, Calanus marshallae, Acartia clausii, Oithona similis, and Centropages abdominalis.

If the total zooplankton biomass were partitioned into relative species contribution, most of the biomass would be made up of individuals of Pseudocalanus sp. and Calanus marshallae. This is because Pseudocalanus is the most abundant copepod and Calanus the largest in body size. This can be seen in the following: the mean relative abundance (percent of total zooplankton numbers) averaged over the summer months at the four stations (1, 3, 5, and 10 miles) were Pseudocalanus, 46.7% of the catch; Acartia longiremis, 20.7%; Acartia clausii, 11.4%; Calanus marshallae, 9.0%. The approximate lengths and dry weights of the adult females were Pseudocalanus, 1.4 - 1.7 mm and 15-20 µg; Acartia longiremis, 1.2 - 1.4 mm, 5-10 µg; Acartia clausii, 1.0 - 1.3 mm, 5-10 µg; and Calanus marshallae, 3.2 - 3.7 mm and 200-300 µg.

ANNUAL CYCLE OF CALANUS ABUNDANCE. The abundance of Calanus

marshallae copepodites I through VI at stations 3 and 10 miles from shore is shown in Figures 4 and 5. At both stations, Calanus were not present from November through December or January. This is a pattern typical of most Calanus populations living in temperate neritic regions, such as Calanus Finmarchicus in the Clyde Sea, Scotland (Nichols, 1933), off Norway (Wiborg, 1954) and in the Gulf of Maine, USA (Bigelow, 1924) for example. It is generally believed that these populations overwinter in the fifth copepodite stage at depths between 150-300 meters in waters beyond the continental shelf. I hypothesize that Oregon Calanus behave in the same way. The tropical neritic copepod, Calinoides carinatus is another member of the Family Calanidae that overwinters. It is an ecological analogue of Calanus marshallae, and is a dominant member of the northwest Africa upwelling system. Late copepodites move offshore and to depths of 500 m during those months when upwelling is not taking place (Binet and Suisse, 1975). It has been shown by Hirche (1978) that an overwintering population of Calanus sp. from a Swedish fjord are in a true diapause state. He found that Calanus sp. brought into the laboratory during the winter floated motionless with their antennules held against their body, would not feed, and furthermore, had only inactive digestive enzymes in their gut walls. These observations should be tested for overwintering Calanus marshallae stage V copepodites.

During the remainder of the year at the 3-mile station, Calanus marshallae copepodites contribute little to the overall zooplankton numerical abundance. There are few periods when C. marshallae are very numerous. During both 1970 and 1971, numbers averaged about 100 individ-

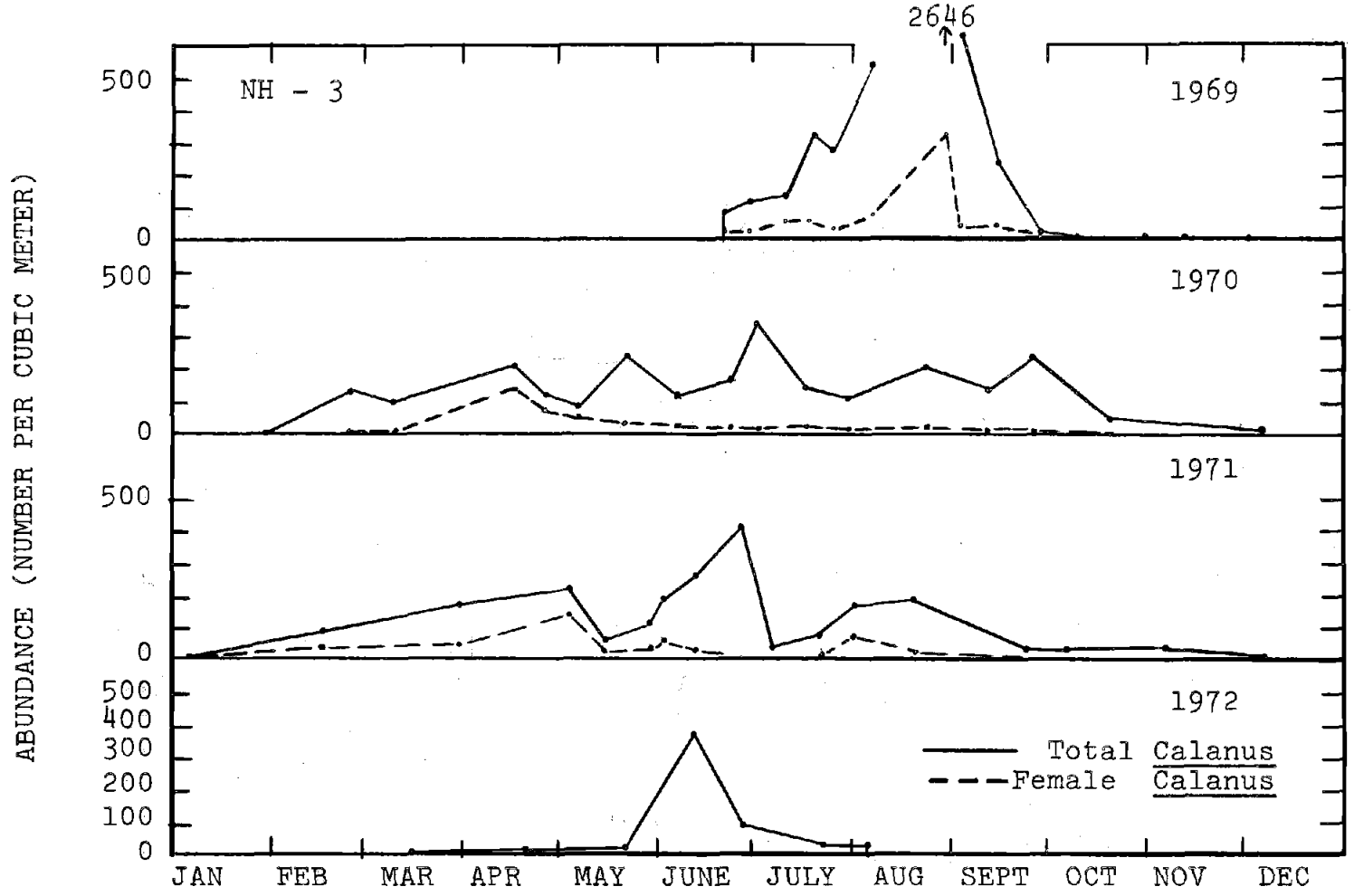


Figure 4. Abundance of Calanus marshallae at a station 3 miles off Newport, Oregon between 22 June 1969 and 5 August 1972.

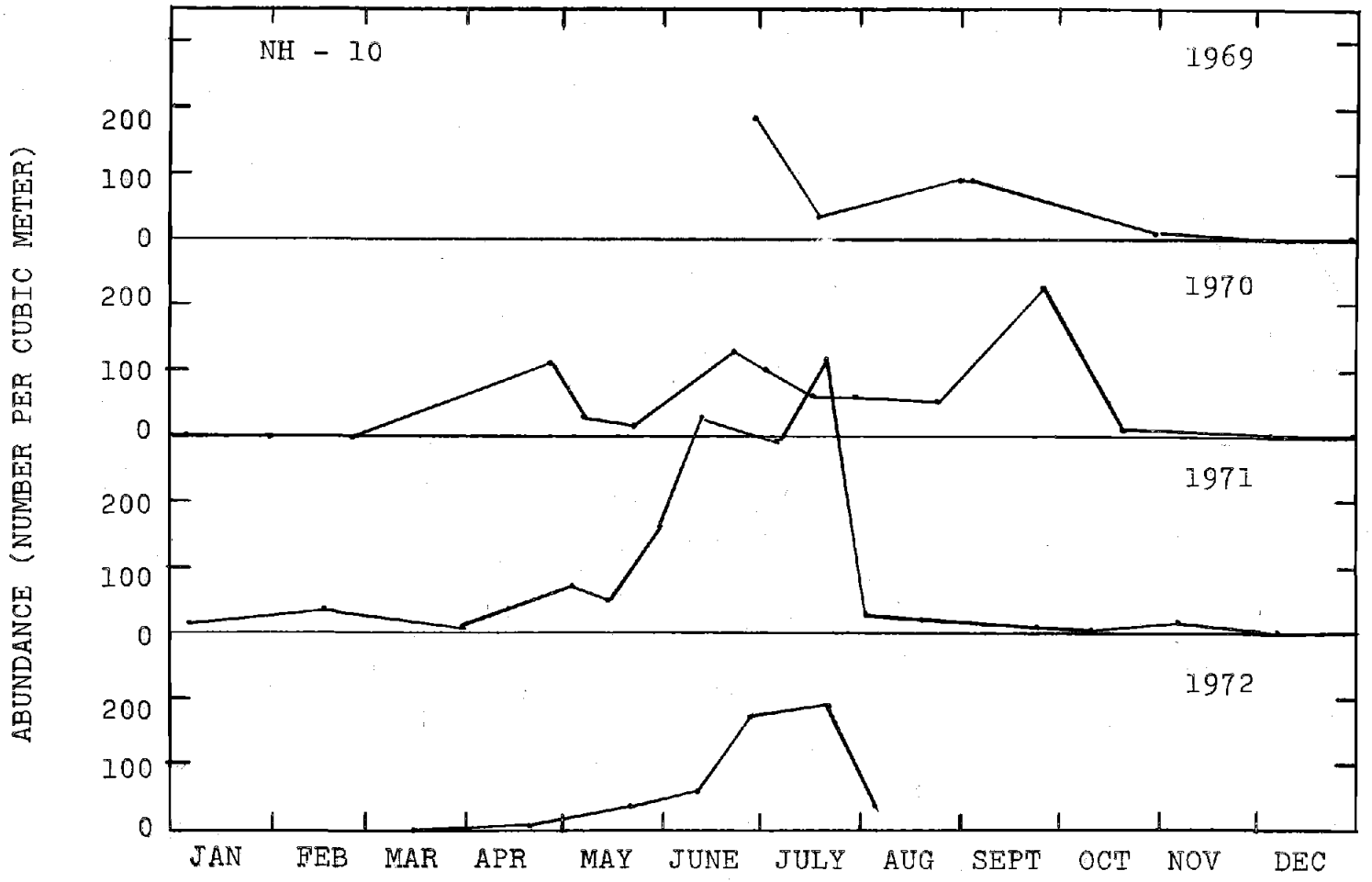


Figure 5. Abundance of Calanus marshallae at a station 10 miles off Newport, Oregon between 22 June 1969 and 5 August 1972.

uals m^{-3} from February through September. By contrast, in August 1969, they reached numbers greater than 500 m^{-3}. Calanus marshallae was virtually absent from shelf waters during all of 1972.

The pattern at the 10-mile station is different. At this mid-shelf location, numbers do not begin to increase until April. Abundance peaks were seen in June and July of all four years, with a smaller peak in September of 1969 and 1970.

The abundances of adult females at the 3-mile station are also shown on Figure 4. They were most numerous in April-May of 1970 and 1971. At the 10-mile station, females are much less abundant. Averaged overall samples collected in April-September, abundances at 10 miles were 9.7 females m^{-3} as compared to 39.0 m^{-3} at the 3-mile station. Males had a regular pattern of occurrence, with the exception of the 1969 data. They occurred from April-July 1970, February-June 1971, May-June 1972, but from July through September 1969.

ECOLOGICAL ZONATION. The annual cycle of Calanus marshallae was not surprising because it was the same as that of the sibling species Calanus finmarchicus from the neritic north Atlantic and North Sea (Marshall and Orr, 1955, p. 67). A surprising observation in the 1969-1972 time series was the onshore-offshore zonation of life history stages. Eggs, nauplii and early copepodite stages of Calanus marshallae tended to be found nearshore, and later copepodite stages offshore. The trend is shown in Table 2. Eggs, nauplii and copepodite I and II were most abundant at stations 1 and 3 miles from shore. Stage III copepodites were abundant at stations 1, 3 and 5 miles. Stage IV were most abundant at stations 3 and 5, and stage V copepodites were most abundant

Table 2. Abundance (number per cubic meter) of Calanus marshallae eggs, nauplii, and copepodites at four distances offshore along the Newport section. The tabled values are averages for 23 upwelling season dates when samples were obtained at each of the four stations on each date. Egg and naupliar abundances are low compared to the 1973 and 1977 data because the net mesh used was too large to quantitatively retain these taxa.

STAGE	2 km	5 km	9 km	18 km
Eggs	21.5	16.5	14.1	10.1
Nauplii	200.9	59.2	15.8	17.7
Copepodite I	24.5	14.0	5.6	4.4
Copepodite II	13.0	9.7	6.7	8.0
Copepodite III	15.6	19.0	17.7	10.4
Copepodite IV	13.8	46.3	50.9	22.2
Copepodite V	3.7	32.8	39.4	36.3
Males	0.1	1.8	3.1	1.5
Females	4.8	33.3	22.9	8.4

at 3, 5, and 10 miles from shore. Adults were abundant only at 3 and 5 miles. As noted by Peterson and Miller (1976), "This observed distribution of stages is probably linked to coastal water circulation patterns. The vertical distribution of the stages must be known before we can understand these observations."

We therefore set out to further investigate this zonation pattern. Vertical distribution of all zooplankton taxa was first studied during the summer of 1973. The data on Calanus marshallae distributions are shown in Figures 6 through 9. It is seen that stage V copepodites were abundant in the surface layer, 20 km from shore. Females were usually most abundant nearshore between 5 and 10 km, but were also found offshore with the stage V copepodites. Eggs were typically most abundant at a depth of 10 m between 3 and 5 miles from shore. They were also found closer to shore and offshore of five miles but abundances in these places were an order of magnitude less. Nauplii were most abundant closer to shore than the eggs, between depths of 10 and 20 m. The fact that stage V copepodites are found predominantly offshore, while the greatest density of eggs and nauplii is found close to shore suggests that for the bulk of the population there is some cycle of transfer both seaward and landward during development and growth. Adults are somehow transported landward where egg laying takes place. Ultimately, their offspring are transported seaward.

Even though this result was suggested from the 1969-1972 data set, the details were unclear. The 1973 data set added much new information but was still inadequate because (1) not enough depths were sampled, (2) there were too many missing data points as a result of malfunction

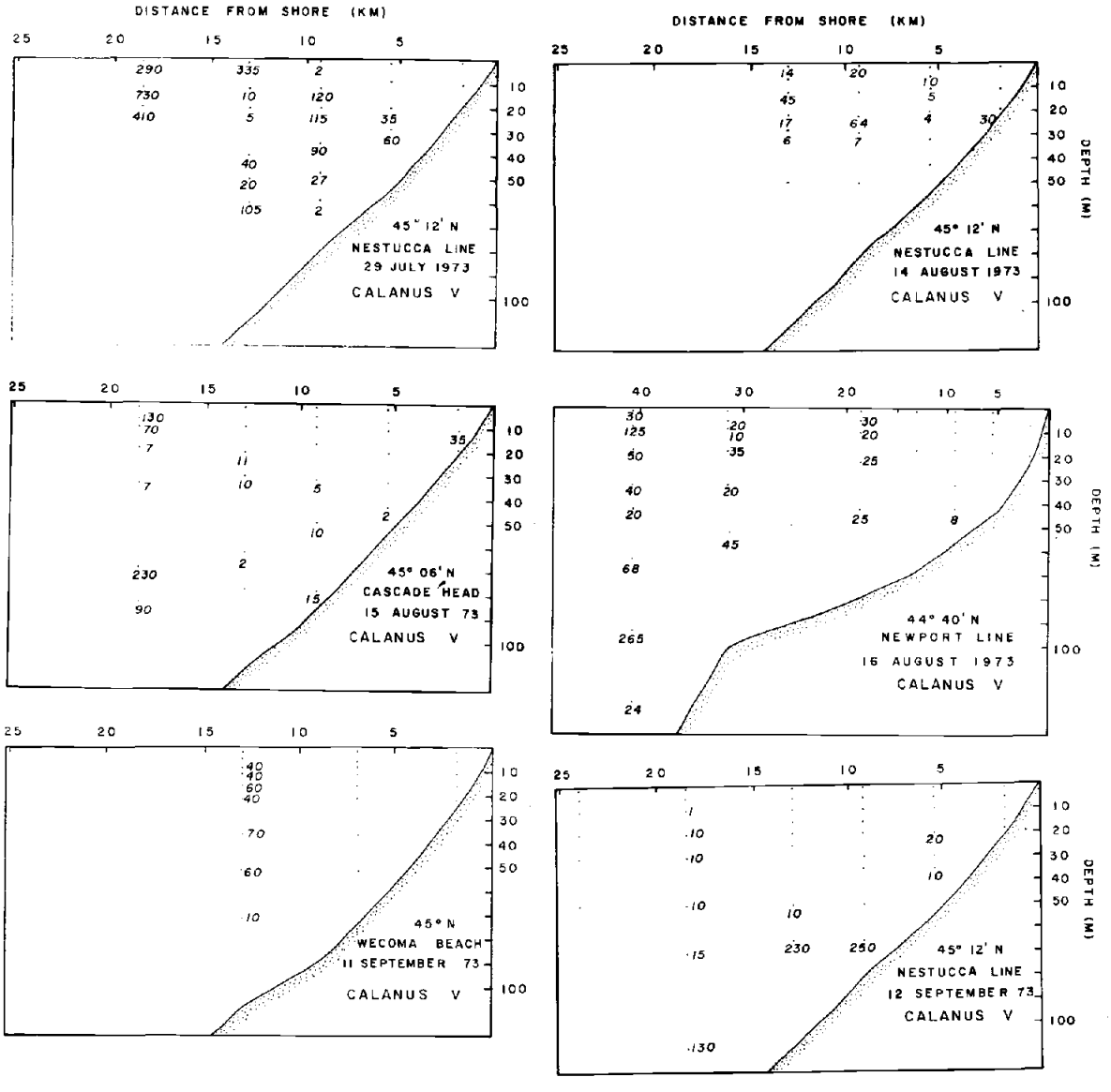


Figure 6. Distribution and abundance (number per cubic meter) of Calanus marshallae stage V copepodites during the 1973 upwelling season. The dots are sampling points.

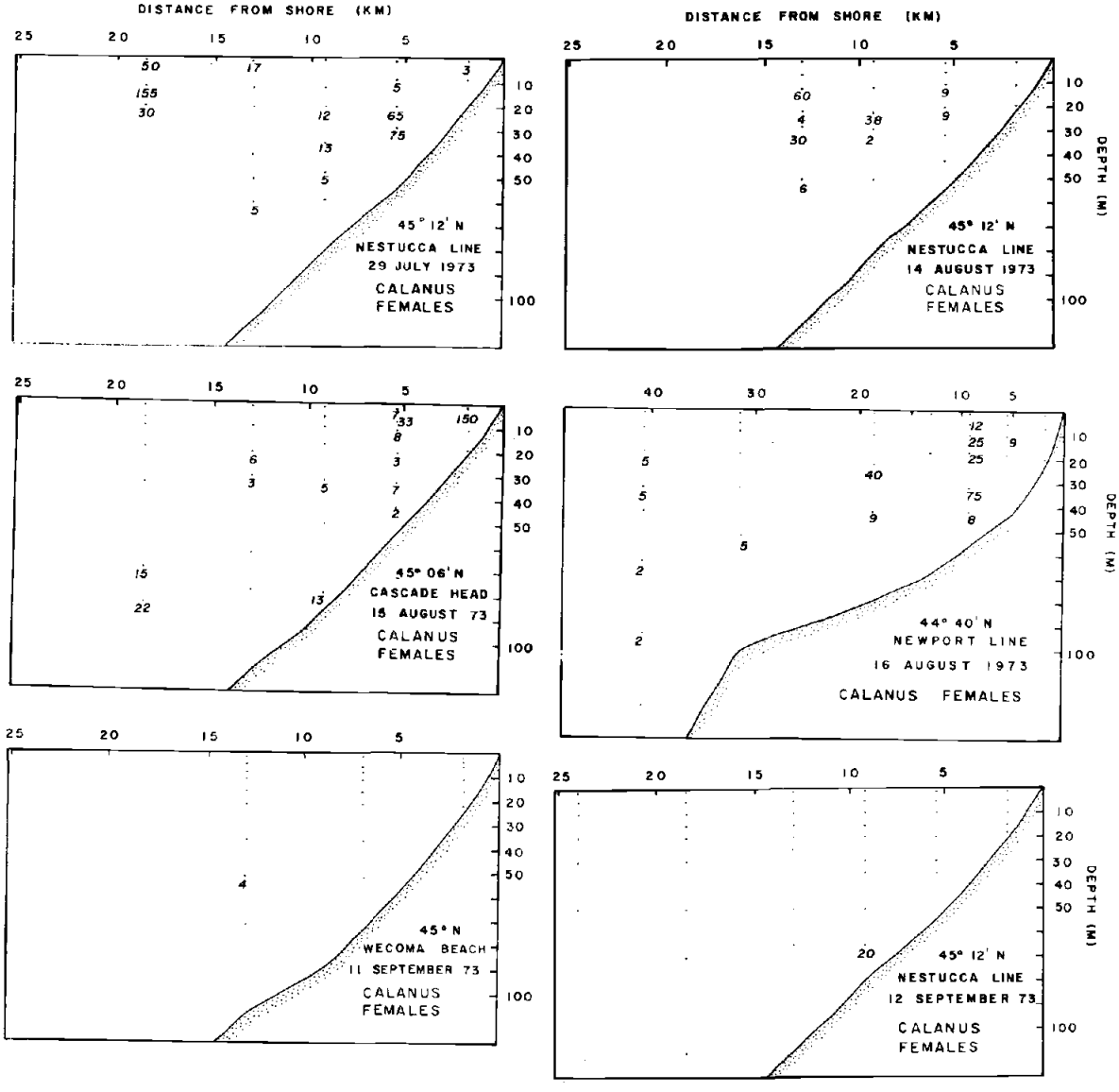


Figure 7. Distribution and abundance (number per cubic meter) of female Calanus marshallae during the 1973 upwelling season.

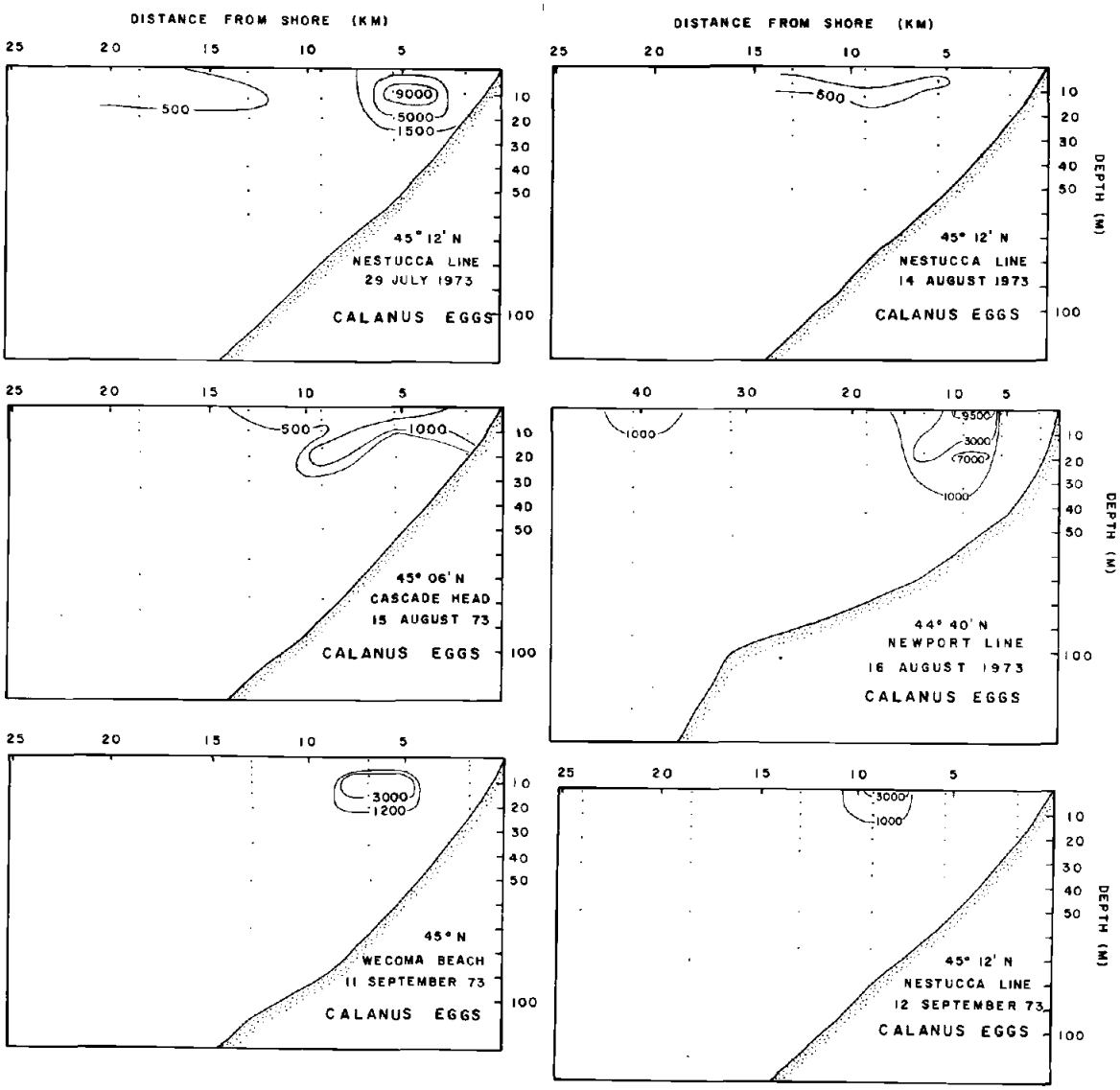


Figure 8. Distribution and abundance (number per cubic meter) of Calanus marshallae eggs during the 1973 upwelling season.

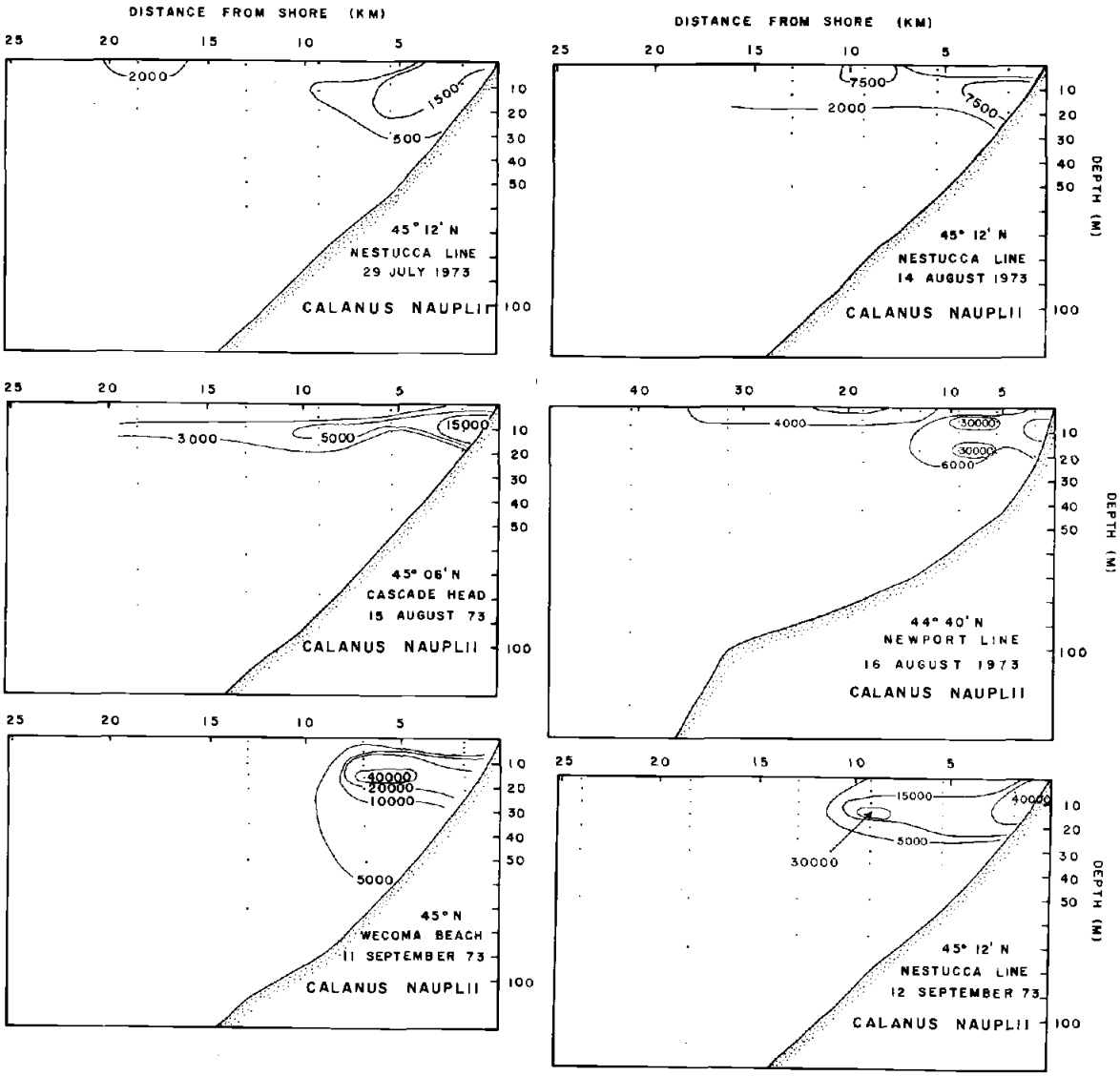


Figure 9. Distribution and abundance (number per cubic meter) of Calanus marshallae nauplii during the 1973 upwelling season.

of the opening-closing nets, (3) only three cruises were made, and (4) distributional data for younger copepodites were lacking because not all of them were present at the times when we sampled. Therefore, we set out to collect an adequate number of samples during the summer of 1977.

The July-August 1977 data from the Sunflower transect line (45° N latitude) are shown in Figures 10-19. Our first cruise on 8 July was a test cruise, and did not produce a complete transect. The data upon which the contour lines are based, are tabled in Appendix I.

The state of the upwelling process is defined by the position of the permanent pycnocline. When both the 25.5 and 26.0 sigma-t isolines intersect the sea surface, upwelling is active. If only the 25.5 line intersects, or if neither line intersects the sea surface, upwelling is relaxed. Active upwelling was seen on 8 July and 4 August. At all other times the system was in a relaxed state. These were not the conditions for which we had hoped, but nature does not always cooperate.

The distribution of phytoplankton biomass was the same as seen on past cruises. The maximum amounts of chlorophyll were in the upper 10 m and within five miles from shore. The maximum was shifted to 7-10 miles during the active upwelling event on 4 August. The maximum remained at this distance on 13 August. The system was just beginning to relax at this time.

Peak abundances of eggs ranged from 0 to 50 per liter. The zero value came about because no eggs were seen on the 13 August cruise. The center of abundance was 1-5 miles from shore on 15, 21, 29 July and 5-7 miles on 4 August. Egg abundance centers corresponded with zones of

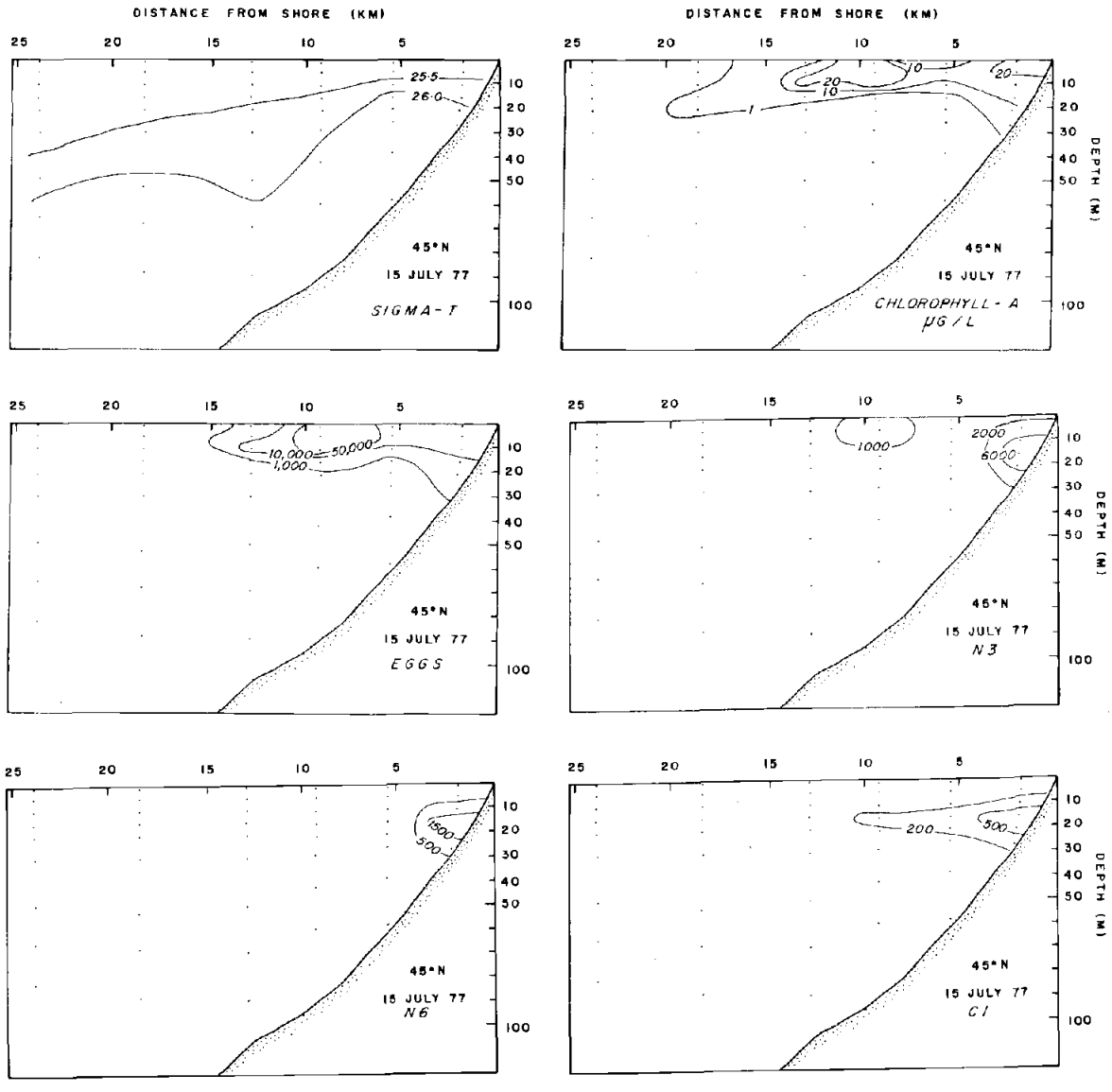


Figure 10. Distribution of density (sigma-t), chlorophyll-a, and Calanus marshallae eggs, N3, N6 and C1 during the 15 July 1977 transect at 45°N latitude. Animal abundances are number per cubic meter.

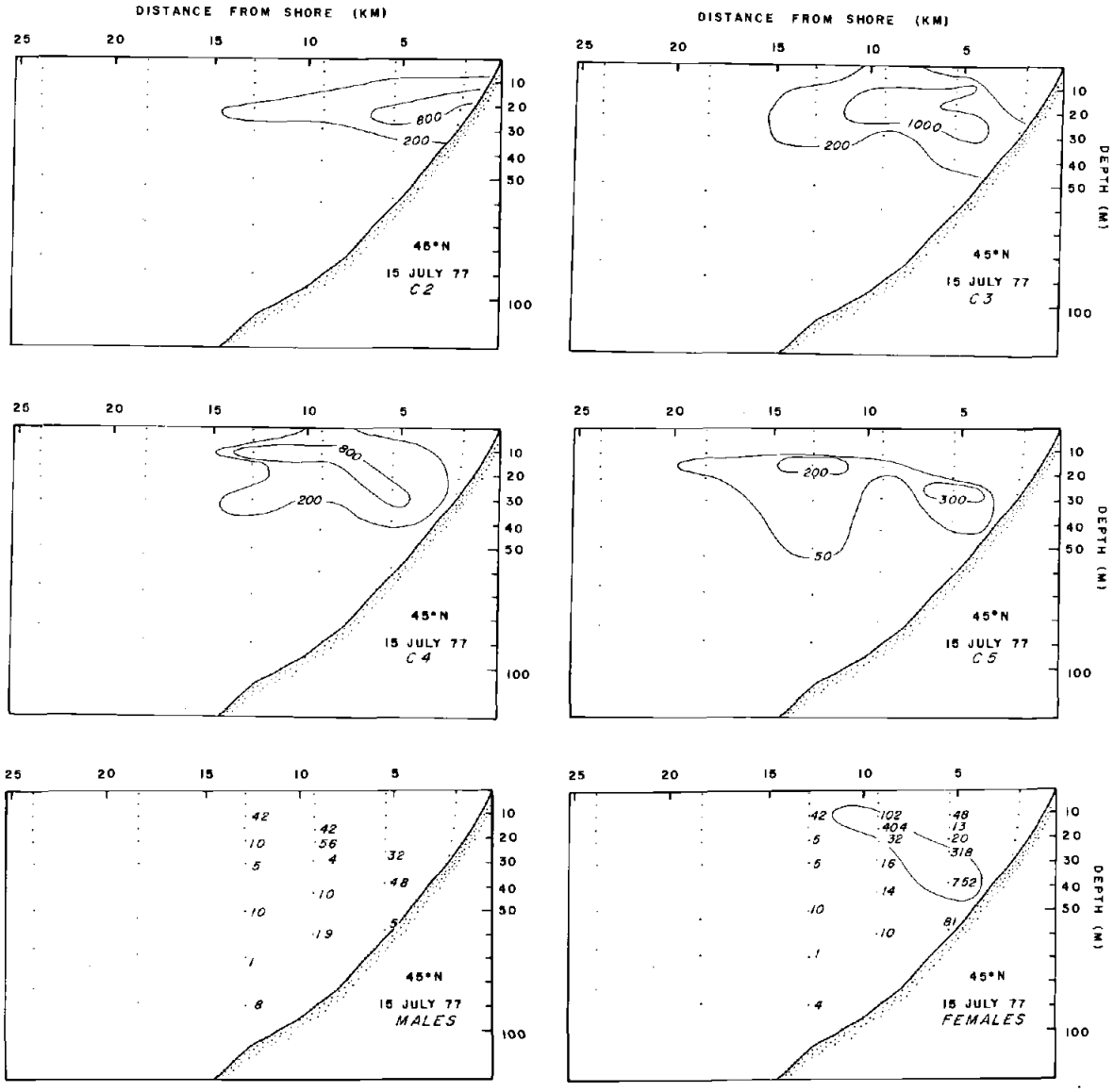


Figure 11. Distribution of C2, C3, C4, C5, male and female Calanus marshallae during the 15 July 1977 transect. Abundances are number per cubic meter.

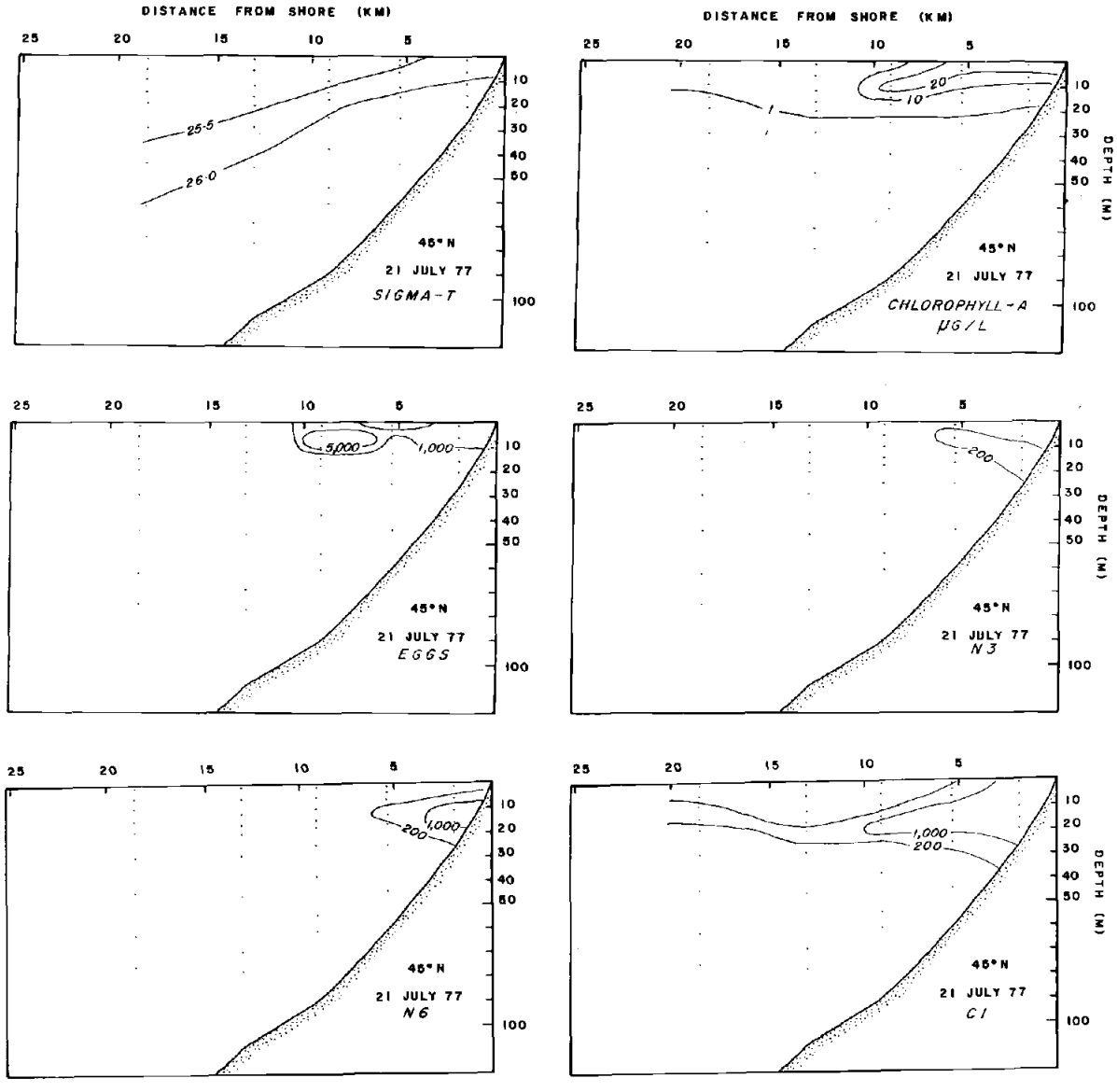


Figure 12. Distribution of density (sigma-t), chlorophyll-a, and Calanus marshallae eggs, N3, N6 and C1 during 21 July 1977. Animal abundances are number per cubic meter.

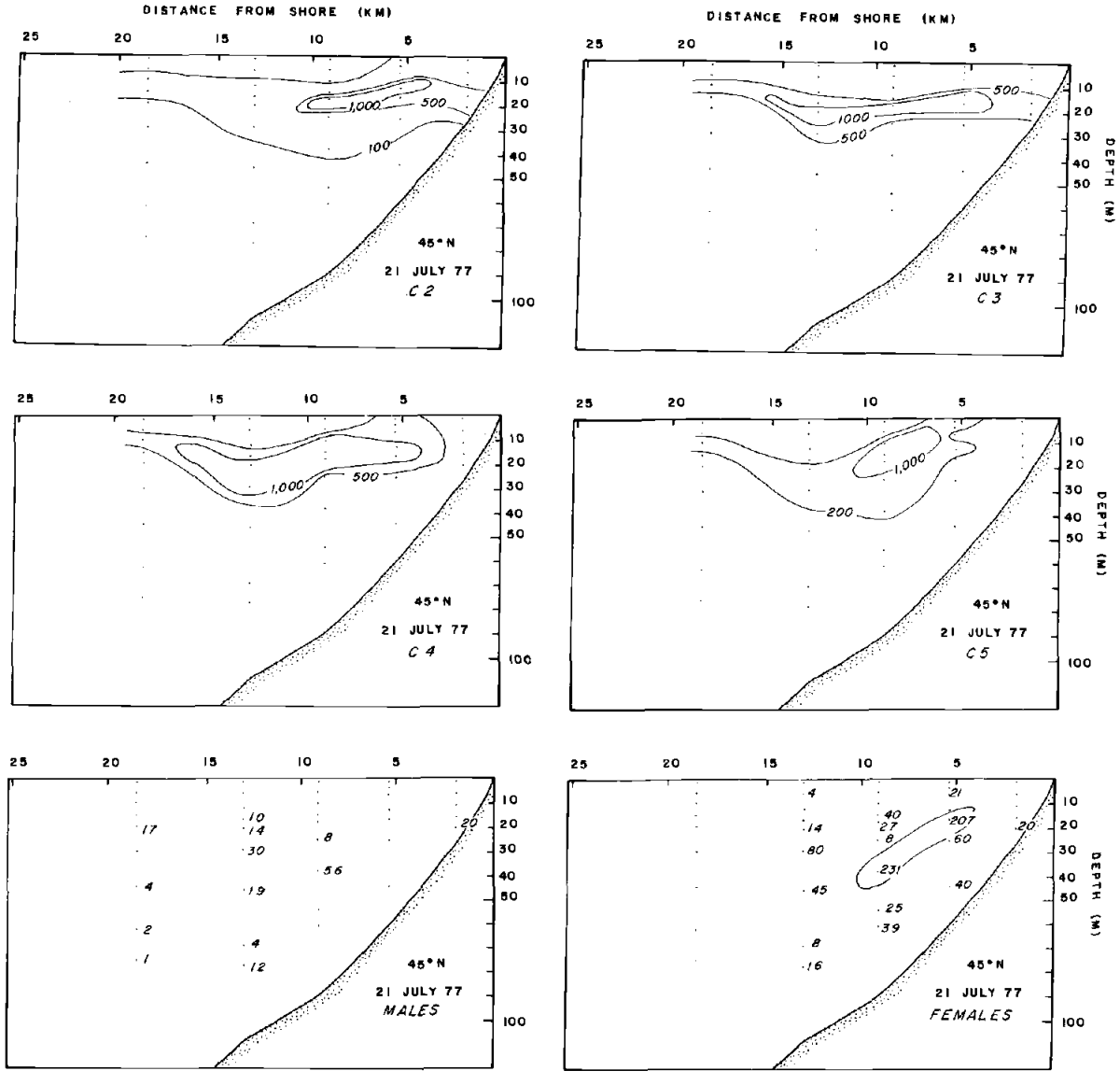


Figure 13. Distribution of C2, C3, C4, C5, male and female Calanus marshallae during 21 July 1977. Abundances are number per cubic meter.

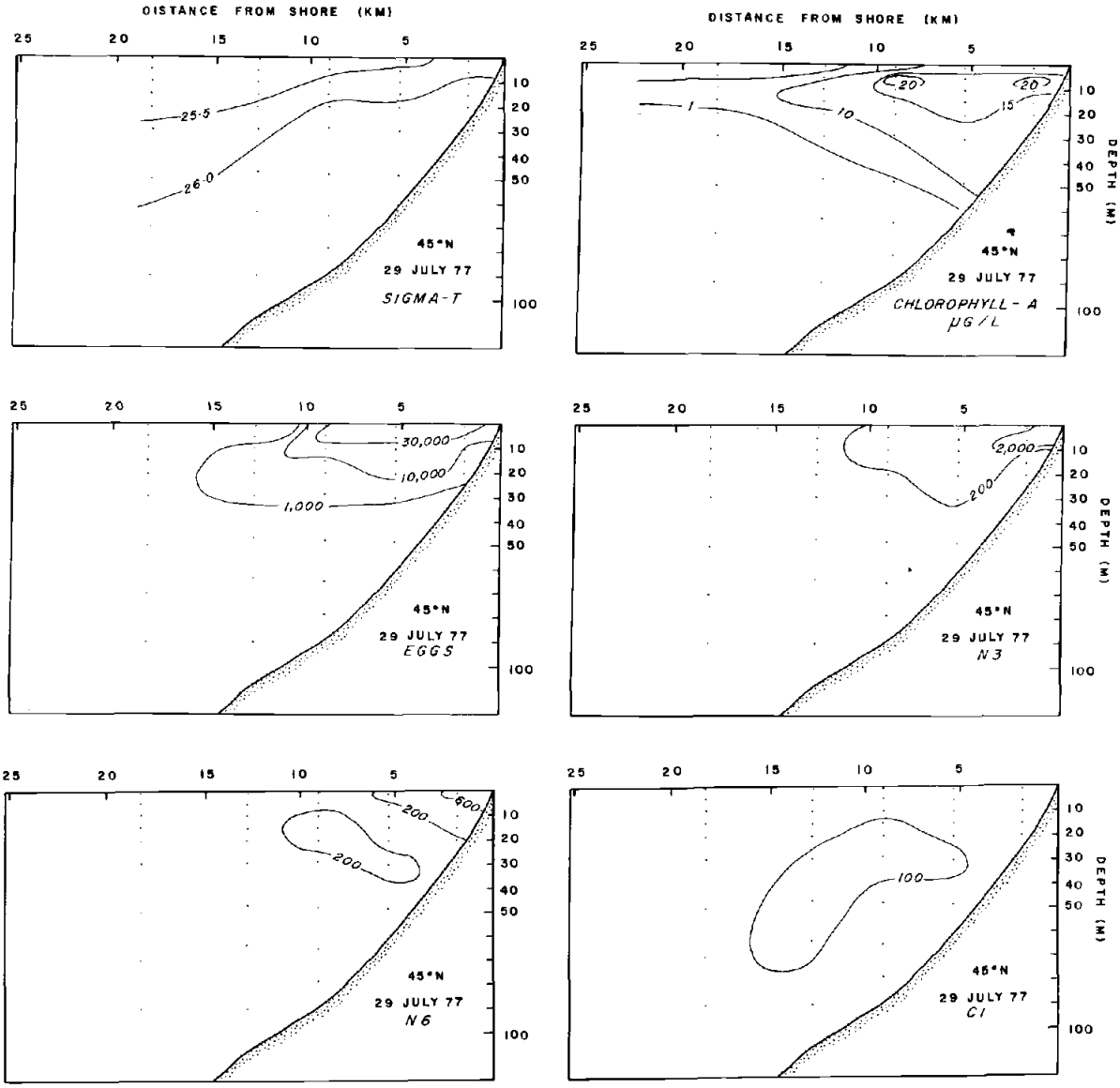


Figure 14. Distribution of density (sigma-t), chlorophyll-a, and Calanus marshallae eggs, N3, N6 and C1 during 29 July 1977. Animal abundances are number per cubic meter.

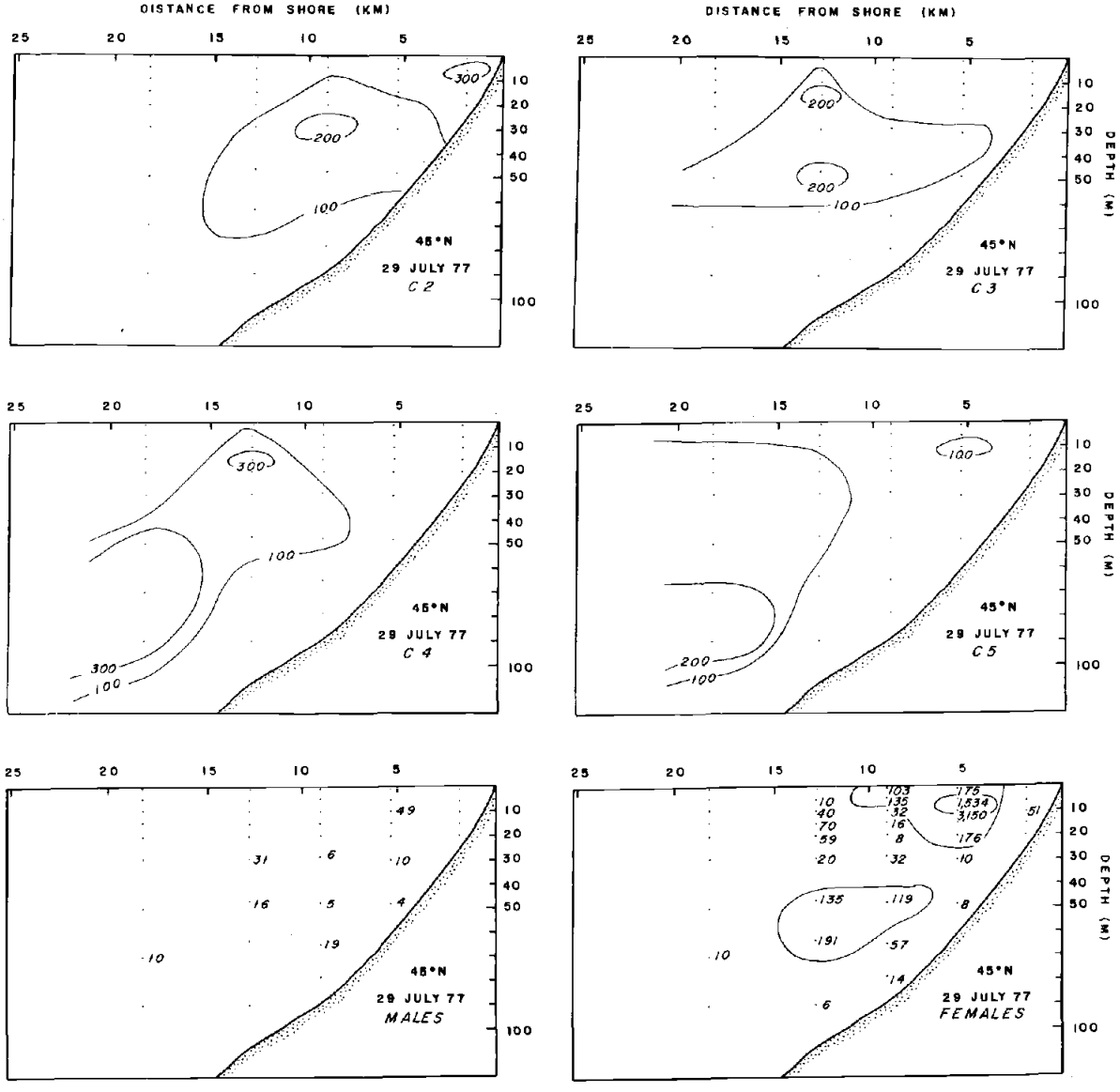


Figure 15. Distribution of C2, C3, C4, C5, male and female Calanus marshallae during 29 July 1977. Abundances are number per cubic meter.

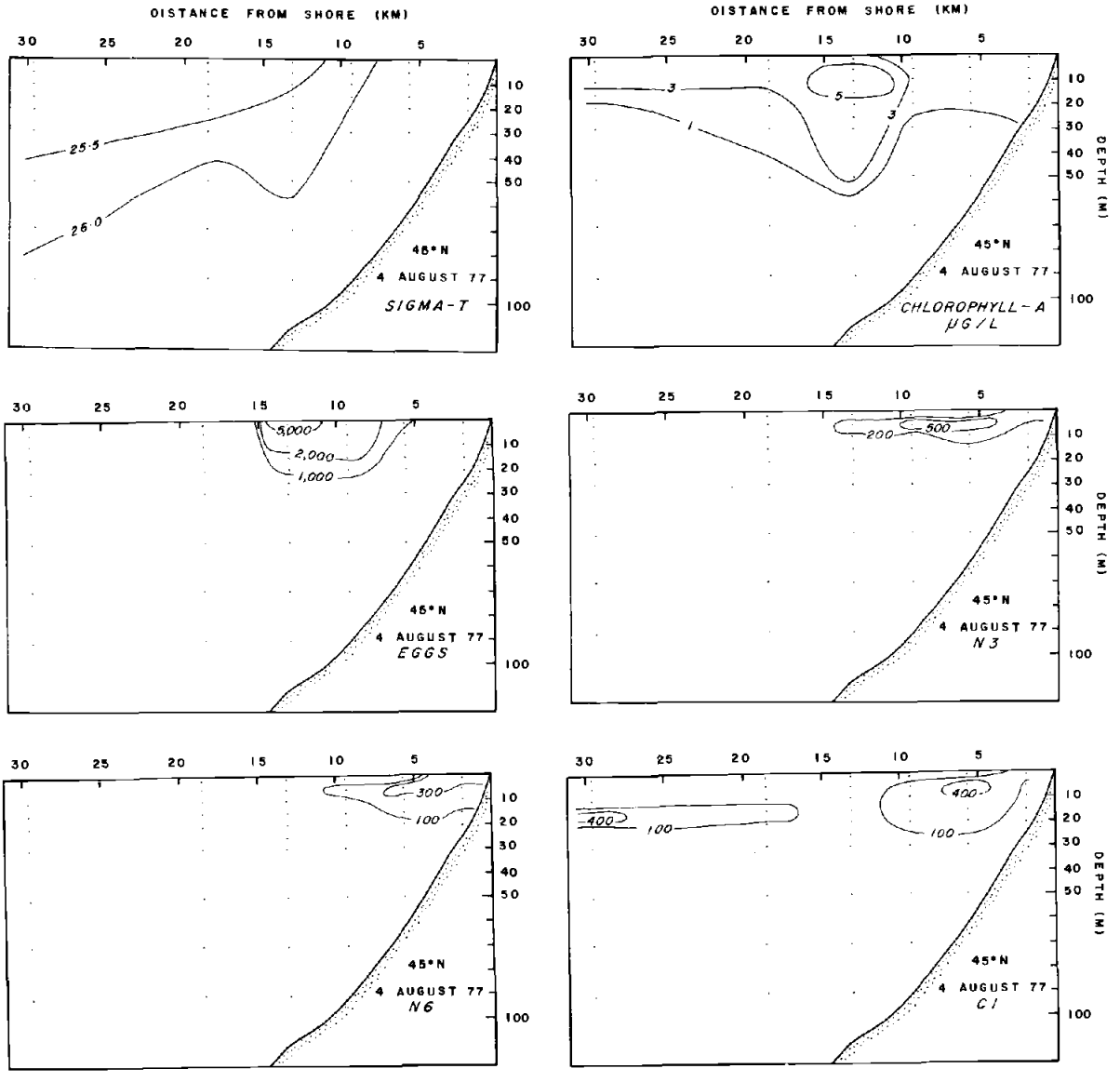


Figure 16. Distribution of density (sigma-t), chlorophyll-a, and Calanus marshallae eggs, N3, N6 and C1 during 4 August 1977. Animal abundances are number per cubic meter.

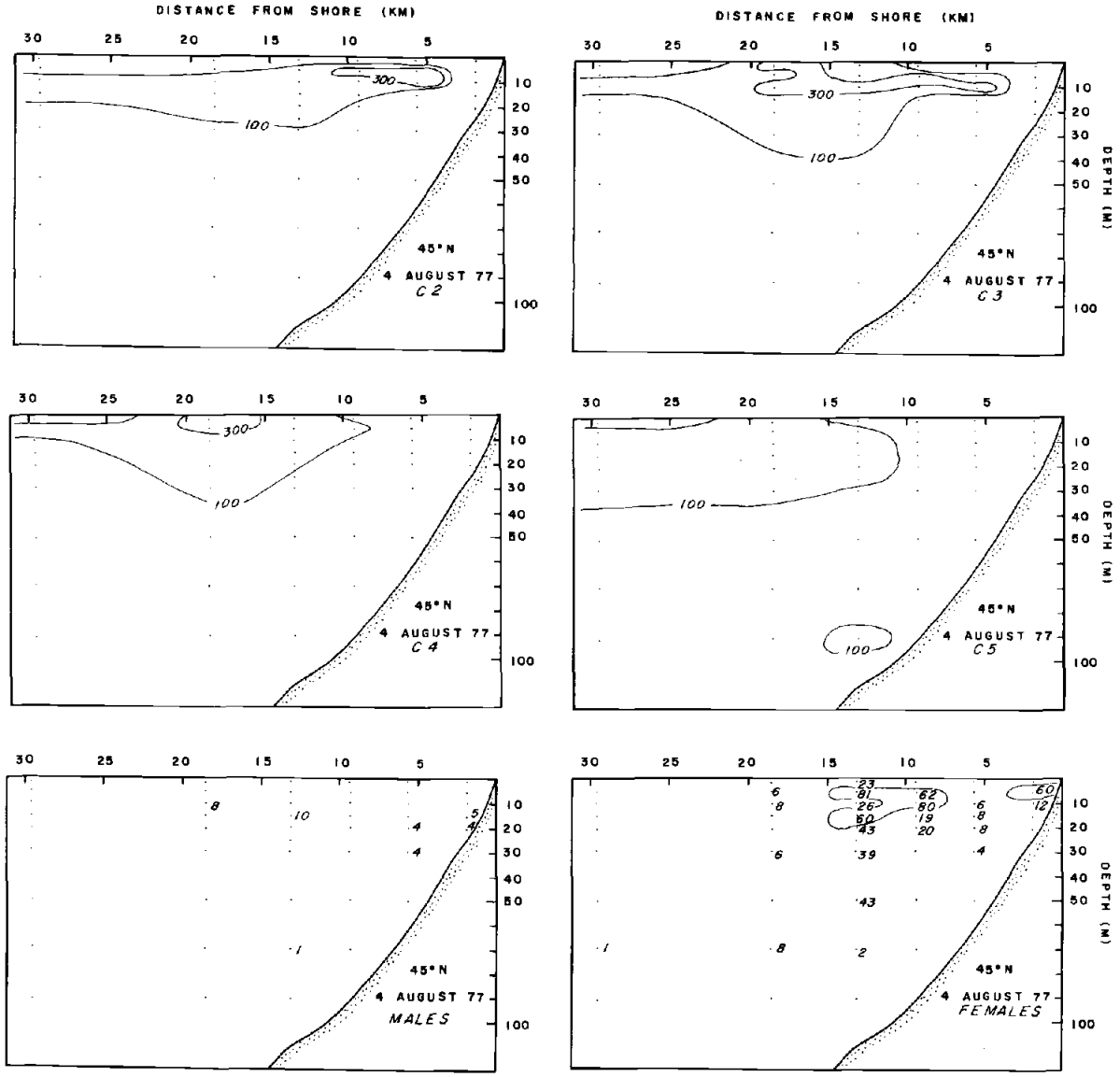


Figure 17. Distribution of C2, C3, C4, C5, male and female Calanus marshallae during 4 August 1977. Abundances are number per cubic meter.

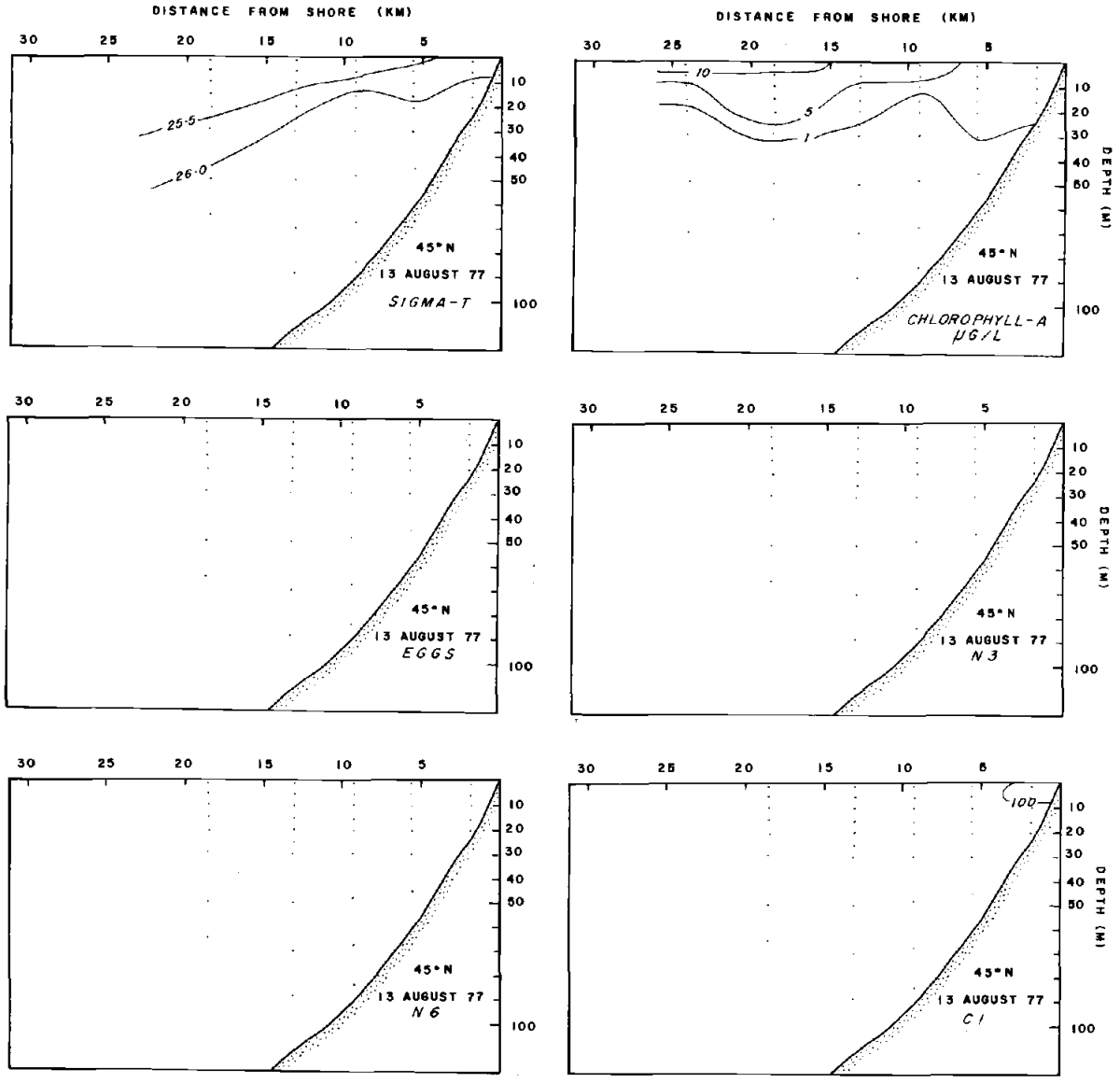


Figure 18. Distribution of density (sigma-t), chlorophyll-a, and Calanus marshallae eggs, N3, N6 and C1 during 13 August 1977. Animal abundances are number per cubic meter. Abundances less than 100 per cubic meter are not contoured.

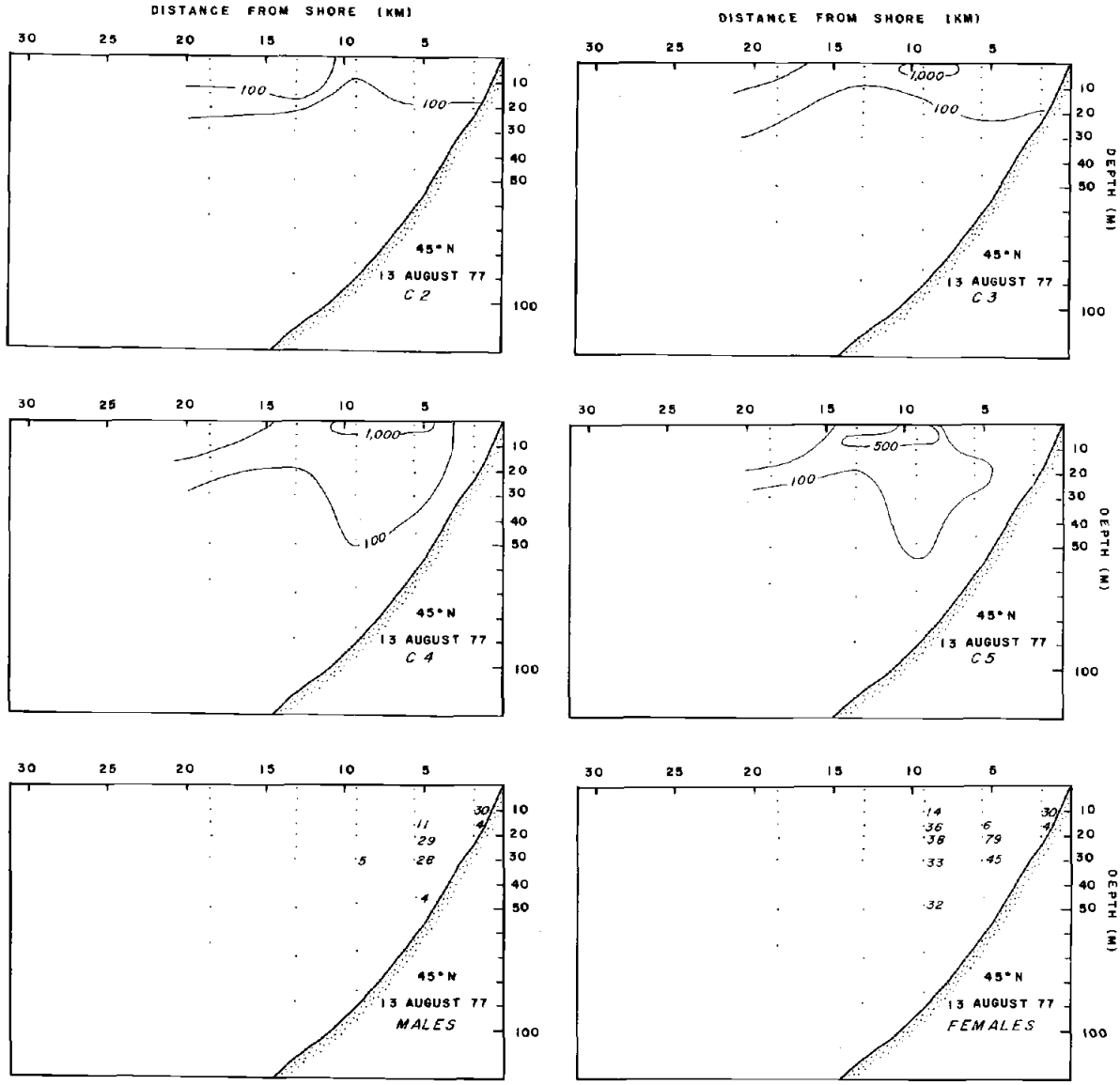


Figure 19. Distribution of C2, C3, C4, C5, male and female Calanus marshallae during 13 August 1977. Abundances are number per cubic meter.

high phytoplankton abundance. This was also the case with the 1973 data.

The nauplii data are unique to 1977, because naupliar stages were differentiated in this data set. I show only the distributions of the third (N_3) and sixth (N_6) stages. The N4 and N5 are always found with the N6. The first two naupliar states were only counted in two transects because they were uncommon and hard to identify. In all cases, the nauplii were at least two miles closer to shore than the eggs. The center of abundance of N_3 was 1-3 miles from shore on the July cruises and three to five miles on 4 August. The N6 were abundant only at one and three miles from shore on all occasions.

The copepodite stages are first to show a seaward shift in distribution. During the July cruises, first stage copepodites (C1) were at least two miles farther to sea than the N6. This shift must be linked to a change in behavior. There is no change in the depth of maximum abundance between N6 or C1 (with the exception of the 29 July cruise), so the behavioral change is not obvious. Perhaps the C1 move upward at night to the very surface and then later return to their usual daytime depth. This would offset their distribution seaward if there were offshore transport in surface waters.

The center of abundance of each successive copepodite stage from C2 to C5 is shifted seaward relative to the younger stages. All of the seaward displacements occur within the upper 20 m of the water column, with the exception of the 29 July transect. On this date, for unknown reasons, the centers of abundance of each progressive copepodite stage from C1 through C5 are both more offshore and deeper in the water column.

The adult females are only found three to five miles from shore, except for 4 August when they were five to seven miles offshore. In all cases, these distances correspond to those where eggs are most abundant. Females are either found at the same point in the water column as their eggs or at most, 10 to 20 m beneath them.

In all 1977 transects, the center of abundance of females occurs deeper in the water column than that of the C5. Additionally, the centers of abundance of females and C5 are separated by at least three to five miles on the 29 July, 4 and 13 August cruises. The separation was not as great on the 15 and 21 July cruises. The separation of stages is evidence for another change in behavior. This seeking of greater depths may be associated with the process of ovary development and egg maturation. The effect of this depth adjustment would be to move the adult stage out of the upper 20 m which are subjected to occasional offshore transport and into deeper waters which have a shoreward component to their flow.

As evidence that the 1977 data are not unusual, the 1973 data on copepodite abundances are shown in Figures 20-23. Data from the four transects where all stations out to 10 miles were sampled are shown. On three of these dates (29 July and 15, 16 August 1973), all of the seaward spreading of stages occurred in the upper 20 m of the water column. On one date (12 September), the seaward shift was accompanied by a deepening of each successive copepodite's center of abundance, just as in the 29 July 1977 data.

In summary, among the copepodites, several patterns occur. In seven of nine transects, all of the seaward shifting of population age

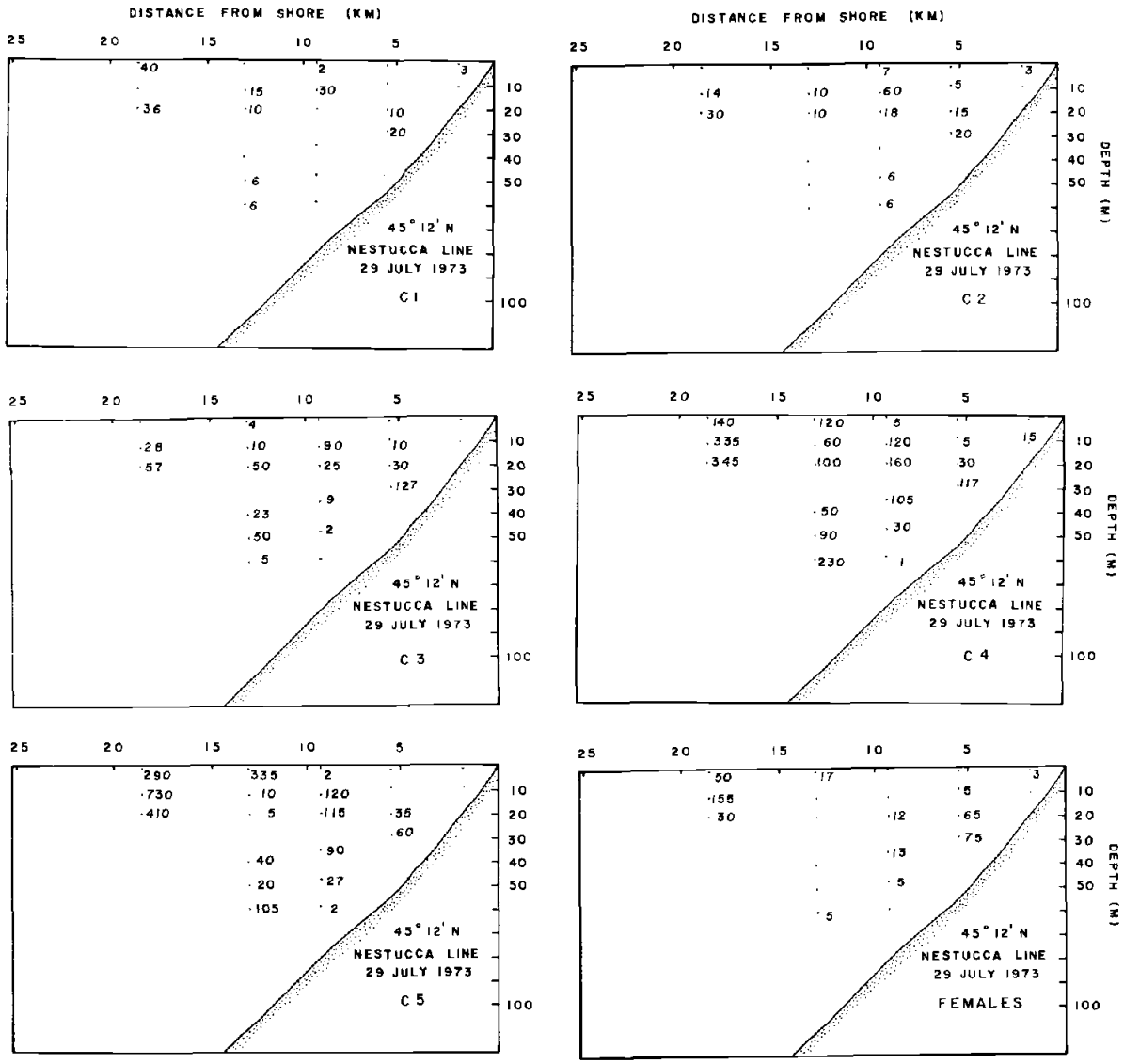


Figure 20. Distribution and abundance (number per cubic meter) of Calanus marshallae copepodite stages C1 through C6 on 29 July 1973.

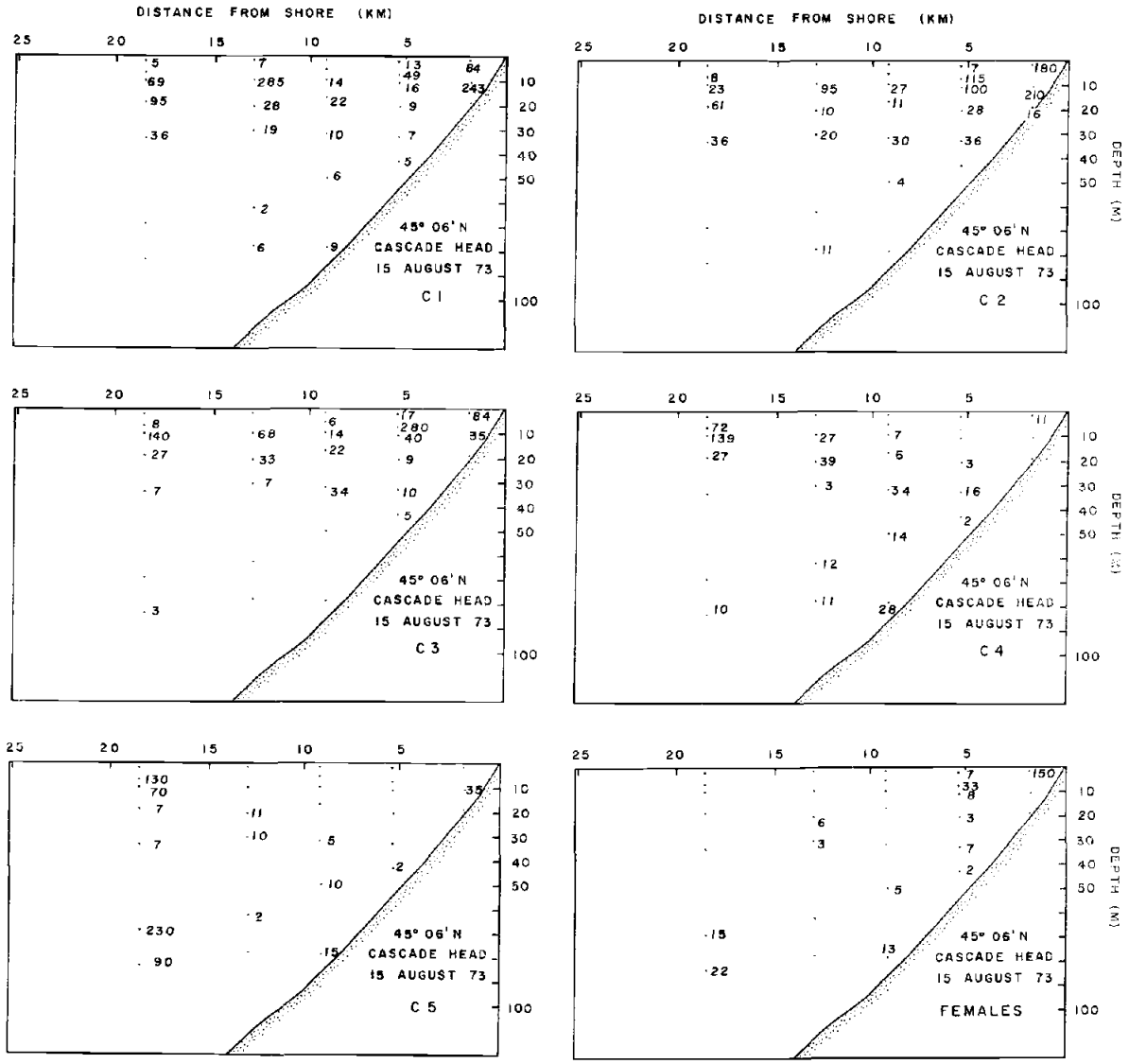


Figure 21. Distribution and abundance (number per cubic meter) of Calanus marshallae copepodite stages C1 through C6 on 15 August 1973.

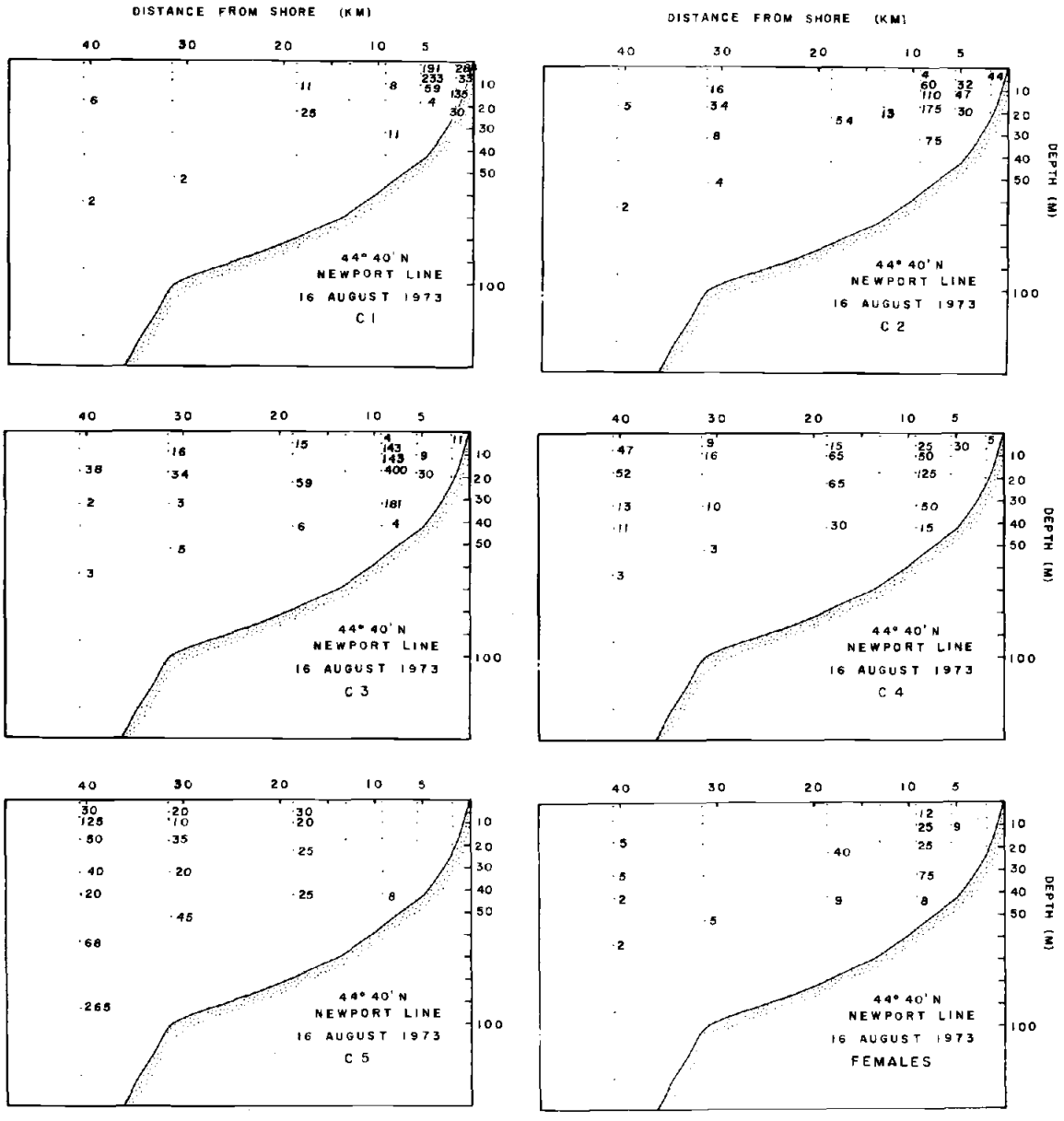


Figure 22. Distribution and abundance (number per cubic meter) of Calanus marshallae copepodite stages C1 through C6 on 16 August 1973.

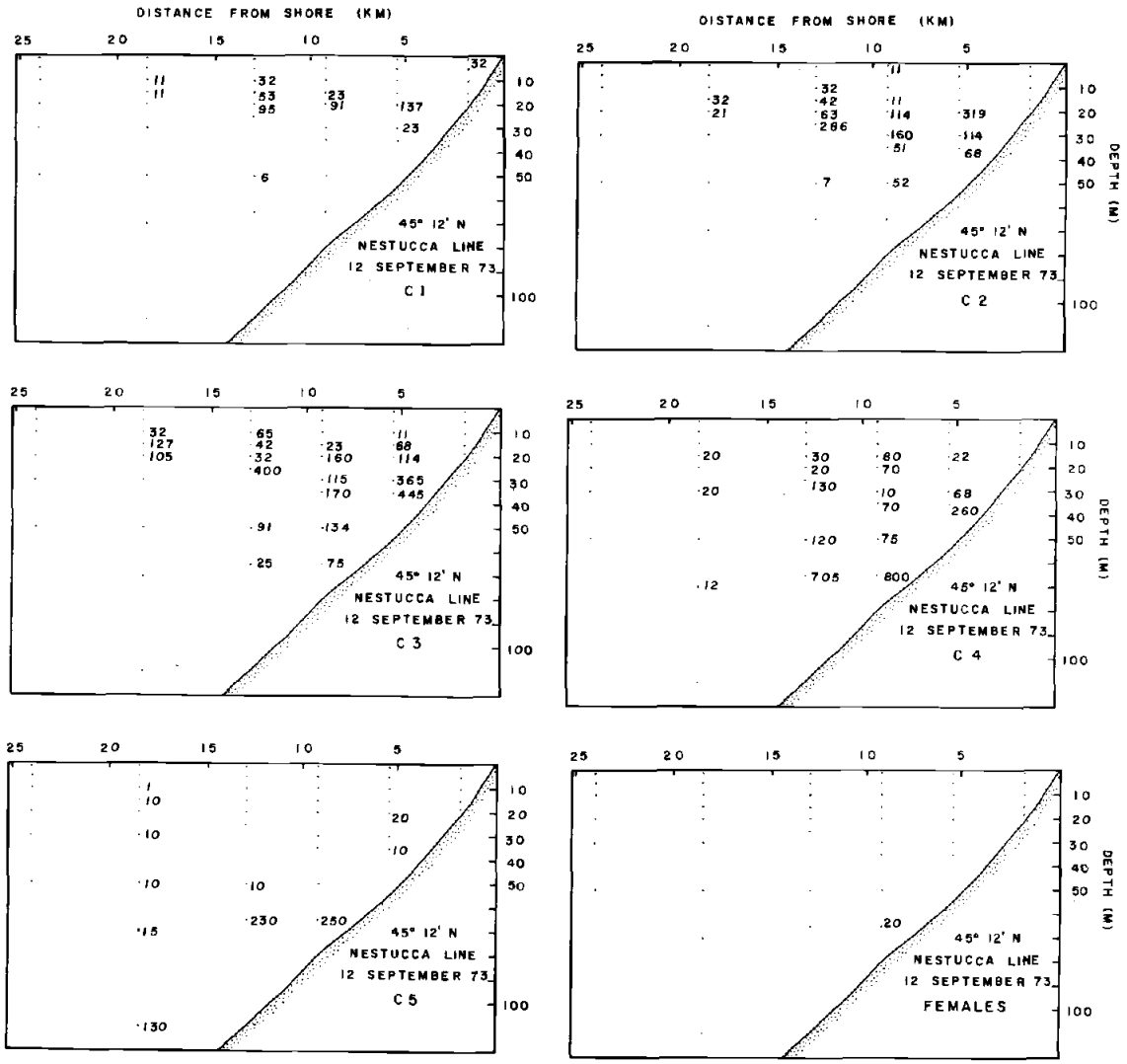


Figure 23. Distribution and abundance (number per cubic meter) of Calanus marshallae copepodite stages C1 through C6 on 12 September 1973.

structure occurred within the upper 20 m of the water column. In two of nine cases, the seaward transfer took place to depths of 50 m. Adults are always deeper in the water column than the C5 stage. In all transects, the adult abundance maximum is closer to shore than that of the C5. Adults and eggs have their greatest abundances at the same distances from shore.

DISTRIBUTIONS OFF WASHINGTON STATE. A nagging problem in all past zooplankton studies completed off Oregon is that we do not know if the distribution patterns seen are unique to the study area. Peterson, Miller and Hutchinson (1979) postulated that the Columbia River plume acts as a low density, surface barrier, stopping seaward surface flow during active upwelling events. Since there is no such thick lens of low salinity water present off the Washington coast in summer, the zonal pressure gradient should be much less steep, and seaward transport of surface water much greater, than off Oregon. Therefore, plankton living near the surface should be transported much farther seaward off Washington than off Oregon. One cruise was made between 21 and 29 July 1977 to examine this hypothesis.

The hydrographic, chlorophyll and zooplankton distributions are shown in Figures 24 and 25 for a transect completed off Cape Shoalwater, Washington (46°44' N) on 24 July and Figures 26 and 27 for a transect off Cape Flattery, Washington (48°20' N) on 27 July 1977. Upwelling was in a relaxed state on both transects. This was unfortunate because it meant that the hypothesis would not be well tested. The water column off both capes was highly stratified. Plant biomass was very high. The same basic zooplankton distribution patterns known for the

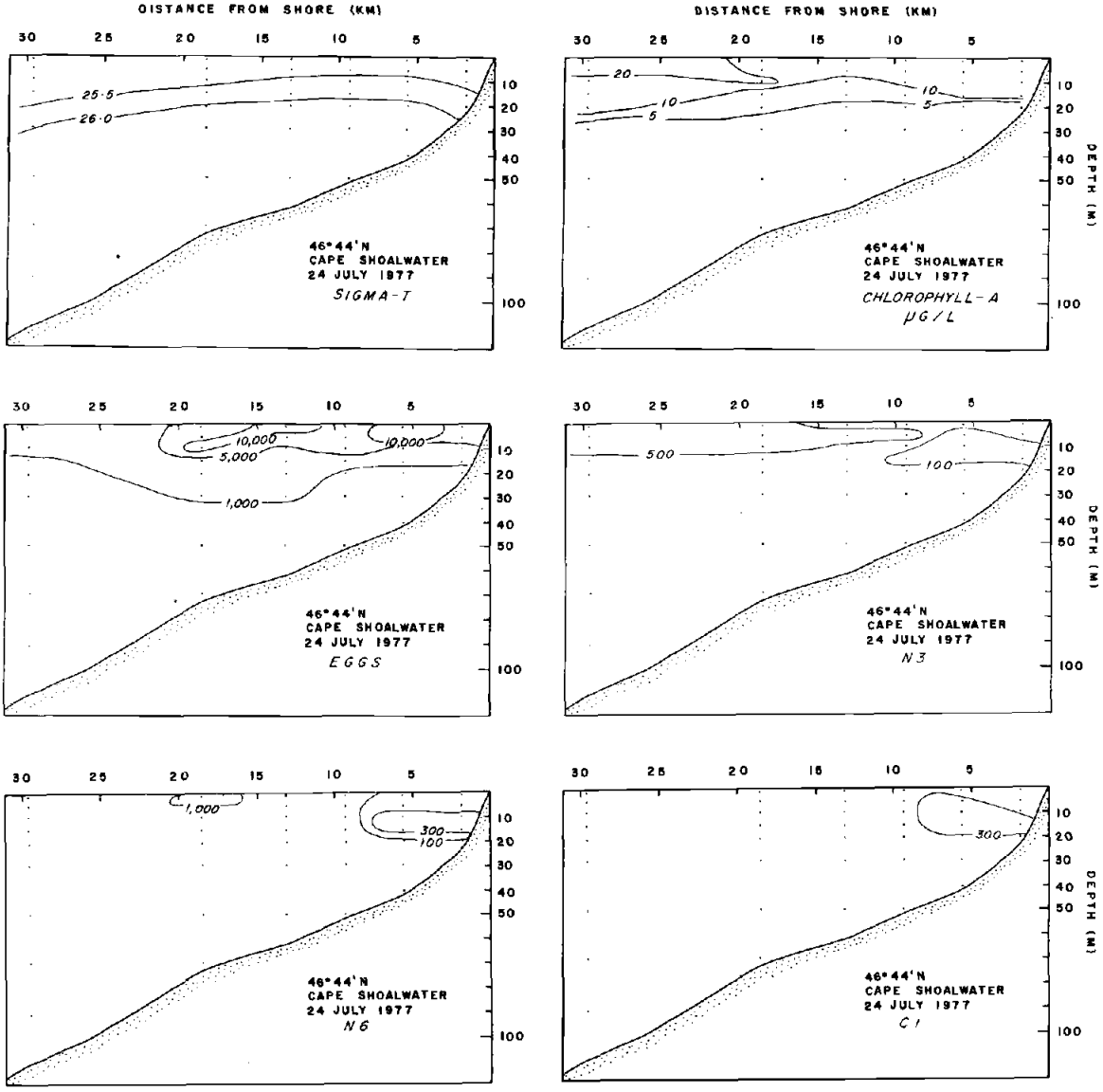


Figure 24. Distribution of density (sigma-t), chlorophyll-a, and Calanus marshallae eggs, N3, N6 and C1 off Cape Shoalwater, Washington, on 24 July 1977. Animal abundances are number per cubic meter.

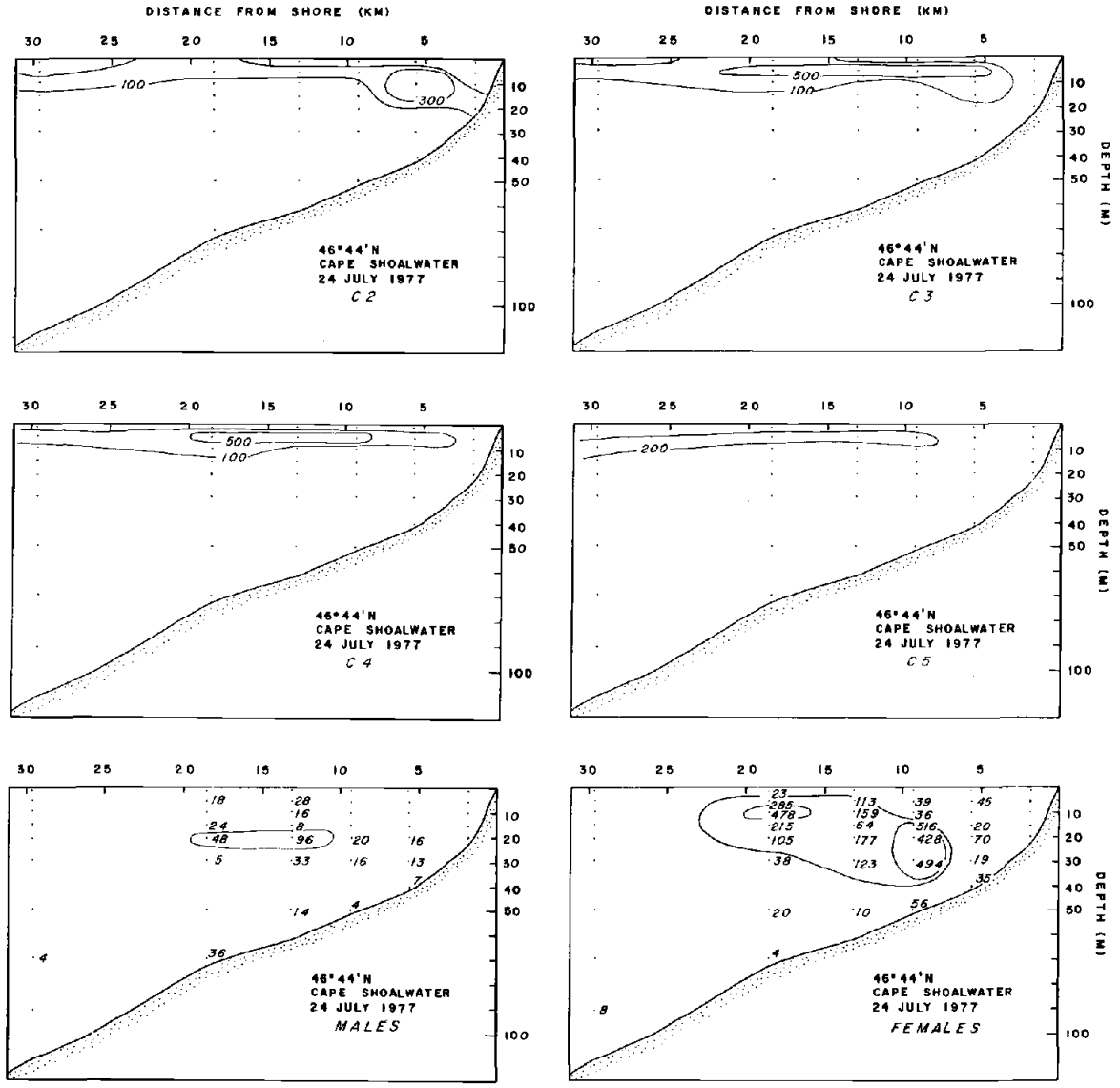


Figure 25. Distribution of C2, C3, C4, C5, male and female Calanus marshallae off Cape Shoalwater, Washington, on 24 July 1977. Abundances are number per cubic meter.

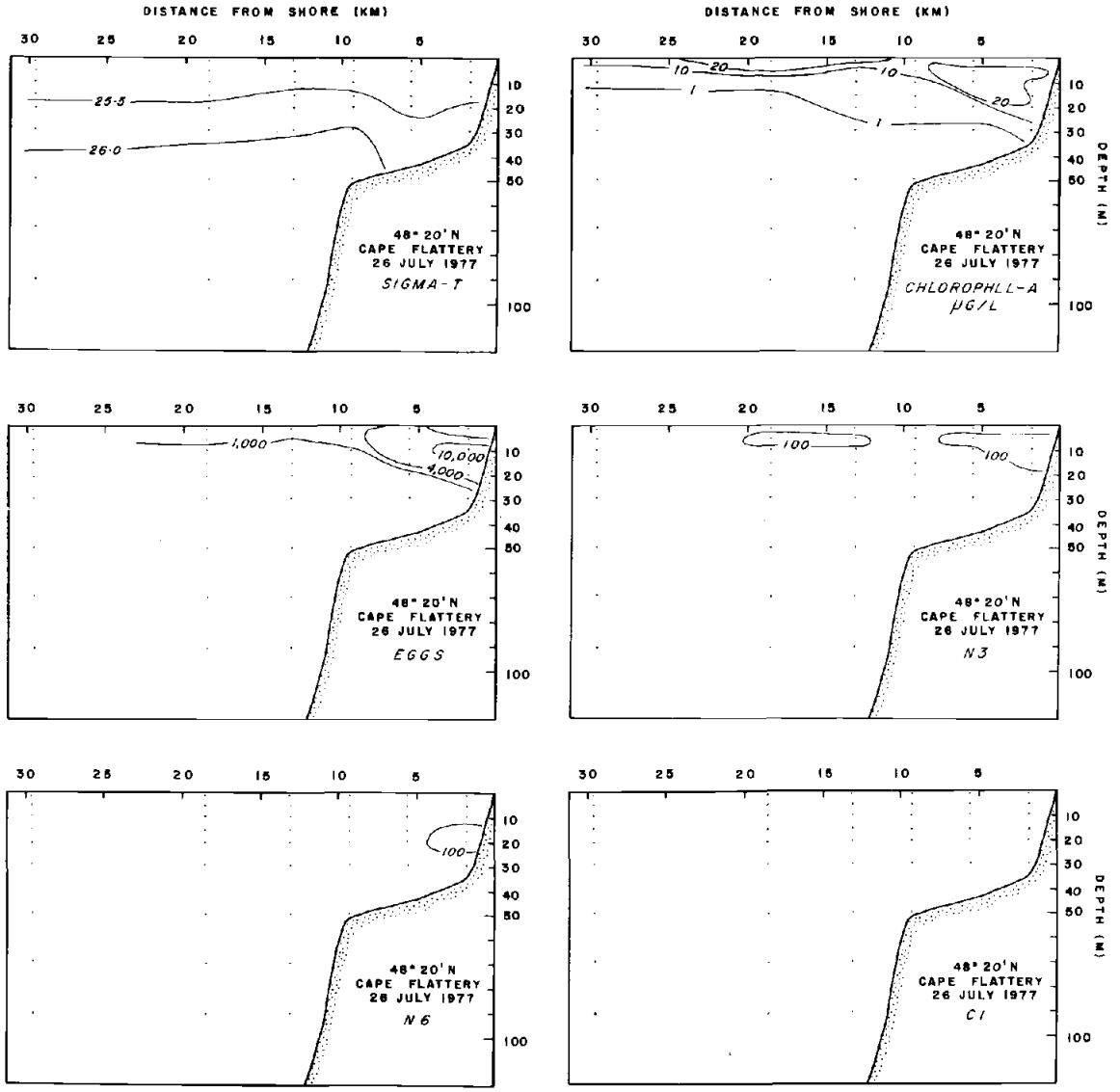


Figure 26. Distribution of density (sigma-t), chlorophyll-a, and Calanus marshallae eggs, N3, N6 and C1 off Cape Flattery, Washington, on 26 July 1977. Animal abundances are number per cubic meter.

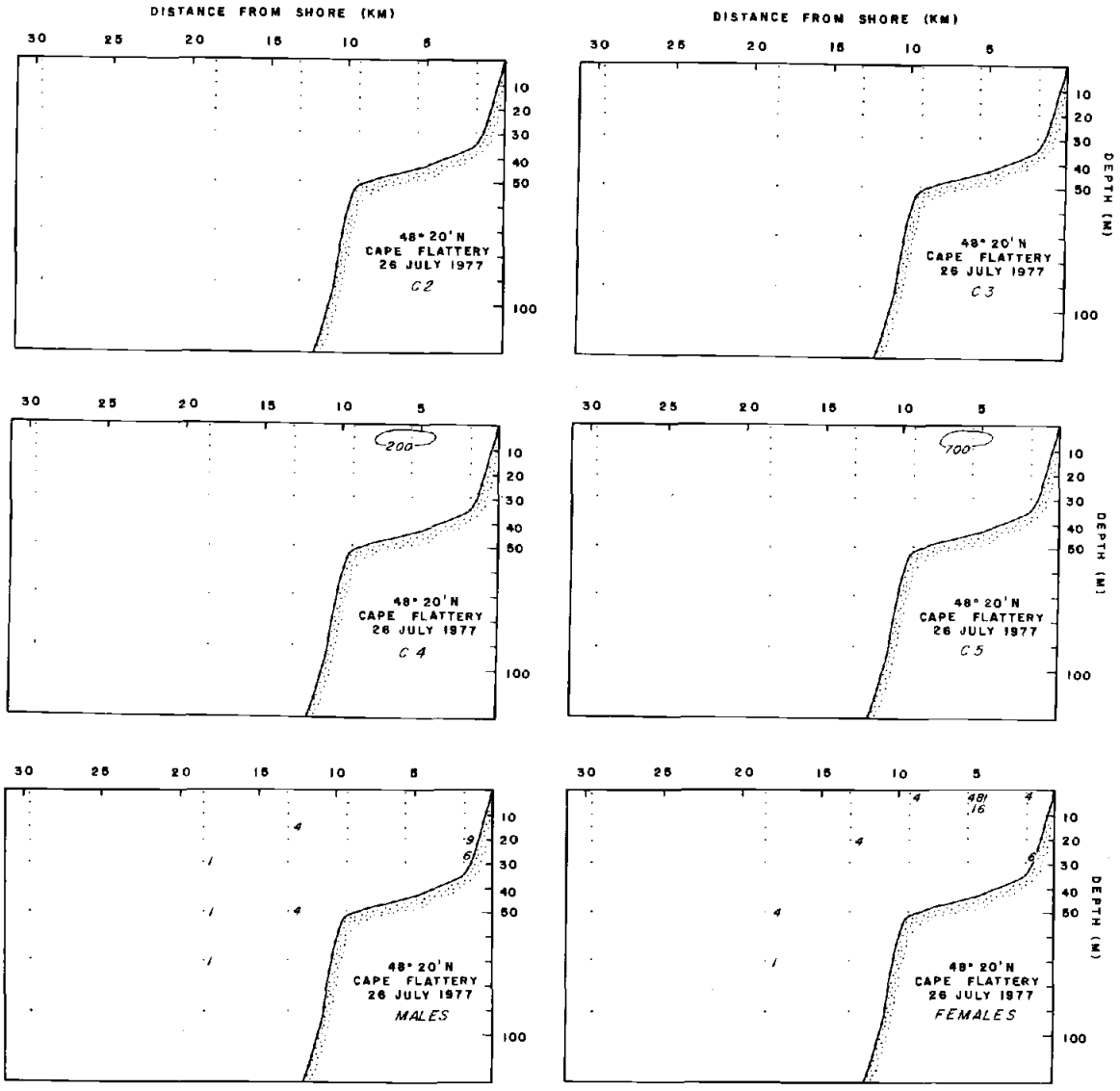


Figure 27. Distribution of C2, C3, C4, C5, male and female Calanus marshallae off Cape Flattery, Washington, on 26 July 1977. Abundances are number per cubic meter.

central Oregon coast were seen. The fourth through sixth nauplii stages were most abundant nearshore off Cape Shoalwater, with older copepodites occurring at increasingly greater distances from shore. Females were deeper in the water column and closer to shore than the fifth copepodite stage. A difference between central Oregon and Cape Shoalwater is that the eggs and third nauplius stage were much more broadly distributed off Cape Shoalwater. This observation does not necessarily support the hypothesis that zooplankton should be abundant farther seaward off Washington than Oregon. The result may be attributable to the fact that the bathymetry is much less steep off Cape Shoalwater. The critical variable in transect comparison is not distance from shore but water depth. This is because alongshore water flow follows the bathymetry closely (Smith, 1974). The effects of bathymetry on phytoplankton chlorophyll distributions are given in Small and Menzies (in prep.), and can be seen in Peterson, Miller and Hutchinson (1979). A water depth of 110 m at the station 16 miles off Cape Shoalwater corresponds to the seven mile station along the Sunflower transects. Eggs were abundant to 16 miles off Cape Shoalwater and to seven miles on the 29 July transect off Sunflower.

The bathymetry off Cape Flattery is again different. The shelf is narrow and cut by the Juan de Fuca Canyon five miles from shore. This feature may affect alongshore circulation patterns, but it is not known how. The zooplankton, however, are not distributed in any pecular way. Eggs and N3 are spread seaward as off Cape Shoalwater, but all other stages are found within five miles of shore.

Neither transect provided an adequate test of the hypothesis that zooplankton should be spread farther seaward off Washington than Oregon. In both transects, most life history stages were retained nearshore. Only two stages (eggs and N3) occurred abundantly farther seaward than expected. Therefore, it would seem that, at worst, only these two developmental stages are subject to losses offshore due to seaward surface flow.

SUMMARY AND CONCLUSIONS

1. Zooplankton are most abundant over the continental shelf off the central Oregon coast in July and August. They are least abundant between November and April.
2. Calanus marshallae make up 9% of the total zooplankton numbers, but a much greater proportion of the total biomass because it is the largest of the dominant copepods. Female Calanus marshallae are 25 times heavier than females of Pseudocalanus sp., the next largest dominant species.
3. Calanus marshallae occur between February and September. Presumably they pass the other months in diapause, in deep water beyond the continental shelf.
4. Calanus numbers begin to increase at nearshore stations several months earlier in the year than at offshore stations. Abundances do not usually increase much during the February-September growing season.
5. Eggs, nauplii, early copepodites and females are found nearshore, and older copepodites are found offshore.
6. In most transects, the seaward shifting of Calanus marshallae population age structure occurred within the upper 20 m of the water column.
7. Adults are always deeper in the water column than C5 and have their abundance maximum closer to shore than C5.
8. The same basic zooplankton distribution patterns known from the central Oregon coast are seen off the Washington State coast.

CHAPTER IV. DEVELOPMENT AND GROWTH

INTRODUCTION

Like other copepods, Calanus marshallae has 13 life history stages. A pelagic egg is followed by six naupliar stages and six copepodite stages. The last copepodite, C6, is tha adult. Determining the rates at which these stages develop is a basic part of any life history study.

Development rate data were gathered for several reasons. First, the total distance from shore which copepodite stages were transported from the very nearshore zone was known from a number of zonal transects. I needed to know the elapsed time for development from the last naupliar stage (N6) to each copepodite stage. This would allow calculation of the average rates at which each stage was transported offshore. Second, in order to decide if field populations are developing at their maximum rate, I needed to know the laboratory development rate under controlled environmental conditions. Third, development data are needed to study copepod growth in terms of change in length and weight with stage. Measurements of the time spent in each developmental stage allows one to calculate change in weight with time.

The following topics are discussed in this chapter: Survivorship and longevity of laboratory animals, development rates at 10°, 11°, and 15°C, variability of developmental rates, variability in development between different families, a comparison of developmental rates in the field to rates in the laboratory, growth of individuals in terms of length vs stage, weight vs stage and weight vs time, and the maternal effects on length of daughters.

DEVELOPMENTAL RATES - LABORATORY MEASUREMENTS

METHODS

Estimates of rates of development of naupliar and copepodite stages of Calanus marshallae come from 19 experiments. Some information pertinent to these measurements is shown in Table 3. Twelve experiments were carried out at 10°C, five at 11°C and two at 15°C. The 10°C experiments began with the eggs of females collected in January and February 1977 from inside the mouth of Yaquina Bay, Oregon and from a station approximately five miles offshore of the bay mouth (44°40'N). The 11°C experiments were carried out using females collected during the summer (June-July) of 1976 from the offshore station. The 15°C experiment was run in August 1977 using females from this same station. The primary data are the measurements made at 10°C. The 11°C experiments were preliminary ones begun in order to determine whether C. marshallae could be raised in the laboratory, and to practice identifying living (and moving) animals. The 15°C measurements were carried out to determine (1) whether C. marshallae could survive at this temperature, and, if so, (2) whether temperature affected its development rate.

All laboratory work was done in a constant temperature walk-in room. Experiments were conducted under continuous low light except for one (experiment I-LD, Table 3) which was maintained under a 12-hour light-dark cycle. In most of the experiments carried out in 1977 (11 of 14) the eggs came from a single clutch of eggs from a different individual. The eggs were kept in 60 mm diameter glass petri dishes.

Table 3. General information about the 19 development rate experiments. Experiments A and B were carried out at 15°C, experiments C through N at 10°C and O through S at 11°C.

EXP CODE	DATE	PARENT	TIME ♀ IN LAB BEFORE EGGS WERE USED IN EXPERIMENT	NUMBER OF INDIV. AT BEGINNING OF EXP.	SURVIVORSHIP TO C5
A	15 AUG 1977	♀ 1	1 day	35 N1	.00
B	"	♀ 2	1 day	27 N1	.19
C	10 JAN 1977	mixed	6 days	63 N3	.30
D	12 JAN 1977	♀ 3	8 days	43 N1	.37
E	23 JAN 1977	♀ 7	19 days	40 E	.13
F	25 JAN 1977	♀ 4	21 days	33 E	.42
G	30 JAN 1977	♀ 7	26 days	48 E	.21
H	4 FEB 1977	mixed	--	50 N3	.56
I-LD	4 FEB 1977	mixed	--	50 N3	.28
J	4 FEB 1977	♀ A	9 days	34 E	.56
K	5 FEB 1977	♀ 4	30 days	31 N2	.61
L	5 FEB 1977	♀ F	10 days	24 E	.17
M	10 FEB 1977	♀ D	15 days	33 N4	.45
N	20 FEB 1977	♀ 5	45 days	40 E	.68
O	18 JUNE 1976	mixed	--	50 N3	.00
P	19 JULY 1976	mixed	--	81 N3	.25
Q	14 JULY 1976	♀ 24	21 days	27 N3	.30
R	18 JUNE 1976	mixed	--	50 E	.18
S	23 JULY 1976	mixed	--	73 N1	.01

After hatching, nauplii were transferred to cylindrical glass containers ranging in volume from 400 ml beakers to one-gallon jars, where all subsequent development took place. Each container was fed a mixture of the diatom Thalassiosira fluviatilis and the flagellate Isochrysis galbana. The plants were grown in batch culture using Guillard's f/2 media (Guillard and Ryther, 1962). Plants were cultured at 12°C and 16°C for use in the 10° and 11°C, and 15°C experiments respectively. New phytoplankton cultures were prepared weekly. Food provided to C. marshallae in growth experiments was always in log-phase and never more than one week old.

Food levels within the experimental containers were occasionally monitored with the aid of a Fuchs-Rosenthal counting chamber. These counts were made too infrequently to be of much use, however. Abundances of T. fluviatilis were between 2000 and 6000 cells ml^{-1} when food was first added. Each container was inspected daily for food buildup or depletion. Fecal pellets were removed by pipette when necessary. Careful attention was given to avoiding accumulation of food particles because mortality of naupliar stages seemed to be high in dense concentrations of phytoplankton. Therefore, small amounts of plants were added daily as needed. It was presumed that food levels were maintained at or above a level which would sustain maximum animal growth rates.

A weekly census was made of the animals in the 10° and 11°C experiments. A census was made at four-day intervals in the 15°C experiments. The water in each experimental container was poured through a 70µm Nitex screen and animals were gently rinsed from the

screen into a plastic dish. The experimental containers were scrubbed with a nylon bottle brush and rinsed several times with fresh water. They were then refilled with seawater, half of which was the water from which the animals had just been removed. Individuals were counted with the aid of a binocular dissecting microscope. Anesthetics were never used. Animals were returned to the experimental containers with a pipette after each was identified to developmental stage.

The raw data are numbers of individuals in each developmental stage on each census date for each experiment. The data were tabled by time since eggs were laid, and stage (Time X Stage). For each census date, counts were converted to percent of the total individuals in each developmental stage. These percent data were then cumulated from youngest to oldest stage on each date, thus representing percent of the population as old as each given stage on each census date. The data are analyzed in that form.

RESULTS

SURVIVORSHIP. The twelve 10°C experiments began with a total of 551 eggs or early naupliar stages. Of this number, 137 individuals reached adulthood. Only one was a male (experiment "K"). It was found that adults are long-lived. Many laboratory-derived females were maintained for more than two months after adulthood was reached. Field-collected females were maintained for up to 77 days before being preserved in formalin. Similarly, the single laboratory male was kept alive for 73 days, and four field-collected males lived 49,51,55 and 61 days before being preserved. Fecal pellets were always numerous

indicating that the males did feed.

Overall survivorship in each 10°C experiment is plotted in Figure 28. Survival from egg or early nauplius to the completion of an experiment ranged from 18 to 68%, with an average of 40% in 11 experiments. (The "M" experiment is not included here since it began with an undetermined number of eggs.) The only pattern which I see in Figure 28 is that mortality is highest between days 0 and 35, becoming nearly zero after this time. By day 35, the median individual had reached the C4 stage. These survivorship data do not necessarily reflect natural mortality. In part, they may represent relative abilities of the different life history stages to withstand frequent handling. Nauplii may be less hardy than copepodites. Nauplii died from unknown causes. Copepodites always died during the molt.

Survivorship in the preliminary experiments conducted during the summer of 1976 at 11°C was low, averaging about 15%. This was probably a result of rough handling.

The 15°C experiments produced the smallest amount of data because survivorship was very low. Seven of nine individuals in experiment "A" died just before the molt into copepodite stage V. The other two successfully molted but were dead at the next census. Experiment "B" produced five females.

DEVELOPMENT AT 10°C. Figure 29 is a set of scattered diagrams of cululative percent of the population that had reached the next stage beyond the indicated stage vs time, using data from the January-February 1977, 10°C experiments. In plotting the data and in subsequent regression analyses, the scale along the ordinate was 0% at the

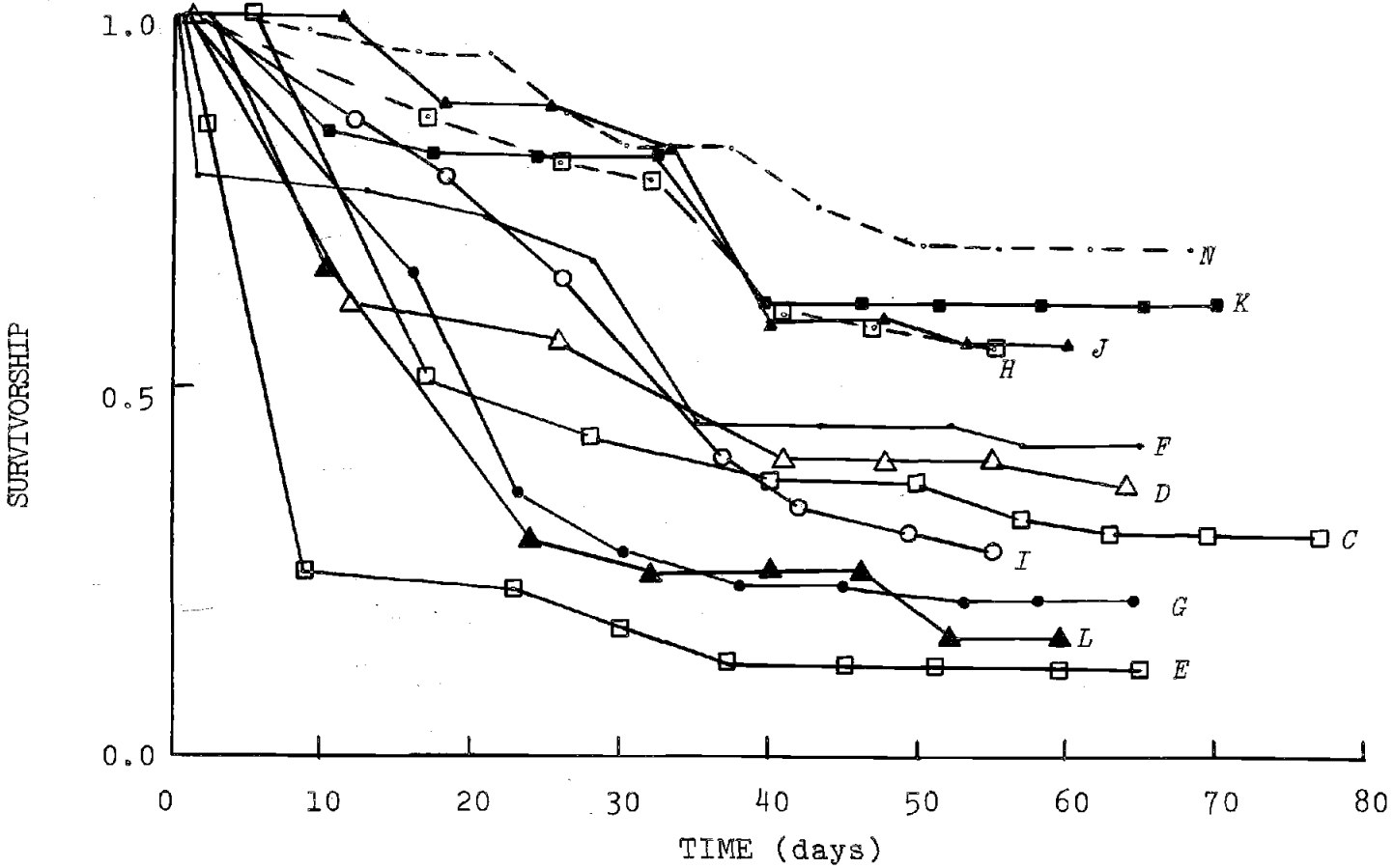


Figure 28. Survivorship (fraction surviving from the beginning day of an experiment) in the 10°C development time experiments. Experiment code letters correspond to those in Tables 3 and 5. Survivorship declines from day 0 to 35 after which mortality is about zero.

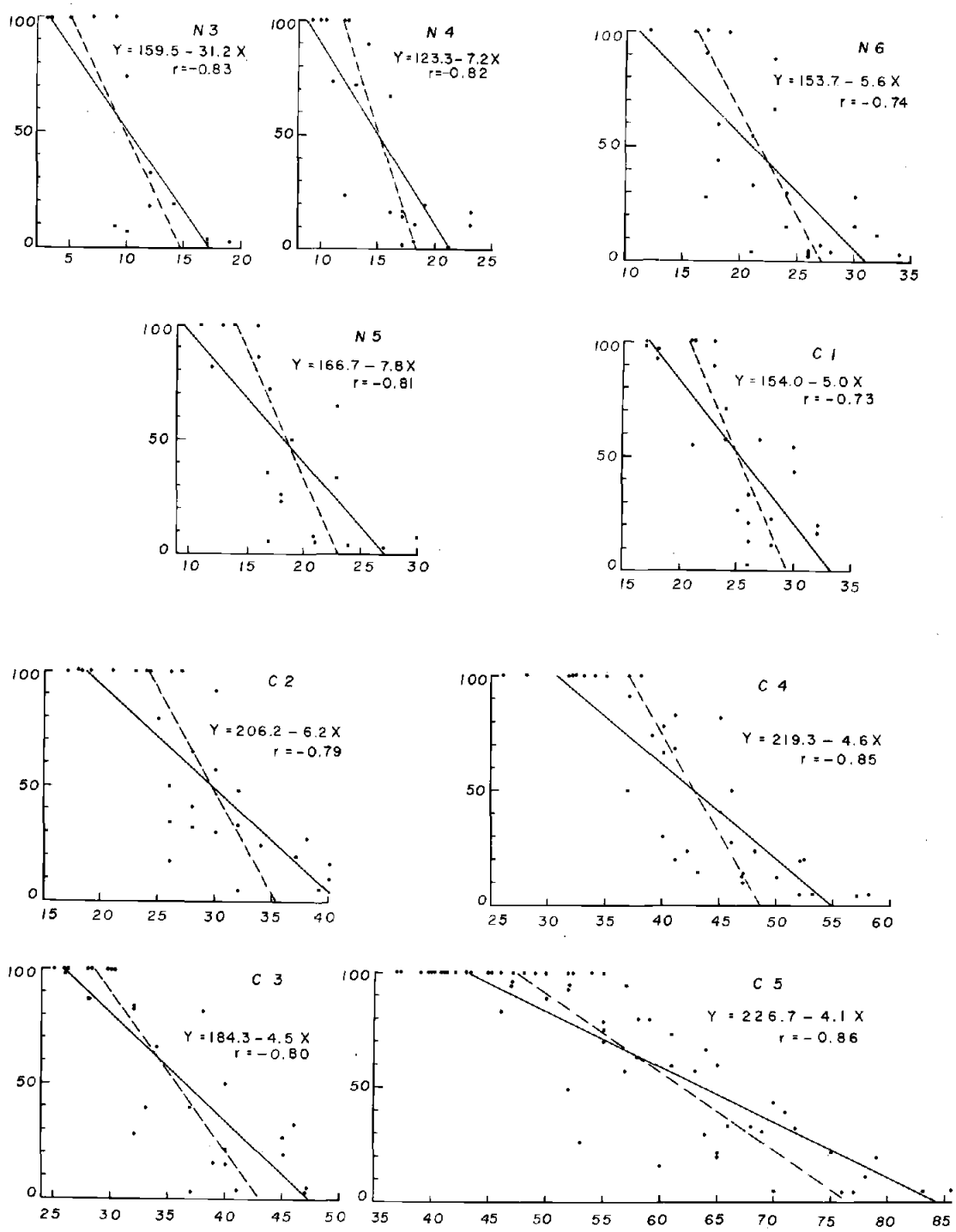


Figure 29. Scatter diagrams of cumulative percent of the laboratory population that had reached the next stage beyond the indicated stage vs. time. The data are from the 10°C experiments. The two lines shown on each panel are regressions calculated from parametric (————) and nonparametric (— — — —) techniques. Regression equations and correlation coefficients are from parametric analysis.

origin ranging upward to 100%. Two regression lines are shown. One was obtained by ordinary least squares methods and the other by the Brown-Mood nonparametric regression technique described by Daniel (1978, p. 343). The regression equations and correlation coefficients shown on each panel are from least squares analysis. The data of interest are the times at which the median individual had reached each successive developmental stage. This is the age of the median individual at each stage. It is the time when 50% of the population had reached the indicated stage and 50% had reached the next stage. Therefore, the nauplius III regression line is used to estimate development time to N4, and N4 line for development to N5, and so on. These times are called "median development times." Estimates of these median development times were arrived at in two ways: (1) by entering $\hat{y} = 50$ in the least squares regression equations and solving for x, the development time, and (2) by inspection from the non-parametric regression lines. Both estimates of development times are listed in Table 4. The two regression methods gave nearly identical results. For all subsequent analyses, the development times calculated from least squares methods will be used.

Estimates of development rates of eggs and the first two naupliar stages come from different sources. Egg development rates (hatching times) are from direct observations on eggs laid at a known time. This straightforward method is only possible if a female lays a clutch of eggs when one happens to be examining her. The probability of this event is low since females only lay one clutch of eggs every 30 hours on the average. Nevertheless, I have 10 observations on hatching time.

The data are 42 h at 9.2°C and 9.4°C, 41.3 h at 9.5°C, 40 h at 10°C, 39 h at 10.8°C, two observations of 39 h at 11°C, 38.8 h at 11.5°C, 37 h at 12°C and less than 24 h at 15°C. Most eggs hatched within 30 minutes of each other so the variance in hatching time is not great. Times to Nauplius I, II and III are also known from direct observations. Both of the first two naupliar stages have a duration of about 0.9 days each. The total time from egg laying to N3 is 3.5 days (based on the mean of four observations). This is nearly the same value as that obtained from regression analysis of development time data (3.4 days).

Table 4 also lists durations of each stage in days and the percentage of the total development time represented by each stage, from N3 to C5. Development from egg to N3 (not shown in Table 4) proceeds very quickly. Only 2.5% of the total development time from egg to adult is taken up by these first three developmental stages. Development slows once the third nauplius is reached. The median individual spends 6.8 days in this stage, which is 10.7% of the total time spent developing into an adult. The duration of successive naupliar stages decreases through the last nauplius stage which takes only 2.6 days. Development becomes progressively slower through the copepodite stages. One-third of the total development time is spent in C5. The median individual reached copepodite V on day 42.9 and adult on day 63.8.

Figure 30 is a plot of developmental stage vs time for the 10°C experiment. Development of the median individual through time from N3 to adult follows a sigmoidal path. Stages N3 and N4 progress slowly, N5-C1 progress rapidly and C4-adult progresses slowly. The sigmoidal pattern is seen most easily when a straight line is plotted. Develop-

Table 4. Median development time (in days) to reach each successive developmental stage in the 10°C experiments.

STAGE	DEVELOPMENT TIME (TIME WHEN MEDIAN INDIVIDUAL REACHED EACH STAGE) NON-PARAMETRIC	LEAST SQUARES	STAGE DURATION (DAYS)	% OF 63.8 d	TRUE RANGE (IN DAYS) WHEN A STAGE WAS PRESENT IN THE EXPERIMENTS RANGE	TOTAL
N3	----	3.4	6.8	10.7	3 - 19	17
N4	10.0	10.2	4.8	7.5	9 - 23	14
N5	15.1	15.0	3.4	5.3	11 - 30	19
N6	18.6	18.4	2.6	4.1	12 - 34	22
C1	21.6	21.0	4.3	6.7	17 - 32	15
C2	25.6	25.3	4.6	7.2	17 - 40	23
C3	29.8	29.9	6.8	10.7	25 - 47	22
C4	35.8	36.7	6.2	9.7	26 - 58	32
C5	41.0	42.9	20.9	32.8	37 - 86	49
FEMALE	62.2	63.8			47 - 93	46

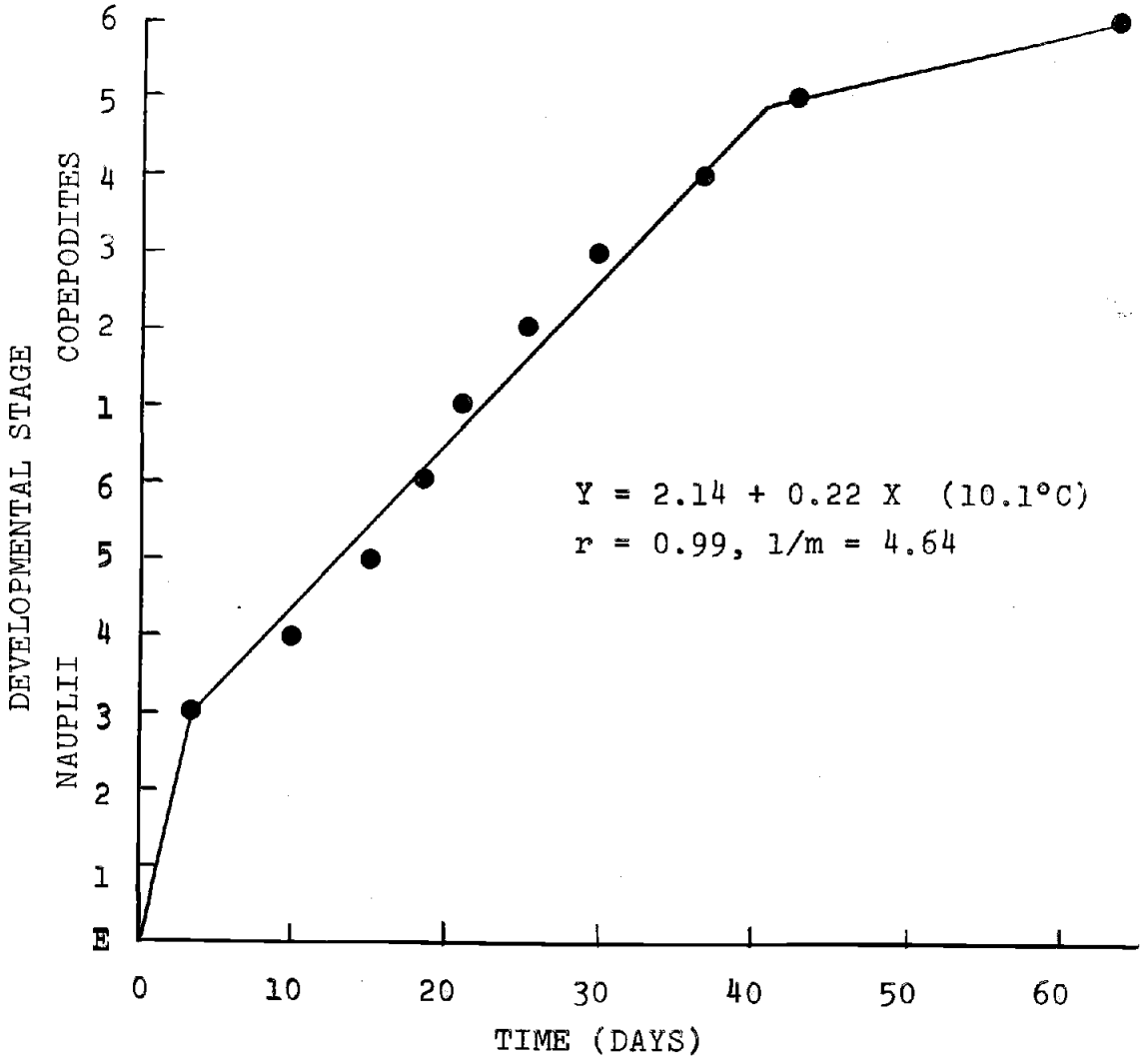


Figure 30. The progression of Calanus marshallae developmental stages through time. The data are times when the median individual had just reached each successive stage, at 10°C. Three distinct growth periods are seen: (1) Development from egg to N3 is rapid, (2) N3 through C5 follows a sigmoidal path which can be approximated by a linear rate of 4.6 days stage^{-1}, and (3) females develop from C5 much slower. Overall development from the third nauplius to adult is sigmoidal.

ment from N3 to C5 was regressed against time. The regression line and equation are shown on the figure. Development from N3 to C5 can be approximated by a linear relationship, progressing at a rate of 4.6 days stage^{-1}. This linear relationship between median development rates and time has been termed isochronal development by Miller, Johnson and Heinle (1977) and has been adopted by McLaren (1978). However, for Calanus marshallae, the true growth pattern is not isochronal, but sigmoidal. Periods of rapid development alternate with periods of slower development.

VARIABILITY IN DEVELOPMENTAL RATES. Figure 31 presents the developmental data in an alternate form. All of the least squares regression lines from Figure 29 are drawn on the same figure but the scale along the ordinate has been reversed, with 100% at the origin. This gives the data a somewhat different meaning. The figure is interpreted as follows: choosing for example, time = 18.4 days and constructing a vertical line at that point, one can see that 77% of the population was older than N4, 50% older than N5, 37% older than N6 and 8% older than C1. The median individual was an N6 on this day. The slopes of the regression lines are a relative measure of the variance in development time. If the variance in development increases with time, the slopes of each progressive line should become less steep. The hypothesis that all slopes (b_1) are equal (b_1,N4=b_1,N5=...=b_1,C5) was tested by calculating the 95% confidence interval estimates for each slope using

$$b_1 \pm \left[t^{.025}_{n-2}\right]\left[S_{b_1}\right]$$

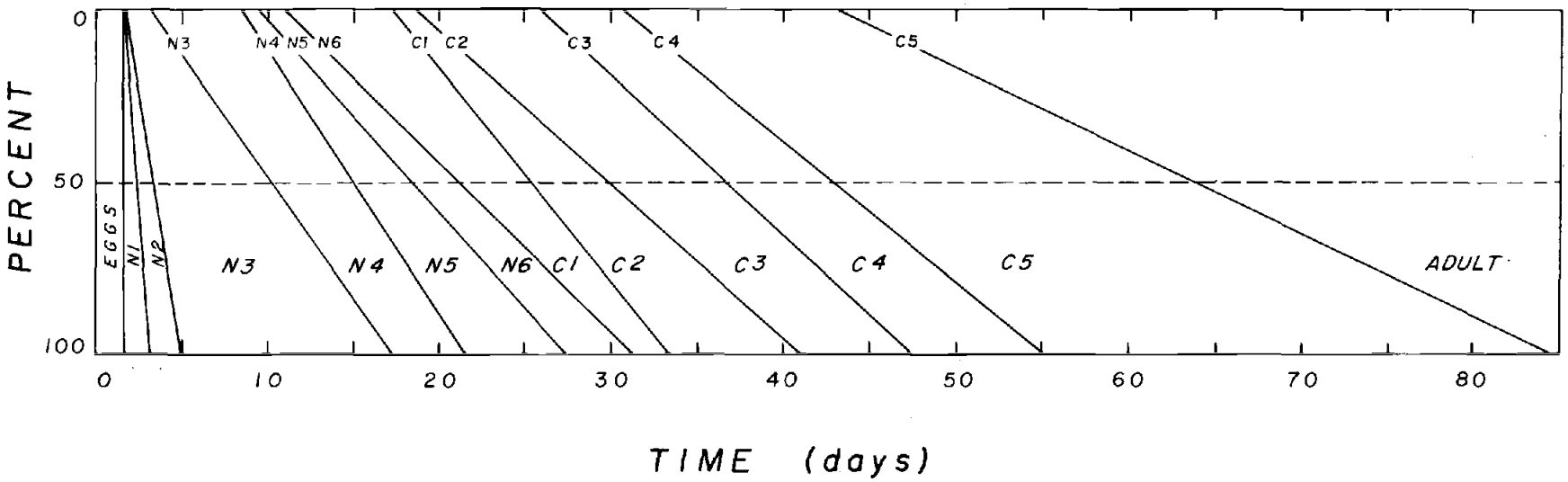


Figure 31. Development of each indicated stage at 10°C showing the least-squares regression lines from Figure 29. The slopes of the regression lines are a measure of the variability of development for each stage. The hypothesis that all slopes are equal was not rejected. Nearly all variability in development from N3 to C5 is installed at the N3 stage. Variability increases greatly in developing from C5 to adult.

where

$$S_{b_1} = \left(\frac{MSE}{SSX}\right)^{1/2}$$

The interval estimates of the slopes were compared and found to include all slopes except that of the C5 regression line. I conclude that the variance in development to all stages from N4 to C5 is about equal. This variance arises during the development of the third nauplius and remains unchanged through C5. There is little variance in egg hatching, N 1 or N2, but great variability in the rate at which C5 individuals develop into adults.

The average slope of the N4 through C5 regression lines was 5.6% day^{-1}. This means that 17.8 days (100/5.6) elapse on the average between the first and last appearance of a given stage. The true range in days when each stage was present in all 10°C experiments is listed in Table 4 (p 65). The median development times are also compared. The average time that stages N3 through C3 were present was 18.9 days. All of this range first appeared at N3. The range begins to spread at C4 and C5. They were present for 32 and 49 days respectively. The implication of these data is that the range in development time of individuals is high. For example, even though the median individual had reached C4, 36.7 days from egg laying and the duration of this stage is 6.2 days, an individual C4 first appeared on day 26 and some were still present one month later, on day 58.

VARIABILITY IN DEVELOPMENT BETWEEN FAMILIES. Although there is some suggestion that variability in development rate among individuals

is high, this problem cannot be studied here because I only have data on development of the median individual averaged from 12 experiments. However, since most of these experiments began from a single clutch of eggs, it is possible to qualitatively examine the variability in development time between families.

The data were analyzed exactly as they were for Figure 29 except that regression lines were calculated from developmental data from each separate experiment. The age of the median individual at each stage was calculated as before by entering $\hat{y} = 50\%$ in the regression equation and solving for x. These development times are listed in Table 5. The missing data in the table arise because only one data point was available for some experiments. Estimates enclosed in brackets come from single data points that were at or near the 50% point for that stage. Due to a shortage of data, only the median development times to copepodite II, III, V, and VI could be analyzed for differences between families.

Several conclusions can be drawn from Table 5. First, the times when 50% of the population had reached each stage from C1 to female averaged from the separate clutch development times are very close to the times calculated from the overall regression. Second, between families, the range in days between the arrival of the median individual to a given stage, is great. In fact, the median individual from a fast-developing clutch of eggs can be nearly two stages ahead of the median individual from a slower developing clutch. Taking "H" and "G" as the most extreme examples, the median C3 appeared on day 32.0 in "H" while the median C1 appeared on day 30.6 in "G".

Table 5. Time in days when 50% of the individuals in a family had reached each listed developmental stage for 12 seperate experiments at 10°C. These times, called median development times (MDT), are from least squares regression of developmental data. Times enclosed in ( ) are inferred from a single data point.

EXP CODE	COPEPODITE STAGE C1	C2	C3	C4	C5	C6	ELAPSED TIME C5 to C6
C		23.2	(<28)	35.7	45.0	65.3	20.3
D		(24.6)	26.0		44.9	68.3	23.4
E	26.1	28.9	31.6	38.0	45.3	68.1	22.8
F		21.9	26.1		(∿39)	59.1	∿20
G	26.7	30.6	35.2	41.8	47.7	61.4	13.7
H		21.5	23.6	32.0	39.1	69.8	30.1
I	18.5	22.2	24.1		36.6	63.0	26.4
J	19.2	22.7	29.6	32.9	40.3	51.9	11.6
K	23.8	27.3	31.8	35.5	42.5	59.8	17.3
L		25.4	32.0	40.9	43.4	52.7	9.3
M	24.7	(27.8)	31.7		42.2	67.7	25.5
N	20.5	24.2	28.9	33.6	40.2	63.5	23.3
AVERAGE	22.8	24.8	29.1	36.3	42.5	62.5	20.0
MDT FROM TABLE 4	21.0	25.3	29.9	36.7	42.9	63.8	20.9

The final conclusion from Table 5 is that if one clutch gets ahead of another clutch for whatever reason, it will not necessarily keep this lead through to the end. This is seen most easily by ranking the data. The "H" clutch was the first to arrive at C2 and C3, the second to C5 but the last to arrive at female. Conversely, "G" was last to arrive at the younger stages but fifth to become a female. The rank-order of arrival to stages C2, C3 and C5 among the 12 clutches was tested for concordance using Kendall's coefficient of concordance, W (Daniel, 1978, p. 326 ff). The result was W = 0.83, significant at the 0.005 level. This means that there is substantial agreement among the ranks as to fast and slow developing clutches. The situation is reversed when rank-order arrivals to stages C3-C5-female and C5-female are examined. In these two cases, no concordance was found. W = 0.39 (χ^2 = 12.8, P$\sim$0.3) and W = 0.54 (χ^2 = 11.9, P$\sim$0.4) respectively. Four of the 12 clutches molted from C5 to female at a much slower rate (C,D,H,I), four of them molted at a faster rate (G,J,K,L) and four of the 12 at an intermediate rate (E,F,M,N) compared to molting during the earlier copepodite stages.

To test these results further, I examined only those eight clutches for which data were available for all stages between C2 and female. Rank-order arrival to stages C2-C3-C4 and C3-C4-C5 were highly concordant (W = 0.87 and 0.85 respectively, P$\sim$0.01) but were not concordant between stages C4-C5-female (W = 0.49, P$\sim$0.15).

The inference which I draw from these descriptive statistics is that molting into adulthood from C5 is controlled by different biological processes than molting into the younger copepodite stages. This is

not surprising because it is at the C5 stage that gonad development is initiated. It is hypothesized that development slows because of the development of ovaries or testes.

DEVELOPMENT AT 11°C. The 11°C data were analyzed by least-squares methods. The development data are listed in Table 6. The median development times at 11°C are somewhat faster than those at 10°C reflecting the effect of temperature on developmental rates. A plot of developmental stage vs time is shown in Figure 32. The developmental pattern is sigmoidal as before. One fact which I want to emphasize with these data is that there is no difference in median development times between families of females collected during the winter (the 10°C experiment) and summer (the 11°C experiment) months.

DEVELOPMENT AT 15°C. The 15°C data were also analyzed by least-squares methods. The data are fewer because only two experiments were carried out and survivorship was low. Therefore, the median development times may have little accuracy. This is particularly true for stages N5, N6 and C1 (Table 6 and Figure 32). Nevertheless, one thing is clear. Compared to the 10° and 11°C data, development at 15°C is greatly accelerated, presumably due to increased temperature. It is a well documented fact (Miller, Johnson and Heinle, 1977; Heip and Smol, 1976; Heinle, 1969) that development time (D) of copepods is related to temperature (T) by a power function of the type $D = a\ T^{b}$. The parameters of this equation were estimated from Calanus marshallae data using least squares analysis after transforming D and T into logarithms. I used time to adult at the three temperatures. The result was

Table 6. Median development times (in days) measured at 10°, 11° and 15°C.

STAGE	10°	11°	15°
N3	3.4	3.4	---
N4	10.2	10.3	5.8
N5	15.0	13.9	8.5
N6	18.4	17.1	8.6
C1	21.0	20.4	8.5
C2	25.3	24.1	13.4
C3	29.9	26.7	15.6
C4	36.7	35.0	19.2
C5	42.9	41.4	27.1
FEMALE	63.8	62.3	35.8

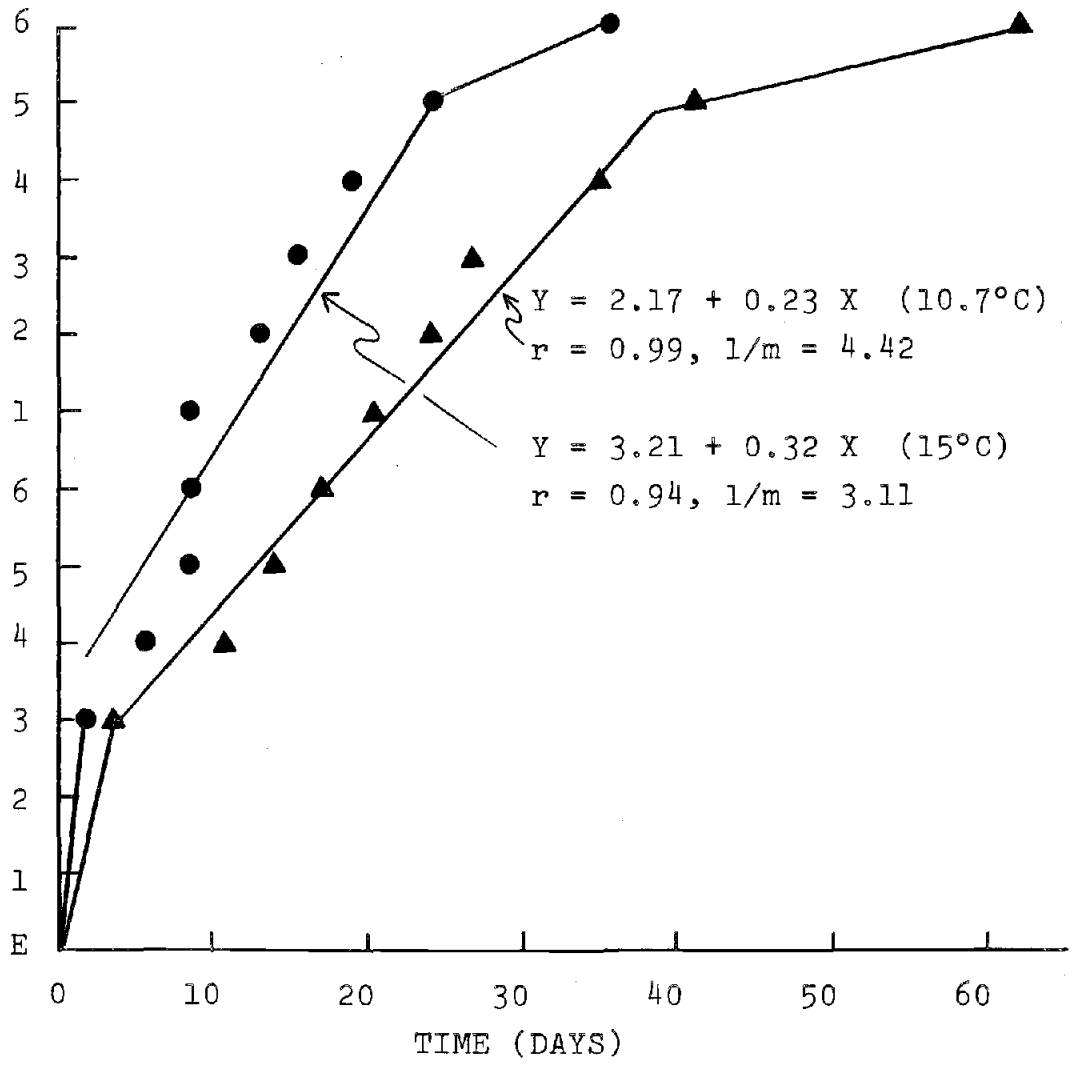


Figure 32. Development of Calanus marshallae at 11° and 15°C. The same sigmoid developmental pattern is seen between stages N3 and female as was seen in the 10°C data shown in Figure 30. Overall development to adult is faster at 15°C than at 10° or 11°C.

$D\ 2223T^{-1.52}$ ($r = .995$). The correlation coefficient is significant at the .06 level. In order to further explore the magnitude of the exponent, I examined the temperature dependence of time to copepodite stages C3, C4 and C5. The equations were respectively, $D = 1274\ T^{-1.63}$ ($r = .999$), $D = 1854\ T^{-1.69}$ ($r = .998$), and $D = 688\ T^{-1.19}$ ($r = .998$). The exponents compare fairly well to Heip and Smol's (1976) data from three harpacticoid copepods ($D = 848\ T^{-1.23}$), to data calculated from Miller, Johnson and Heinle (1977) for Acartia tonsa ($D = 1107\ T^{-1.66}$), and to data calculated from Heinle and Flemer (1975) for Eurytemora affinis ($D = 557\ T^{-1.27}$). My data compare less well to data on Calanus finmarchicus ($D = 420\ T^{-0.94}$) calculated from McLaren (1978) and Pseudocalanus minutus ($D = 164\ T^{-0.73}$) calculated from McLaren (1974). If time to adult were shorter in Calanus marshallae, the intercept (a of the power function) would be smaller in magnitude thus nearer to values calculated for the closely related form C. finmarchicus. This suggests the possibility that C. marshallae is more sensitive to temperature changes than C. finmarchicus.

EFFECTS OF FOOD CONCENTRATION ON DEVELOPMENTAL RATES. No attempt was made to carefully study development rates as a function of food concentration. All experiments began with a dense suspension of a mixture of the diatom Thalassiosira fluviatilis and the flagellate Isochrysis galbana. It was assumed that this would constitute "excess food." Judged by my naked eye, suspensions of phytoplankton in my laboratory experiments were much more dense than natural phytoplankton in a coastal sea water sample. Levels of Thalassiosira fluviatilis at the beginning of a census interval were monitored occasionally,

and ranged from about 2000 to 6000 cells ml^{-1}. These numbers were converted to carbon units in order to facilitate comparison of my work to other works. Based on Coulter Counter measurements, the mean cell volume (V) of my T. fluviatilis clone was approximately 2100 μm^3 $cell^{-1}$. Using the Strathmann (1967) equation, Carbon = 0.378 $V^{0.758}$, my T. fluviatilis carbon $cell^{-1}$ was 125 pico grams. This equates to 250 to 750 µg carbon per liter, over the range of 2000 to 6000 cells ml^{-1}.

Other published studies on the effects of food concentration on developmental rates suggest that laboratory development rates are not strongly influenced by food concentration. Harris and Paffenhoffer (1976) and Paffenhoffer and Harris (1976) found no difference in generation time (egg to adult) for the temperate coastal copepods Temora longicornis and Pseudocalanus elongatus, in experiments carried out at food levels of 25, 50, 100, and 200 µg carbon per liter, and 12.5°C. Development rates of Calanus helgolandicus were the same at food levels of 218, 400 and 800 µg carbon per liter, but retarded at 118 µg carbon per liter (Paffenhoffer, 1970). Food levels in my experiments were comparable to Paffenhoffer's intermediate values. I tentatively conclude that food levels maintained during my laboratory measurements were adequate and that the animals were developing at their maximum rates. Careful measurements of development rates of Calanus marshallae in the laboratory over the range of 50 to 500 µg carbon per liter are needed before one can be certain that the above conclusions are not false. One need not carry out frequent and detailed censuses as I did, however. Food effects could be studied simply by measuring time from egg to first copepodite, for example.

DEVELOPMENT RATES - FIELD OBSERVATIONS

Great difficulties exist in studying copepod developmental rates from field data. First, one is dealing with a population of pelagic animals. This means that the population under study is constantly moving with the water currents. One can never be certain of sampling the same group of animals repeatedly. Second, distinct cohorts must be present. A massive spawning must take place over a short time period, followed by an interval of quiescence. Third, sampling variability is extreme for zooplankton because they are not randomly distributed spatially or temporally. This can lead to spurious results. Fourth, a lesser problem is that one must sample at a frequency commensurate with the duration of each developmental stage. Finally, one must use plankton nets with meshes small enough to capture most of the developmental stages.

It might be possible to monitor the change in age with time of a cohort at sea if one or the other of two conditions are met: (1) the cohort is trapped within a cyclonic eddy of known dimensions and location, or (2) the cohort is initiated at all points along hundreds of miles of coastline in an oceanographic regime where flow within the upper layers is uni-directional. If the first condition is met then one can assume that the same population is being sampled (see for example, Cushing and Tungate, 1963). If the second condition is met, one can study cohorts because the spatial component is minimized by development being initiated at the same time at all points in space. Therefore, with luck, periodic sampling along a fixed line of stations

situated normal to the water flow could result in data on time rate of change of age structure of the cohort as it moves past the observer.

A plausible scenario can be offered in support of the second of the above two alternatives. Off the Washington, Oregon and northern California coasts from late spring through summer, coastal upwelling is the dominant oceanographic process. Upwelling events are periodic, alternating between active and relaxed events. The main upwelling center is along a line source located about 5 to 10 miles from shore. Protracted upwelling events have the effect of transporting female Calanus marshallae from offshore deep water into the nearshore zone where egg laying takes place. During an active upwelling event, phytoplankton are in low abundance but after an event, large phytoplankton blooms develop nearshore. Since egg laying is strongly food dependent (see Chapter V of this dissertation), egg laying rates will be high and a massive spawning event will take place during relaxation of the upwelling. This spawning event could easily take place at most points along the coast which are influenced by coastal upwelling. The spawning event would be terminated when food levels drop as another active upwelling event begins. Since all of the above sequence of events depends ultimately upon the wind, one cannot predict when or even if a cohort will be initiated. So, one must go to sea on a regular basis and hope for the best.

METHODS

Several data sets collected off Oregon are available for study of development rates in the field. Although none of the samples were

collected explicitly for the study of development, some useful information may be gleaned from them. One data set is the three-year time series of zooplankton samples collected between 22 June 1969 and 5 August 1972 at stations 1, 3, 5, and 10 miles off Yaquina Head, Oregon (44°40' N latitude; one mile north of Newport, Oregon). These samples were taken at approximately two-week intervals with bongo nets of 0.24 mm mesh towed obliquely through the entire water column.

Another data set was taken during July-August 1977. It has high spatial resolution at weekly intervals but the time series lasted only six weeks. These samples were taken along one hydrographic line at 45° N with a plankton pump. The data are shown in Figures 10-19.

The final set is a brief series of four samples taken weekly between 28 July and 18 August 1978 at one station five miles off Newport, Oregon, with a 0.12 mm mesh net towed obliquely from 40 m to the surface.

RESULTS

The 1969-1972 data offer the best chance to look for cohorts because the length of the time series is three years. One problem with the data is that the plankton net mest was too large to quantitatively retain the eggs and most naupliar stages of Calanus marshallae. Therefore, I am restricted to the use of the copepodite data alone. An additional and unfortunate problem is that the approximately 14 day sampling intervals were so great that at least two developmental stages could pass during the intersampling period. Cohorts can only be seen if abundance modes persist for at least this

long. If cohorts are present, the temporal resolution of development times may not be very accurate. With these problems in mind, I set out to analyze the data.

The data (previously unpublished) are abundances of Calanus marshallae copepodite stages, expressed as numbers per cubic meter, at stations 1,3,5, and 10 miles from shore. The data were standardized by converting to percent in each stage at each station. In order to reduce the dimensionality of the data (date x stage x station), the percentages of C1, C2 and C3 were each averaged over stations 1, 3, and 5, and C4, C5, male and female were averaged over all four stations, giving a date x stage array. This averaging is justified because the region of greatest abundance of the C1-C3 is usually within the first five miles from shore. C4-C6 range over the entire shelf, but are usually more abundant offshore than onshore.

Percentages in each stage on each of 46 sampling dates are shown in Tables 7 through 10. Modes in relative stage abundance are seen in all of the data, with perhaps the best definition in the years 1970 and 1971. Cohorts do exist and can be traced simply by following modes. At times, successive reappearances of modes within a single stage are seen (for example, C1 on 6 May 1970 reappearing on 16 June 1970). These give an estimate of total generation time. Other periods are much more sketchy, giving only estimates of the time spent passing through three or four developmental stages (for example, C2 to female from 3 to 28 September 1969). Developmental periods during each year are listed in the tables.

Table 7. Relative abundance of copepodite stages of Calanus marshallae (% of total C. marshallae) during 1969. Stages C1, C2 and C3 are averaged over stations 1, 3, and 5 miles from shore. Stages C4, C5, male and female are averaged over stations 1, 3, 5 and 10 miles from shore. See text for more details.

DATE	INTERVAL BETWEEN SAMPLING	C1	C2	C3	C4	C5	♀	♂
22 JUNE 1969		5.1	14.2	51.6	29.8	19.8	5.1	1.5
29 "	7 days	4.7	0.6	4.3	28.3	21.3	8.2	6.3
10 JULY	11 days	6.9	21.8	11.2	18.3	20.3	18.3	3.3
18 "	8 days	1.1	6.6	4.0	11.4	28.0	9.9	2.8
25 "	7 days	23.9	8.9	25.0	9.1	30.5	7.7	4.8
6 AUG	12 days	25.1	22.4	17.1	13.1	5.8	15.5	0.7
26 "	20 days	22.8	25.1	39.1	10.7	0.0	0.0	0.0
30 "	4 days	0.0	3.7	30.7	53.5	11.0	6.5	0.2
3 SEPT	4 days	0.3	0.3	9.3	62.3	17.0	7.0	0.9
14 "	11 days	0.0	2.9	4.0	28.1	56.9	11.4	0.0
28 "	14 days	0.0	0.0	0.0	0.0	----	38.7	0.0
8 OCT	10 days	0.0	0.0	0.0	0.0	0.0	0.0	0.0

COHORT	INCLUSIVE DATES	INCLUSIVE DEVELOP. STAGES	DURATION	MEAN SURF. TEMP.	COMPARABLE LABORATORY DURATION (10°)
1	22 June-23 July	C3 - ♀	31 days	11.6°C	33.9 d
2	31 July- 3 Sept	C1 - C4	33 days	10.6°	16 d
2	31 July-14 Sept	C1 - C5	45 days	10.2°	22 d
2	~16 Aug -14 Sept	C2 - C5	29 days	10.4°	17.6 d
2	3 Sept-28 Sept	C4 - ♀	25 days	10.6°	27 d

Table 8. Relative abundance of copepodite stages of Calanus marshallae (% of total C. marshallae) during 1970.

DATE	INTERVAL BETWEEN SAMPLING	C1	C2	C3	C4	C5	♀	♂
25 FEB 1970		57.3	22.7	9.1	1.4	5.0	7.3	0.0
9 MAR	12 days	40.6	14.3	15.9	11.9	2.4	0.4	0.0
27 APR	50 days	9.3	12.5	13.6	21.5	13.8	27.4	3.7
6 MAY	9 days	43.5	16.1	3.8	4.9	11.0	23.6	12.0
4 JUNE	29 days	9.2	30.2	27.9	18.9	6.7	6.1	1.0
23 JUNE	19 days	1.8	7.9	26.8	10.9	11.2	15.5	4.0
2 JULY	9 days	2.4	13.4	29.4	18.0	6.9	8.5	1.1
16 JULY	14 days	46.7	15.4	9.3	11.5	9.0	9.3	1.4
29 JULY	13 days	26.3	8.9	15.1	11.0	3.1	2.8	0.0
13 AUG	15 days	16.9	24.4	39.4	14.5	4.4	2.2	0.0
23 AUG	10 days	8.8	10.4	27.2	31.6	19.1	8.0	0.0
11 SEPT	19 days	40.3	12.9	1.9	5.2	9.9	2.9	0.0
25 SEPT	14 days	15.0	3.8	7.3	18.1	23.3	1.8	0.3
9 OCT	14 days	0.0	0.0	0.0	0.0	100.0	0.0	0.0

COHORT	INCLUSIVE DATES	INCLUSIVE DEVELOP. STAGES	DURATION	MEAN SURF. TEMP.	COMPARABLE LABORATORY DURATION (10°)
1	∿1 MAR - 6 MAY	C1 - C1	67 days	10.3°C	64 days
2	6 MAY - 16 JULY	C1 - C1	71 days	10.0°	64 days
2	4 JUNE- 13 AUG	C2 - C2	70 days	9.7°	64 days
2	∿17 JUNE- 18 AUG	C3 - C3	62 days	9.7°	64 days
3	16 JULY- 11 SEPT	C1 - C1	57 days	10.3°	64 days

Table 9. Relative abundance of copepodite stages of Calanus marshallae (% of total C. marshallae) during 1971.

DATE	INTERVAL BETWEEN SAMPLING	C1	C2	C3	C4	C5	♀	♂
6 JAN 1971		0.0	0.0	1.1	7.9	39.3	45.3	6.1
16 FEB	41 days	45.4	5.6	4.1	0.3	0.5	43.6	5.2
30 MAR	42 days	0.4	5.2	9.4	9.0	21.7	24.5	5.9
3 MAY	34 days	8.0	8.3	11.5	9.2	7.5	40.6	11.6
14 MAY	11 days	30.9	7.7	13.8	12.5	6.8	22.2	4.6
29 MAY	15 days	1.2	1.3	6.9	22.1	13.3	11.6	5.9
12 JUNE	14 days	34.2	14.3	14.5	20.0	21.8	5.5	1.4
28 JUNE	16 days	0.0	1.2	3.0	29.7	31.8	0.4	0.0
6 JULY	8 days	1.6	3.2	18.4	47.8	29.1	6.2	0.3
21 JULY	15 days	0.0	0.0	1.7	15.4	41.4	16.7	0.2
2 AUG	12 days	0.9	0.9	2.9	1.1	43.0	51.4	0.0
19 AUG	17 days	54.3	7.1	3.4	1.1	17.0	7.2	0.0
23 SEPT	35 days	0.0	1.1	2.3	12.1	56.7	0.9	0.9
11 OCT	18 days	42.4	16.9	3.3	1.0	1.0	0.0	1.0
6 NOV	26 days	21.1	16.2	33.4	24.3	8.6	0.0	0.0

COHORT	INCLUSIVE DATES	INCLUSIVE DEVELOP. STAGES	DURATION	MEAN SURF. TEMP.	COMPARABLE LABORATORY DURATION (10°)
1	16 FEB -14 MAY	C1 - C1	87 days	9.5°C	64 days
2	6 JULY- 2 AUG	C4 - ♀	27 days	11.7°	27 days
3	2 AUG -19 AUG	Egg- C1	17 days	15.0°	21 days
3	19 AUG -11 OCT	C1 - C1	53 days	13.1°	64 days
(2?)	(?)20 JUNE- 2 AUG	C1 - ♀	43 days	12.5°	43 days

Table 10. Relative abundance of copepodite stages of Calanus marshallae (% of total C. marshallae) during 1972.

DATE	INTERVAL BETWEEN SAMPLING	C1	C2	C3	C4	C5	♀	♂
22 MAY 1972		21.7	34.8	15.9	14.6	9.8	4.7	5.7
11 JUNE	20 days	0.0	0.0	4.8	30.9	31.8	1.7	0.2
28 JUNE	17 days	0.4	2.1	6.4	15.3	39.0	5.7	0.7
21 JULY	23 days	10.4	5.5	15.4	16.1	26.4	26.1	0.0
5 AUG	15 days	34.0	7.1	22.9	11.7	22.3	16.8	0.0

COHORT	INCLUSIVE DATES	INCLUSIVE DEVELOP. STAGES	DURATION	MEAN SURF. TEMP.	COMPARABLE LABORATORY DURATION (10°)
1	22 May-28 June	C2 - O	37 days	10.1°C	39 days

The pattern from each of the four seasons of data is the appearance of cohorts in February, May, July and in some years, September. Four complete cohorts were seen during the February-September 1970 growing season, as evidenced by four distinct modes in C1 relative abundance. Three cohorts moved through the 1971 season.

The 1977 data are shown in Figure 33. The profiles of abundance with depth were integrated by the trapezoid method thus converting abundances of each developmental stage to numbers beneath a square meter water column extending from 1 m to the deepest depth sampled. Numbers per square meter were summed over all stations on each date giving an abundance x date table. These are the data shown in Figure 33.

Two cohorts are seen. In order to analyze the development rates of these cohorts, the area within each cohort was calculated then the fractional stage when half of the total area was attained, was estimated. These "area-midpoints" are connected by straight line segments. Development over the cohort existence time is then compared to times for the same amount of development to take place in the laboratory. The 8 July-29 July 1977 cohort began at a point 0.6 between C2 and C3, and ended midway between C4 and C5. This cohort developed slowly. Twenty-one days elapsed in the field where 10.9 days would pass in the laboratory for these fractional stages to develop. After 29 July, the cohort was evidently lost. The second cohort was first seen on 15 July 1977 and was still present on 13 August, our last sampling date. Laboratory times of 26.1 days compare well to the 29 days estimated from the field for development of N4 to C4.

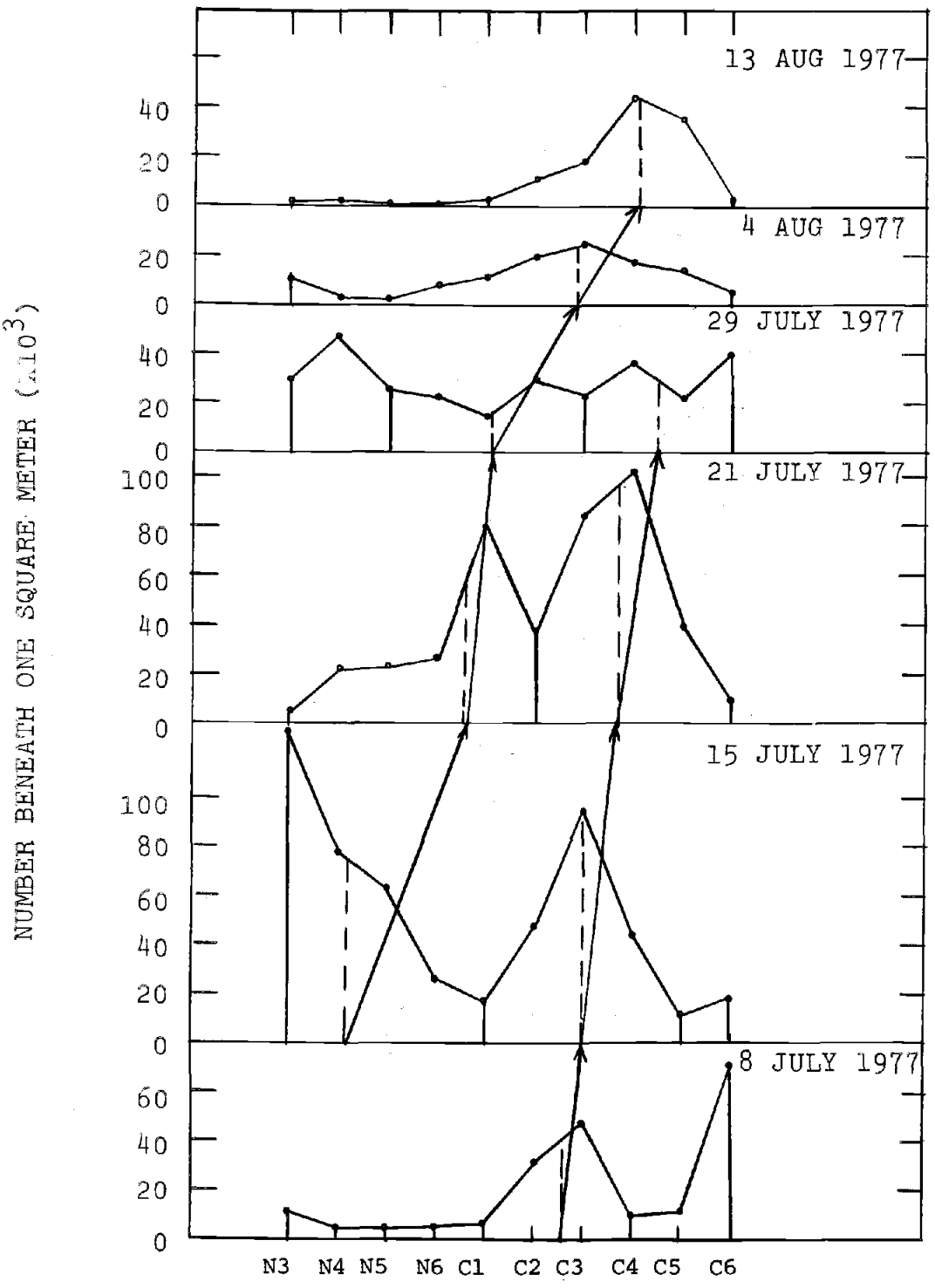


Figure 33. Development of cohorts during July-August 1977. Two cohorts were seen.

Development in the field during 28 July-18 August 1978 is shown in Figure 34. A clear cohort was initiated sometime before 28 July. On this date, a mode of N3-N4-N5 was present. This mode persisted through 18 August, developing to C3 in 21 days. This compares well to a laboratory time of 19.7 days from N4 to C3. Area midpoints were calculated. The fractional developmental stages over the cohort time span were N4+0.25 to C3+0.1. The laboratory time for this developmental interval was 19.2 days.

There is little doubt that cohorts exist and that they can be traced in nearshore copepod populations. This can only happen by synchronous egg laying along a line source extending hundreds of miles along the Washington and Oregon coast. It is hypothesized that both the synchrony and event nature of egg laying are initiated and controlled by the discontinuous upwelling events described earlier.

Table 11 summarizes the development time information gleaned from the above field data sets. The inclusive dates between modes of the indicated stages and the time in days between modes are compared to laboratory development times which were measured at 10°C. Also listed is sea surface temperature averaged over the inter-mode period. There are two striking features in this table. First, the sea surface temperature changes little during winter, spring and summer months, with the exception of August and September 1971. Second, the duration of developmental periods in the field are remarkably similar to laboratory development times. Developmental rates seen in the field were as fast as laboratory rates in 12 of 19 cases, slower than the laboratory in 5 of 19 cases and faster in 2 of 19 cases. These latter

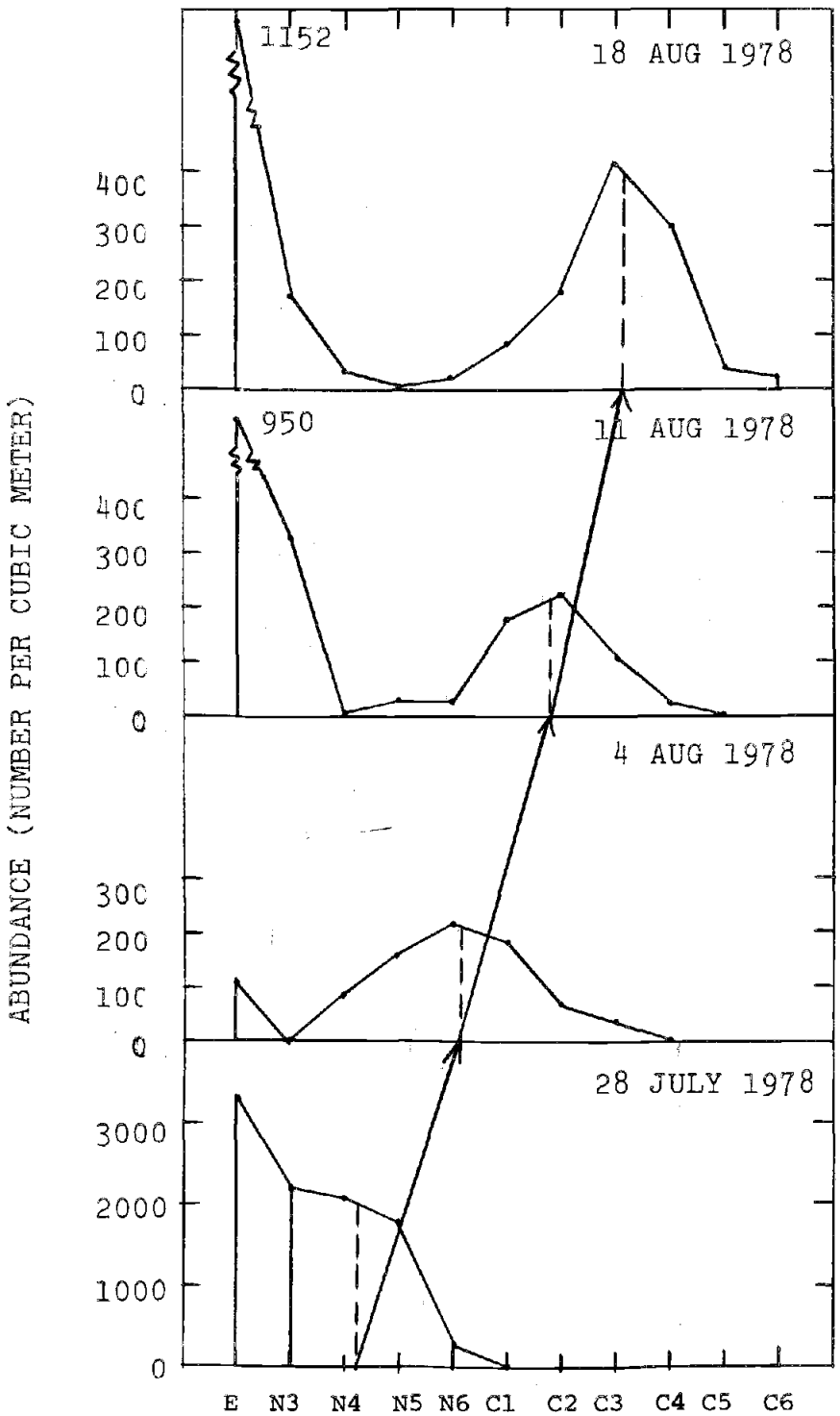


Figure 34. Development of a cohort in August 1978.

Table 11. A listing of cohorts identified in the 1969-1972, 1977 and 1978 data sets. Duration in the field is compared to development in the laboratory at 10°C. Field and laboratory development times are compared in Figure 35.

COHORT	INCLUSIVE DATES	INCLUSIVE DEVELOP. STAGES	FIELD DURATION	MEAN SURF. TEMP.	COMPARABLE LABORATORY DURATION (10°C)
	(1969)				
1	22 JUNE-23 JULY	C3 - ♀	31 days	11.6°C	34 days
2	31 JULY- 3 SEPT	C1 - C4	33 days	10.6°	16 days
	31 JULY-14 SEPT	C1 - C5	45 days	10.2°	22 days
	∿16 AUG -14 SEPT	C2 - C5	29 days	10.4°	18 days
	3 SEPT-28 SEPT	C4 - ♀	25 days	10.6°	27 days
	(1970)				
1	∿ 1 MAR - 6 MAY	C1 - C1	67 days	10.3°C	64 days
2	6 MAY -16 JULY	C1 - C1	71 days	10.0°	64 days
	4 JUNE-13 AUG	C2 - C2	70 days	9.7°	64 days
	∿17 JUNE-18 AUG	C3 - C3	62 days	9.7°	64 days
3	16 JULY-11 SEPT	C1 - C1	57 days	10.3°	64 days
	(1971)				
1	16 FEB -14 MAY	C1 - C1	87 days	9.5°	64 days
2(?)	∿20 JUNE- 2 AUG	C1 - ♀	43 days	12.5°	43 days
2	6 JULY- 2 AUG	C4 - ♀	27 days	11.7°	27 days
3	19 AUG -11 OCT	C1 - C1	53 days	13.1°	64 days
	2 AUG -19 AUG	Egg- C1	17 days	15.0°	21 days
	(1972)				
1	22 MAY - 28 JUNE	C2 - ♀	37 days	10.1°	38 days
	(1977,1978)				
1	8 JULY-29 JULY 77	C2 - C4	21 days	12.0°C	11 days
2	15 JULY-13 AUG 77	N4 - C4	29 days	11.5°	26 days
3	28 JULY-18 AUG 78	N4 - C3	21 days	10.6°	19 days

two fast rates occurred in late-summer 1971 when the surface waters were 3-5 °C warmer than usual, This temperature increase would accelerate development.

Figure 35 shows the regression of development time in the field against development in the laboratory using the data in Table 11. The slope of the regression line was not significantly different from 1.0 ($t = 1.02$, $P = 0.01$, 17 degrees of freedom). I conclude that field and laboratory developmental rates are generally the same. This relationship has two possible implications. If one assumes that laboratory animals were properly cared for under satisfactory conditions of food, light and temperature, then one must conclude that animals are developing in the field under conditions of adequate resources. Food is not limiting. On the other hand, if one assumes that developmental rates in the field are at their maximum, then one can conclude that the laboratory measurements were carried out without undue hardship to the animals and that the laboratory animals were not growing in some odd way peculiar to laboratory conditions.

It is not possible to resolve this dilema because I have no precise measurements of the effects of food concentration on development times. However, during the summer of 1976, concurrent with the five "adequate food" developmental rate experiments, four experiments were carried out using "low food". In these experiments, food was added at concentrations 0.1 of the amounts added to the adequate food beakers. Development progressed for 21, 22, 31 and 40 days respectively after which an order of magnitude more food was added. Table 12 summarizes the results. There were two clear effects. First,

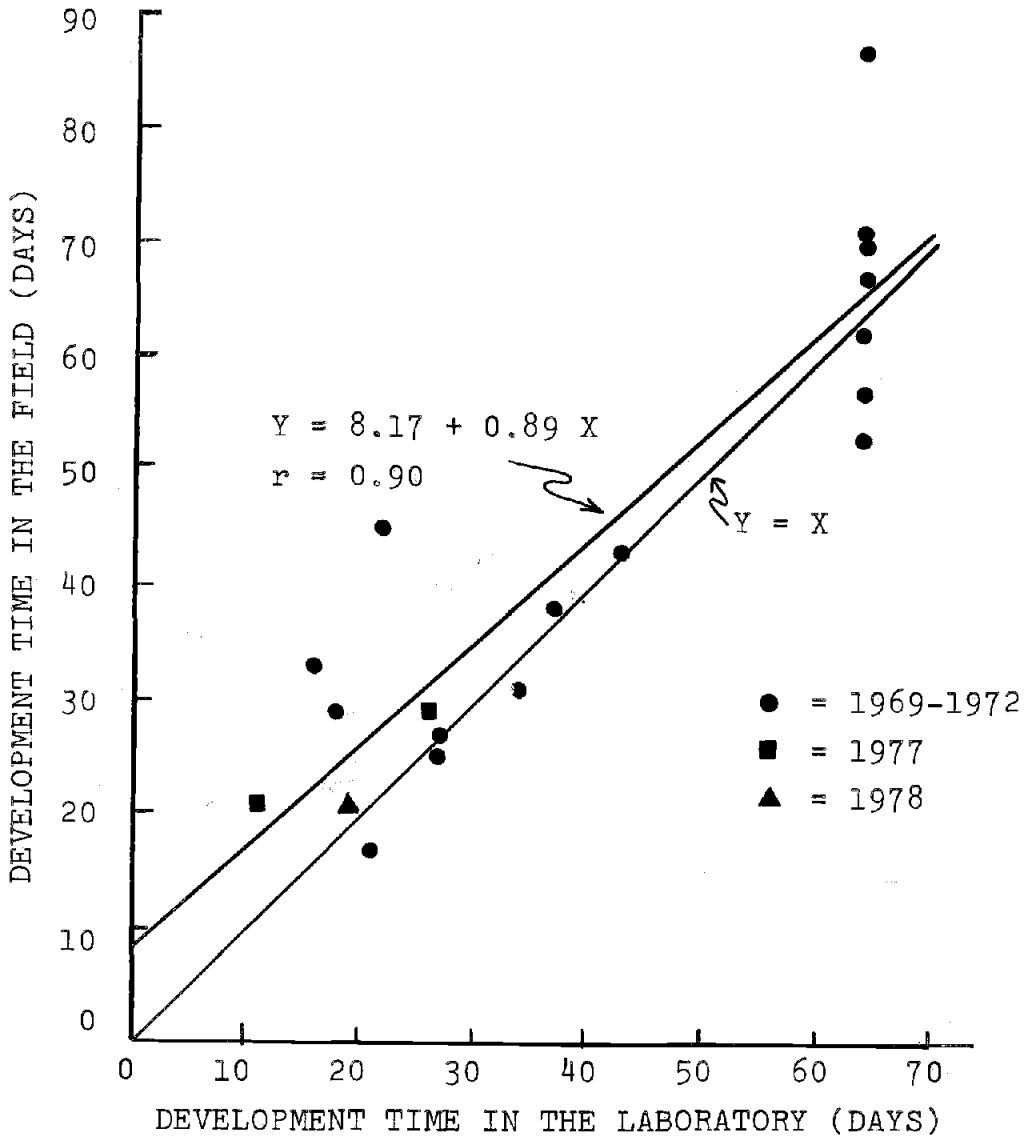


Figure 35. A scatter diagram of development times in the field vs. development times in the laboratory. The data are from Table 11. The slope of the regression line was not significantly different from 1.0 which means that field and laboratory development rates are the same.

Table 12. Results of the low food experiments. Growth rates are retarded if food levels are too low. At the end of the low food period, animals were behind the high food beakers by two to five developmental stages. After being fed higher levels of food, groups 1 and 2 recovered and grew at rates equal to animals that were always adequately fed. Groups 3 and 4 did not recover.

EXPERIMENT	DAYS ON "LOW FOOD"	STAGE OF MEDIAN IND. ON FINAL DAY OF "LOW FOOD"	MEDIAN STAGE ON HIGH FOOD AT NEXT CENSUS	MEDIAN STAGE ON HIGH FOOD AT TERMINATION	ELAPSED TIME ON HIGH FOOD	EXPECTED TIME IF FOOD WAS ADEQUATE
1	21	N4-N5	N5,24.1	♀,70.3	46.2 d	48.8 d
2	22	N3-N4	N4,24.8	C5,57.7	32.9 d	32.7 d
3	31	N4-N5	N6,36.3	C3,53.7	17.4 d	11.5 d
4	40	N5-N6	N6,40	C2,57	17 d	6.9 d

at the end of the low food period, animals in the low food beakers were behind the high food beakers by two and one-half to five developmental stages. Second, after again being fed adequate amounts of food, the first two experimental groups recovered and grew at rates equal to the animals which were always fed adequate amounts of food. The other two experimental groups did not recover completely. Development did progress faster than during starvation, but never as fast as the adequately fed group. This suggests that after three to four weeks of near-starvation conditions, the animals had metabolized so much of their protein that they were unable to completely repair the damage to their bodies.

To further explore starvation effects, I maintained nauplii in filtered seawater. Eggs were collected from females kept in 100 ml of membrane-filtered seawater. The containers were examined at one to three day intervals and dead individuals were removed. Five experiments were carried out using Calanus marshallae eggs and one experiment was done with C. pacificus eggs. The results are shown in Figure 36. In all cases, the developing individuals reached the third naupliius stage. Development did not progress beyond this stage. The N3 survived well until day 11 or 12, after which mortality rates were high. Since the time from egg laying to N3 is 3.5 days, the N3 stage can survive for 8 to 10 days without feeding.

Peterson, Miller and Hutchinson (1979) hypothesized that zooplankton living in the very nearshore zone one to three miles from shore can experience several-week periods of relatively low phytoplankton concentration during active upwelling events. Both the ability of

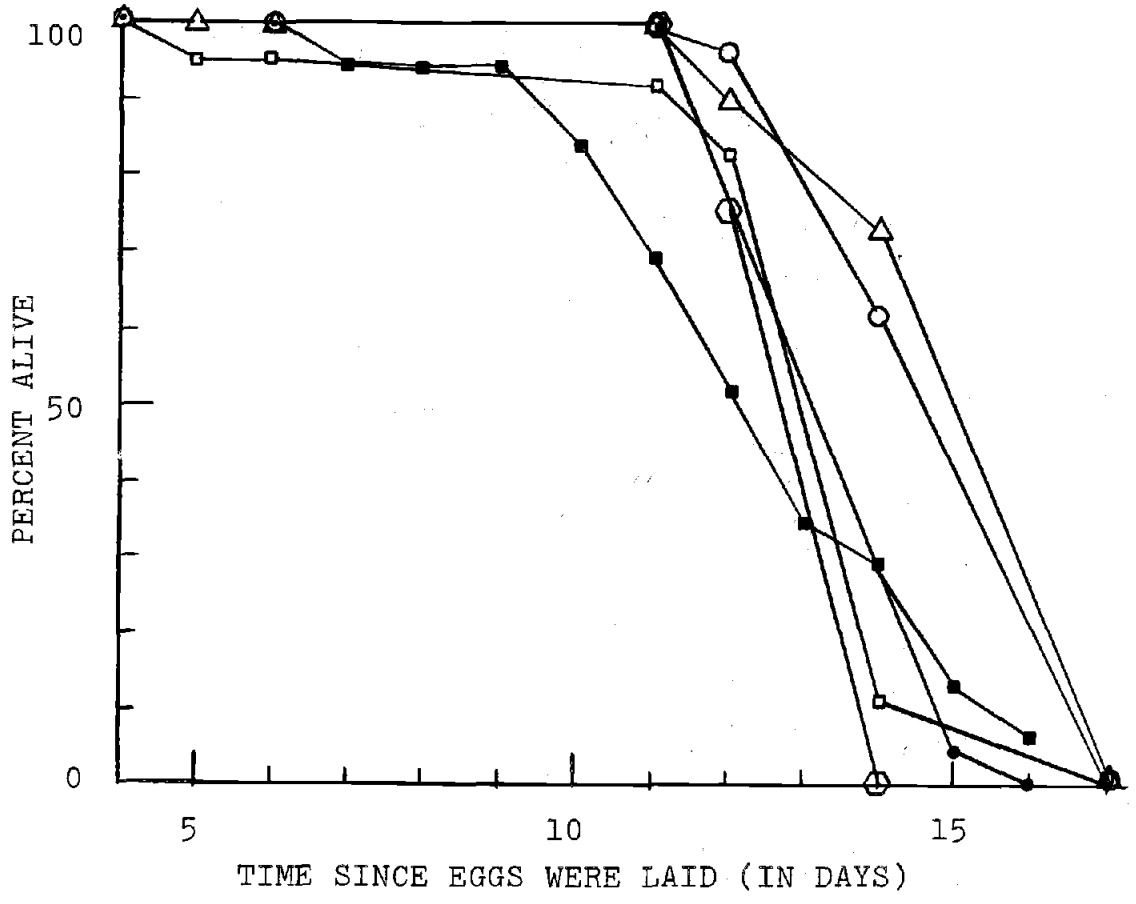


Figure 36. Survivorship of starved N3 of Calanus marshallae (open symbols) and C. pacificus (■).

Calanus nauplii to recover their growth rates after 21 days of low food, and their ability to survive for 10 days without any food at all, would be highly adaptive traits for survival in the Oregon upwelling zone. These traits have not necessarily evolved as an adaptation to life in this region, but would be adaptive to this environment.

GROWTH

Individuals grow in both length and weight. In copepods, length increases occur only at each molt, and are thus incremental. Weight is probably gained almost continuously, but since it is not possible to assign an age to an individual, weight gains must also be treated as incremental. The measurement data then are length vs. stage and weight vs. stage. Neither is a continuous function.

METHODS

Length measurements were made with a Wild M-5 binocular dissecting microscope equipped with an ocular micrometer. Measurements were made to the nearest micrometer division at 50 x for eggs and nauplii and 25 x for copepodites. Total length was measured from the tip of the head to the end of the furcae (excluding furcal setae). Laboratory animals were measured alive without anesthetics. Field material was measured from formalin-preserved specimens.

Weights were estimated only from living material. In most cases, individuals were collected from the field and dried on the same day. Copepodites were removed with a pipette, transferred to a paper towel, rinsed briefly with distilled water, transferred to a small piece of aluminum foil, then dried in an oven at 60°C. Eggs and nauplii were

collected with a pipette, transferred to a piece of Whatman filter paper and rinsed. The filter paper was scanned beneath the dissecting microscope and the animals were counted, then rolled into a stack using a dissecting needle. This was transferred to a piece of foil and dried at 60°C. All weighings were done on a Cahn Gram Electrobalance. Dried animals were transferred to tared pans and weighed. Eggs and N3 were dried in lots of 50 to 100 individuals each. N4 to N6 were dried in lots of 15-20, and C1 through C3 in lots of two to eight individuals. Since Calanus marshallae is a large copepod, it was possible to weigh individual C4, C5 and adults thus obtaining data on length-weight relationships.

RESULTS

CHANGE IN LENGTH WITH STAGE. We have seen that nauplii and copepodites of Calanus marshallae develop at approximately the same rates from N3 to C5. Growth rates expressed in terms of body length are very different.

Figure 37 is a plot of total length vs. developmental stage. It compares data from the summer of 1976 experiments done at 11°C (LAB-76), the winter of 1977 development time experiments at 10°C (LAB-77), and from measurements made on field-collected material. The years 1969 and 1977 were arbitrairly chosen as representative of field animals. It can be seen in the figure that change in length with stage occurs in two linear phases. Nauplii increase in body length at the rate of 0.06 mm per stage which is one-eighth the rate for copepodites of 0.51 mm per stage. There were no statistically significant differences between mean total length of any naupliar stage grown in

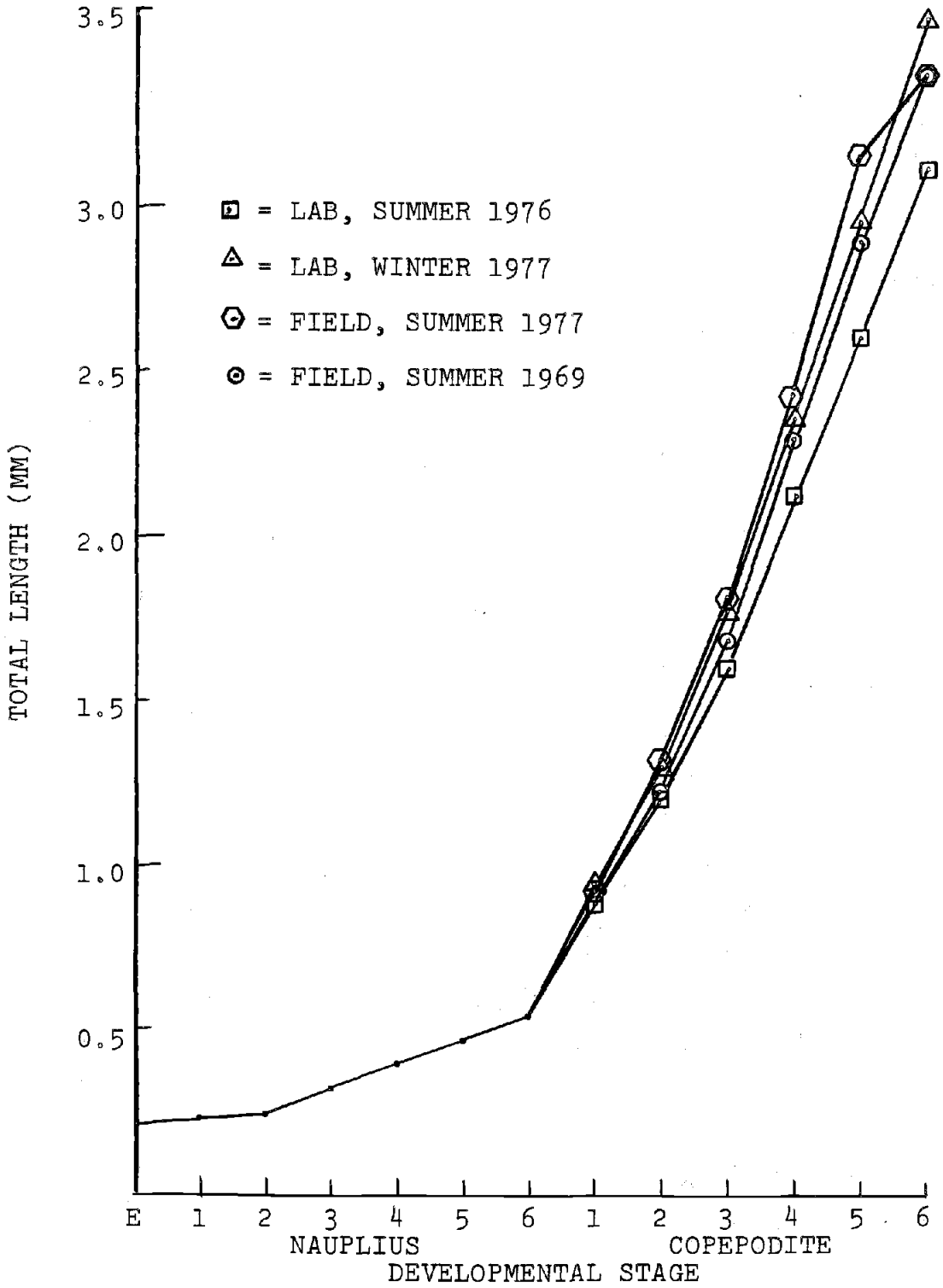


Figure 37. A comparison of total lengths of laboratory-reared and field-collected Calanus marshallae developmental stages.

the laboratory compared to those grown in the field, based on paired t-tests. However, average total lengths of each of the six copepodite stages from LAB-77 were significantly greater than LAB-76 copepodites. Only C4 and C5 from the field in summer of 1977 were significantly longer than LAB-77 specimens. LAB-77 females were significantly longer than field females ($t = 7.04$, 270 degrees of freedom). This fact supports my belief that food levels in development experiments at 10°C were at an adequate level, and that the food used, Thalassiosira fluviatilis and Isochrysis galbana, were of adequate nutritional quality.

According to Brook's Rule (see Miller, Johnson and Heinle, 1977), the ratios of body lengths of successive stages are nearly constant. The data on average body lengths of Calanus marshallae which were plotted in Figure 37 are listed in Table 13 along with the body length ratios. Relative growth in length is slowest in naupliar stages, rapid between N6 and C1 and moderately high between the early copepodite stages. The rate of relative growth decreases through the late copepodite stages. Five growth periods are seen: (1) between N2 and N6, the growth increment is 1.22, (2) from N6 to C1, 1.67, (3) C1 through C4, 1.36, (4) C4 to C5, 1.26 and (5) C5 to female, the growth increment is 1.16.

MATERNAL EFFECTS ON TERMINAL SIZE. Laboratory-reared females (LAB-77) were significantly longer than field females. A puzzling part of these data was that the range in length of laboratory-raised females was much greater than field females (Table 14). This fact suggests the following two hypotheses: (1) Since the laboratory

Table 13. Total length (L) and growth increment (I) of laboratory and field Calanus marshallae. The growth increment = $L_{(\text{stage } i+1)}/L_{(\text{stage } i)}$. Length is mm.

STAGE	(LAB - 76) L	I	(LAB - 77) L	I	(FIELD-77) L	I	(FIELD-69) L	I
E	.22							
N1	.21							
N2	.25	1.19	.25		.25			
N3	.33	1.32	.32	1.28	.33	1.32		
N4	.40	1.21	.41	1.28	.42	1.27		
N5	.48	1.20	.49	1.20	.48	1.14		
N6	.55	1.15	.55	1.12	.55	1.15		
C1	.88	1.60	.95	1.73	.93	1.69		
C2	1.19	1.35	1.30	1.37	1.31	1.41	1.23	1.38
C3	1.60	1.34	1.77	1.36	1.81	1.38	1.69	1.37
C4	2.12	1.32	2.36	1.33	2.43	1.34	2.35	1.39
C5	2.62	1.24	2.96	1.25	3.16	1.30	2.90	1.23
♀	3.12	1.19	3.57	1.21	3.41	1.08	3.41	1.17

Table 14. A comparison of total length of laboratory and field female Calanus marshallae. Laboratory-reared females were significantly longer than field females ($t = 7.04$, 270 degrees of freedom).

	LAB 1977		FIELD 1977	
SIZE CLASSES	TOTAL	%	TOTAL	%
2.60 - 2.76 mm	0	0.0	1	0.1
2.80 - 2.96	0	0.0	1	0.1
3.00 - 3.16	2	2.0	79	6.1
3.20 - 3.36	14	14.1	400	30.8
3.40 - 3.56	22	22.2	572	44.1
3.60 - 3.76	44	44.4	213	16.4
3.80 - 3.96	16	16.2	29	2.2
4.00 - 4.16	1	1.0	2	0.2
Total	99		1297	

conditions represent a nearly constant environment with adequate amounts of food, the great range in terminal size cannot be ascribed to environmental effects. It may be due almost entirely to genetic differences between females. (2) Since the larger (>3.8 mm) females are seldom seen in the field, they may be selectively eaten by some unknown predator.

The first hypothesis was examined by regressing terminal size of daughters against that of their mothers. This regression was possible because most of the LAB-77 development time measurements began with eggs from a known mother. Data were available for nine families. They are shown in Figure 38. The trend of the data suggests that larger mothers have the smaller daughters on the average. However, the slope of the regression line was not significantly different from zero (sample F = 3.24, critical F = 3.92 with 1,98 degrees of freedom). Only 3 % of the variability in terminal size of all daughters was explained by size of their mothers. I conclude that the sizes of mothers have little influence on sizes of their daughters. Terminal size of daughters is extremely variable. It will be shown later in this dissertation that fecundity is independent of body size as well. Therefore, it would appear that there is no reproductive advantage in being large. In fact, large size may be selected against.

CHANGE IN WEIGHT WITH STAGE. The dry weight (W) vs. stage data are plotted in Figure 39. Weight increases between the egg and N4 progress slowly. From N4 through female, weight is gained at an overall weight-specific exponential rate of 0.73 µg per µg per stage. The trend of the N4 through C2 stages suggests a slower growth rate

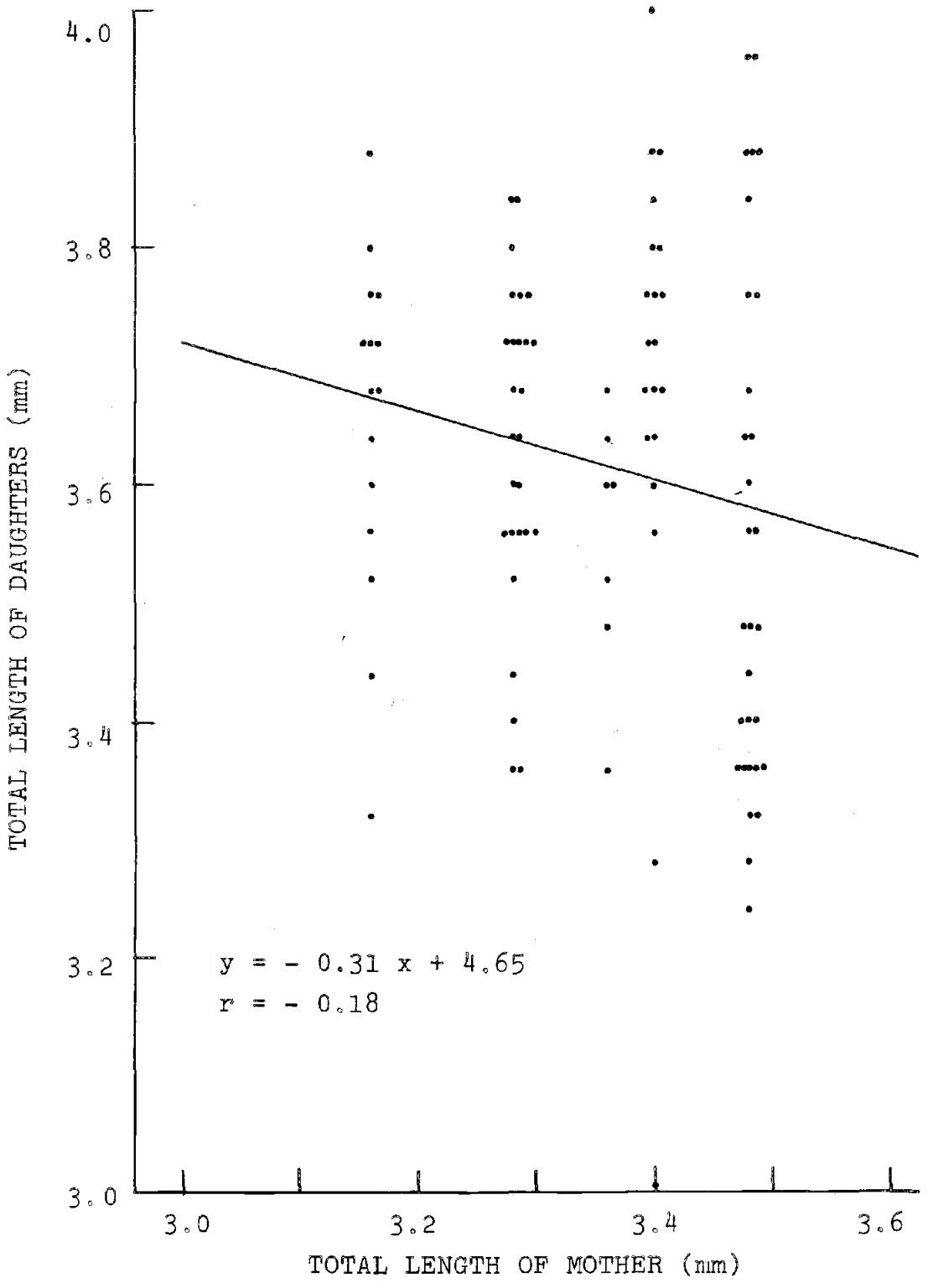


Figure 38. Scatter diagram of length of daughters vs. length of mother, for Calanus marshallae.

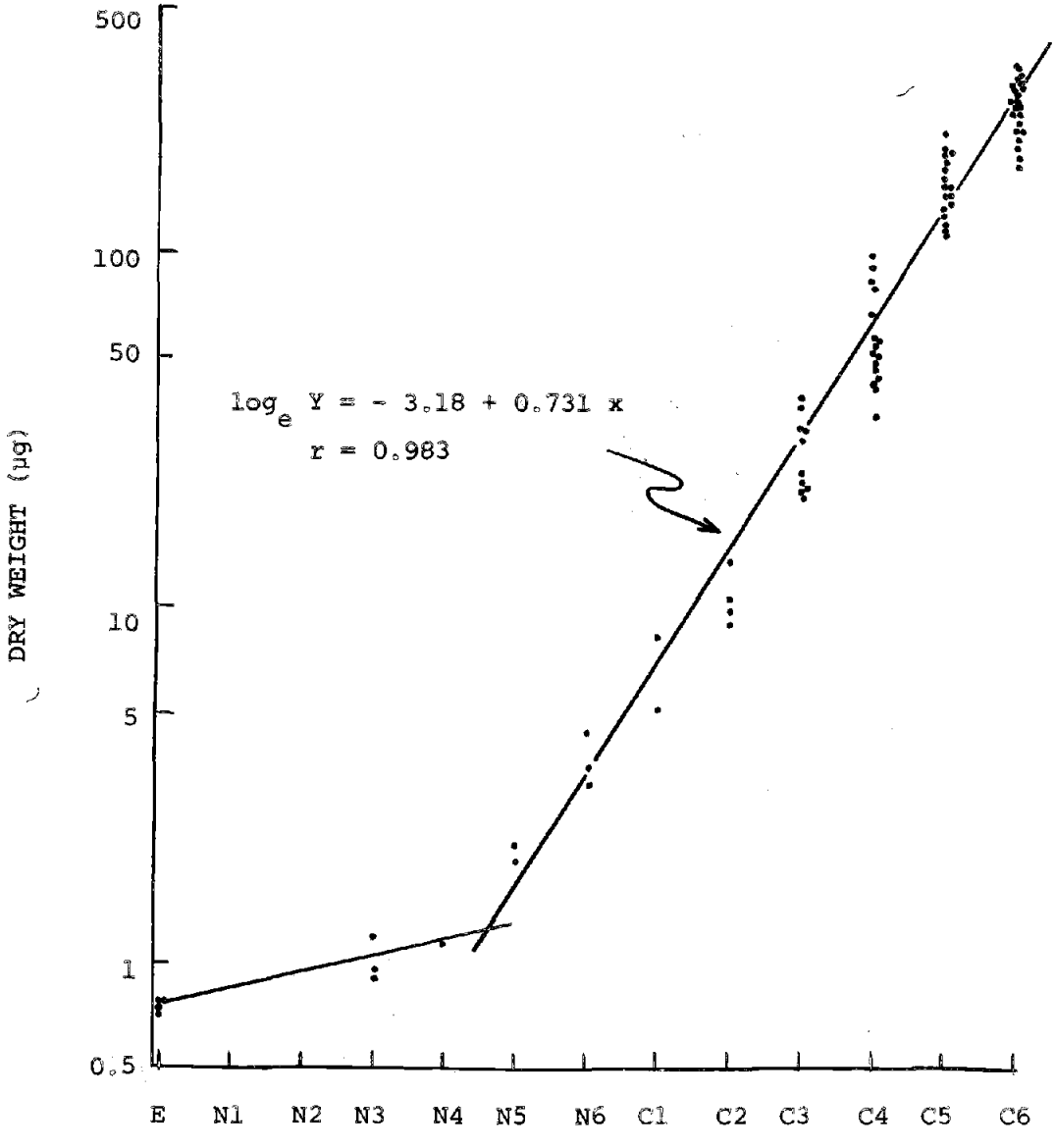


Figure 39. Change in weight with stage for Calanus marshallae. Weight changes are exponential from N4 through C6 (females).

during this developmental period. Regression of log W on stage gives a growth rate of 0.55 µg per µg per stage. The older copepodites (C3 to C6)progress at a rate of 0.76 µg per µg per stage.

LENGTH-WEIGHT RELATIONSHIPS. Copepod weight (W) is roughly proportional to the cube of length (L) times some constant, thus is described by the power function, $W = a L^{b}$. The coefficients are found by least squares methods after transforming both L and W to logarithms. Length-weight data are needed to allow better estimates of copepod biomass from preserved samples. One may calculate biomass from enumeration data and average weight per stage data for each developmental stage, but better estimates become possible if length and weight relationships have been established. It is particularly important to have such data if the animals in question are subjected to great seasonal oscillations in length as a result of a strong seasonal temperature gradient. This latter reason does not apply to Calanus marshallae because they are not subject to a variable temperature regime. Environmental temperatures seldom deviate from 8° to 12°C.

The length-weight data for Calanus marshallae are shown in Figure 40. The measurements on copepodite stages C1, C2 and C3 are of low quality because the lengths are averages from a group of animals different from those which were weighed. The C4, C5 and C6 data were taken properly. That is, they are sets of lengths and weights from many separate individuals. The overall regression of C1 through C6 was $W = 4.13 L^{3.28}$ ($r = 0.97$). If only C4 through C6 are included in the regression, the relationship is $W = 2.00 L^{3.92}$

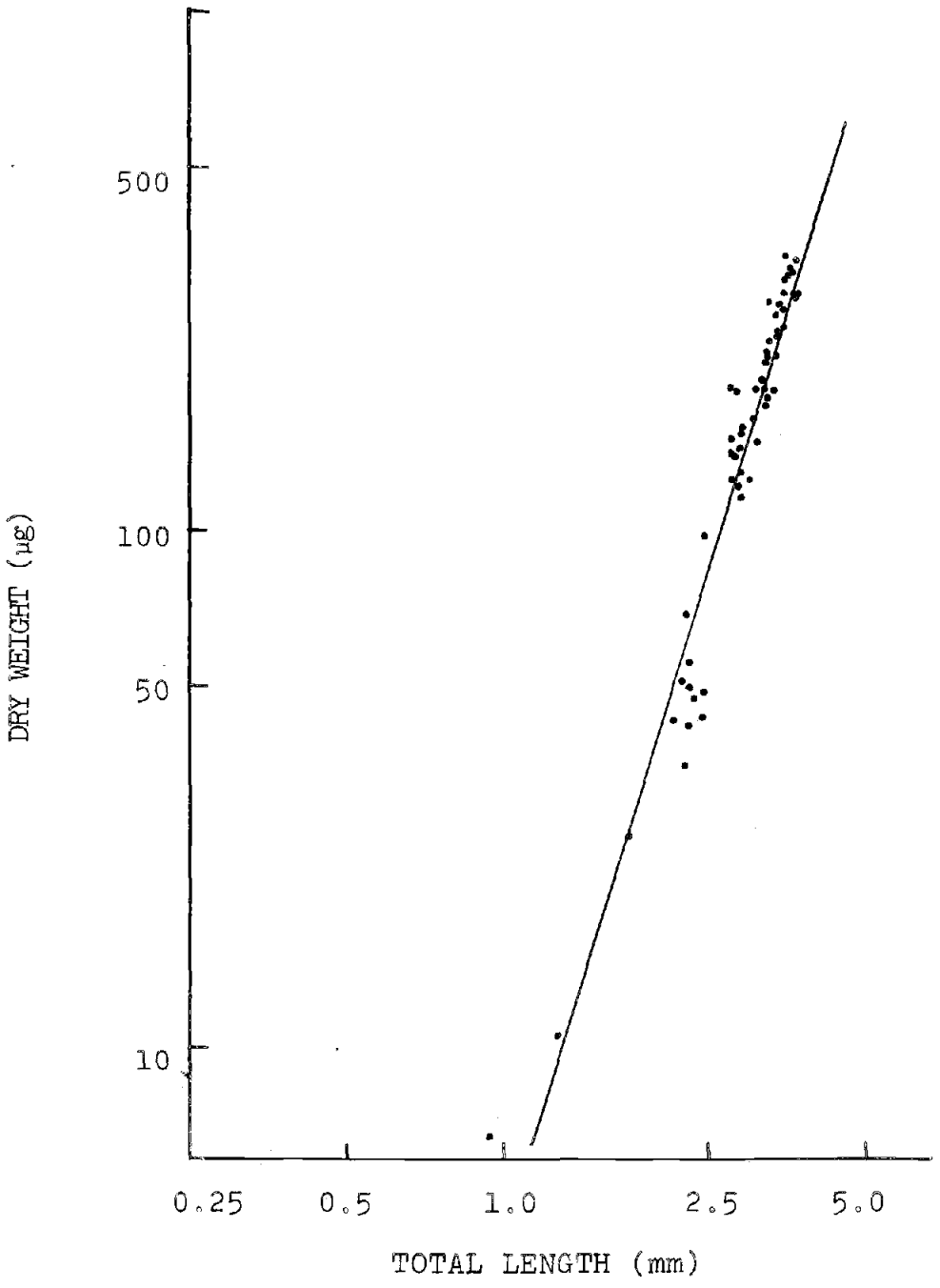


Figure 40. Length-weight relationship for Calanus marshallae.

($r = 0.96$). A cubic relationship ($W = aL^3$) does not apply for Calanus marshallae older copepodite stages.

CHANGE IN WEIGHT WITH TIME. The functional relationship between change in weight with time was examined by plotting dry weight vs. the median development time of each naupliar and copepodite stage. I used the development time data from the winter 1977 (10°C) experiments. The time rate of weight change is thus not directly measured, but rather, comes from converting the developmental stage data into stage duration data and cumulative elapsed time. A further restriction on the data is that I only have weights for various stages, so therefore have no knowledge of the variance of weight with time within any stage. This problem arises because it is not possible to determine the age of an individual within a developmental stage. Therefore, strickly speaking, I am not justified in describing the data with a continuous function. Nevertheless, in order to explore the general relationship between change in weight and stage, I have fitted the data by least squares methods after transforming the weight data to natural logarithms. The result is shown in Figure 41. Three growth phases are seen: (1) from egg through N4, weight is gained at a rate of approximately 0.05 µg per µg per day, (2) from N4 through C5 the growth rate is 0.176 µg per µg per day, and (3) from C5 to female, growth is extremely slow at a rate of 0.024 µg per µg day. Even though growth rate on a per stage basis was nearly constant from N4 through female, growth on a daily basis is considerably different. The great change between C5 and female arises because of the long time interval between recruitment of females from C5.

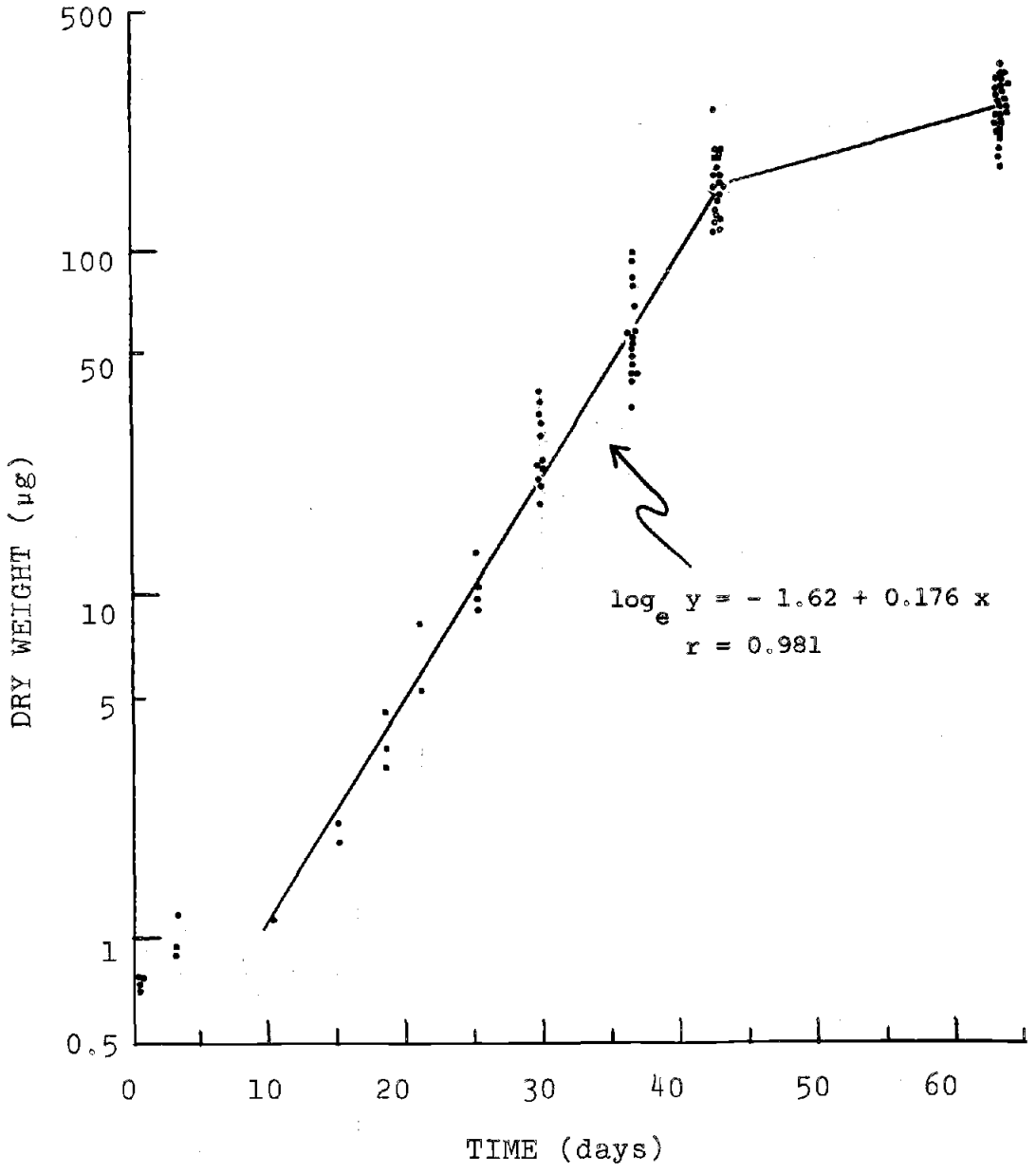


Figure 41. Change in weight with time for Calanus marshallae. Three growth phases are seen: (1) from day 0 to day 10, (Egg to N4), (2) from day 10 to day 43, (N4 to C5), and (3) from day 43 to day 63, (C5 to female).

DISCUSSION

My simplified methods of maintaining Calanus marshallae in the laboratory seem to have produced results comparable to other published studies on pelagic copepods. Survivorship in my primary experiment at 10°C from egg to adult averaged 40 % (range 18-68 %). Mullin and Brooks (1967, 1970) raised Rhincalanus nasutus in continuous culture at La Jolla, California. In no case did more than 30 % of their animals survive from egg to adult. They also raised Calanus helgolandicus (= C. pacificus) from egg to adult with 25 % and 53 % survival at 10° and 15°C respectively. In another set of experiments, they raised Rhincalanus nasutus at 10°C with 10 and 40 % survival, and at 15°C with 44 and 77 % survival. Paffenhoffer (1970, 1976) raised Calanus helgolandicus from La Jolla, CA with excellent success. Survivorship ranged from 59 to 86 % on diatom food at levels above 50 µg carbon per liter, and was nearly 100 % when fed the dinoflagellate Gymnodinium splendens. Johnson (1974) raised Acartia californiensis from Yaquina Bay, Oregon at 20 °C with 21 and 36 % survival in two experiments. Paffenhofer and Harris (1976) and Harris and Paffenhofer (1976) had 30.4 % survival (20-44 % range) for Pseudocalanus elongatus and 37.2 % survival (14-57 % range) for Temora longicornis from the North Sea. Landry (1978) raised Acartia clausii from San Juan Island, Washington with 85 % survival from N1 to adult. High mortalities did occur in some experiments but these were not included in his development time analyses (Landry, 1975). Finally, Pace (1978) had 25% survival of Acartia tonsa at 14 °C and 21 % survival of

Acartia californiensis at 25°C from Elkhorn Slough, California.

Survivorship of Calanus marshallae was 0 and 19 % at 15°C from egg to adult in two experiments. This is not surprising because 15°C is above the temperature at which Calanus are usually abundant in the field. They are most abundant over the range of 8° to 12°C. As seen in Table 11, the usual surface temperature is 10°-11°C.

Since laboratory survival of Calanus marshallae was as good as that of most other pelagic species of marine copepods which have been studied, I conclude that my experimental methods were adequate and that weekly handling of individuals had no great effect on their mortality. As previously mentioned, nauplii died from unknown causes. Copepodites almost always died while molting which is the same observation made by Ramont and Gross (1942) in their studies of Calanus finmarchicus.

There are only a few complete studies on developmental rates to which I can compare my Calanus marshallae data. Johnson (1974) and Landry (1975, 1978) found that median development times for Acartia californiensis and A. clausii respectively, progressed at a constant daily rate from N1 through adult. Such growth was called "isochronal development" by Miller, Johnson and Heinle (1977). Pace (1978) found a constant developmental rate from N1 through C4 for A. californiensis and from N1 through C5 for A. tonsa. Growth slowed as the terminal age was approached. Slow growth in his experiments probably resulted from inadequate nutrition. He used natural seawater in his copepod culture flasks, renewing half of it every two days. Additional food was not added.

Isochronal development is said to occur in Eurytemora affinis, E. herdmanni (Katona, 1971 cited in Miller et al, 1977) and in Pseudocalanus (see McLaren, 1978). The general rule seems to be that given adequate nutrition, some pelagic copepods will develop at some constant rate in terms of developmental stages per day, over a large fraction, if not all, of their development from egg to adult.

Calanus marshallae appears to be an exception to this rule. Even though a plot of stage vs. cumulative median development time can be well-fitted to a straight line over the range N3 to C5, the trend of the data is clearly sigmoidal. Development is faster than the constant rate calculated from linear regression from egg to N3 and between N5 and C1. Development is slower than predicted between N3 and N5, and C1 to C5. Development from C5 to female was about one-fifth as fast as the isochronal development rate. These patterns were seen in all of the data from three experimental temperature, 10°, 11° and 15°C, so they are surely real.

The possibility does exist that the older developmental stages were underfed, therefore not developing at their theoretical maximum rates. However, 19 separate experiments were conducted at three temperatures and in none of them was there ever any indication of isochronal development through the adult stage. During the progress of these experiments the problem of inadequate nutrition troubled me. Experiments H through N were fed large amounts of food once or twice daily after the C4 stage was reached. In experiments M and N, suspensions of Thalassiosira fluviatilis in the experimental containers were so dense that the water was colored yellow-brown. Water

discoloration does not occur below about 6000 to 8000 cells per ml. This extreme measure did not alter the developmental rates. I therefore feel confident that the laboratory development data are correct and free of bias. Even if there were nutritional deficiencies, the sigmoid shape of the growth curve would probably not change. If food were inadequate for whatever reason, growth of all developmental stages should be equally affected. Each intermolt period would be lengthened or shortened proportionally.

If isochronal growth from egg to adult can be taken as the general rule, why then is Calanus marshallae so different? A tenet of Darwinism is that natural selection will shape the life history of a population in a manner dictated by the immediate physical and biotic environment. Miller, Johnson and Heinle (1977) suggested that predation mortality by zooplanktivorous fish on older copepodites of Acartia species in Yaquina Bay, Oregon is high. They hypothesized that due to high mortality rates of older stages, quick arrival to adulthood and early reproduction would be favored by selection. In Calanus marshallae, we see the opposite pattern. Development to N3 is rapid, followed by near-isochronal development to C5, and extremely slow development to adult. If differential mortality rates have shaped this developmental pattern, then we can hypothesize that the pattern evolved in response to constantly high egg, N1 and N2 mortalities, moderate death rates through the other naupliar and copepodite stages, followed by a greatly enhanced survival rate of C5 and adults. Under this scheme, selection would favor those phenotypes that hatch quickly and move directly to the third nauplius. There would be no great

penalty for slow development to C6 once C5 is reached. This model would further predict that reproduction need not be initiated after the adult molt had been reached, and that reproduction should be iteroparous. Murphy (1968) has used a computer model to show that under conditions of uncertain survival of pre-reproductive individuals and a relatively stable survival of reproductive individuals, iteroparity is advantageous. The Calanus developmental model is further explored in the General Discussion of this dissertation.

The total development time from egg to adult was 64 days at 10°C. This time is considerably longer than that measured in the laboratory by Mullin and Brooks (1970) for the copepod Calanus helgolandicus. At 10°C this species completed its total development in 43 days. At 15°C, time from egg to adult was 23 days. Paffenhofer (1970) worked with the same species at the same geographical location and found times of 21 and 25 days at 15°C. My 10° and 15°C estimates for Calanus marshallae are each 34 % longer than those for C. helgolandicus.

McLaren (1978) predicted the generation lengths of a sibling species of Calanus marshallae, C. finmarchicus, from Lock Striven, Scotland, to be 46.5 days at 10°C. This estimate was arrived at by taking a laboratory measured egg to adult time of 33 days at 14-15°C and adjusting it by using a temperature function derived from egg hatching times. The laboratory data are from Nicholls (1933). These latter data are of extremely dubious quality because conditions of rearing are not known and temperatures were never routinely measured. Only three individuals survived to adulthood from an undetermined number of eggs. However, the temperature-adjusted laboratory estimates

did agree well with data based on cohort development in the field. The possibility exists that Nicholls could have been working with Calanus helgolandicus. This species does develop to adult in about 45 days at 10°C. It is common knowledge that during the early studies of Calanus finmarchicus during the 1930's through the 1950's, C. finmarchicus and C. helgolandicus were not differentiated in any of the field or laboratory studies (see Marshall and Orr, 1955, p. 7). The two species are definetely known to be sympatric (Fleminger and Hulsemann, 1977).

There is no reason to believe that my values of development time are in error simply because they do not agree with Calanus helgolandicus. Calanus marshallae is a different species. Similarly disparate development times are seen between several Acartia species. At 12°, 15° and 20°C, Acartia tonsa from Chesapeake Bay develop from egg to adult female in 21, 11, and 7 days respectively (Miller, Johnson and Heinle, 1977). Acartia clausii from San Juan Island, Washington develops in 25, 20 and 13 days at the same temperatures (Landry, 1976). Acartia californiensis from Yaquina Bay, Oregon develop in 37, 22 and 12 days at those same temperatures. The differences between species are great. For some reason, the life history of Acartia tonsa has evolved so that development is much more rapid than in other estuarine Acartia species.

The subject of estimating development rates from field data has been reviewed by McLaren (1978). This work is significant because it has brought together all published field data on temperate pelagic marine copepods, in an attempt to look at generation times in the

field. He found sufficient published data on seven species. They were Calanus finmarchicus, Pseudocalanus minutus, Microcalanus pygmaeus, Centropages hamatus, Temora longicornis, Acartia clausii and Oithona similis. All estimates of generation times were made possible because of the appearance of cohorts in the field. Generation lengths were predicted from two kinds of laboratory data. The first kind of predictions are those calculated from a temperature function of development time based on egg hatching times. This assumes that development to adult is a known and constant multiple of egg hatching times. This has been shown to be true for Acartia clausii (Landry, 1975) and Pseudocalanus (Corkett and McLaren, 1978, cited in McLaren, 1978). The second kind of prediction is from laboratory estimates of generation lengths based on development time experiments like the ones which I carried out. The result of his efforts which is germane here is that generation lengths in the field were close to times predicted from a variety of laboratory data. Field development times were usually the same as or somewhat longer than laboratory times. This was the result which I obtained for Calanus marshallae when development rates in the field and laboratory were compared.

Both McLaren and I would like to conclude that field populations are developing at the same rates as laboratory populations because food is not limiting. However, the conclusion cannot be drawn without making a circular argument. The assumptions need rigorous testing. McLaren assumes (1) that the various Belehradek temperature functions derived from egg hatching data can adequately describe stage duration

and generation lengths of different copepod species, (2) that isochronal development is widespread, and (3) that laboratory development rate measurements were made under conditions of an abundant supply of high quality food. The key assumption in my work are that laboratory food levels were high enough to sustain maximum growth rates, and that handling of the animals did not affect their development.

Perhaps we need not worry about uncoupling the arguments, or about rigorous testing of the assumptions. There are now so many data on the one-to-one relationship between field and laboratory developmental rates that one can hardly doubt that field populations of pelagic copepods, at least temperate coastal representatives, usually develop under conditions of adequate food abundances. I share McLaren's opinion that food abundance probably has little influence on setting a copepod's life history pattern and therefore on its contribution to secondary production. Careful ecological studies are needed to understand the details of life history phenomena.

Change in weight with time (growth) of Calanus marshallae seems to be different from other pelagic copepods. The comparisons are hard to make though, because so few species have been studied in sufficient detail. For C. marshallae, growth is exponential between the N4 and C5 stage, a 33 day interval. Weight at any time between day 10 (= N4) and day 43 (= C5) is described by $W_t = W_{10} e^{kt}$, where W_{10} = 1.15 µg dry weight. The growth coefficient (k), was 0.18 µg per µg per day at 10°C. From C5 to adult, the growth

coefficient drops to k = 0.024. For both Rhicalanus nasutus and Calanus helgolandicus, the growth coefficients are only constant over much shorter developmental intervals. Growth rate slowed with time but the details are unclear because development was divided into three phases: N1 to C1, C1 to C4, and C4 to adult (Mullin and Brooks, 1970), or N1 to C1, C1 to C3 and C3 to C5 or C3 to C6 (Paffenhofer, 1976). Recall that I produced developmental data for each developmental stage. Paffenhofer and Harris (1976) and Harris and Paffenhoffer (1976) continue to pool developmental into arbitrary groups: Egg to C1, C1 to C3 and C3 to adult. This means that it is impossible to know the growth details. In both cases, Pseudocalanus elongatus and Temora longicornis growth coefficients tended to be greatest between stages C1 to C3.

The most complete growth data are those of Miller, Johnson and Heinle (1977) and Landry (1978), on Acartia californiensis and A. clausii respectively. In both species, growth is exponential from N1 or N2 to the adult. It seems then that when detailed studies are carried out (such as these two and my own), growth is found to be exponential over a large fraction of the developmental stages. The growth aspect of life history cannot really be known without detailed developmental rate data.

SUMMARY AND CONCLUSIONS

1. Laboratory survivorship was as good as or better than most other comparable studies. I conclude that my simplified experimental methods were adequate.

2. Development in the laboratory was studied at 10°, 11° and 15°C. Development from eggs to N3 progressed extremely rapidly, taking 3.5 days at 10°C. Development from N3 to C6 followed a sigmoidal growth model, with slow growth from N3 to N5, fast growth between N5 and C1, and slow growth between C5 and C6. Development from C5 to C6 took about 22 days at 10°C.

3. Variability in development did not change between N3 and C5. On the average, 17.8 days elapsed between the first and last appearance of any given stage in a laboratory cohort.

4. Between-family variability in development time is high. The median individual in some clutches can be as much as two developmental stages ahead of the median individual from other clutches. However, rank-ordered arrival times to C5 are not concordant with rank-ordered arrival times to female, for 12 clutches studied. This suggests that molting into adulthood is controlled by different biological processes than molting within the naupliar and copepodite stages. It is hypothesized that development slows from C5 to C6 because the sex organs are developing.

5. Development (D) is temperature (T) dependent. Time from egg to female is given by the power function, $D = 2223\ T^{-1.52}$.

6. Development in the field could be studied because cohorts were often seen. They appear in February, May, July and in some years, September.

7. Development times obtained from field cohorts were the same as those obtained in the laboratory. Since every effort was made to assure adequate quantities of high quality food in the laboratory, I feel that my laboratory data correctly represent maximum developmental rates. Therefore, I conclude that field populations are developing under conditions of adequate food levels.

8. Growth in length of both field and laboratory animals follows a separate linear model in the naupliar and copepodite stages. The growth rates were 0.06 mm per day for nauplii and 0.51 mm per day for copepodites. Laboratory raised and field-collected nauplii were the same lengths. Older copepodites from the field were longer than laboratory individuals. Laboratory raised females were significantly longer than field-collected females.

9. Total lengths of daughters and total length of mothers are not related. Only 3 % of the variability in daughter terminal length was explained by total length of their mothers. Females greater than 3.8 mm made up only 2 % of the field population but 17 % of the laboratory population. It is possible that these large females are selectively eaten in the field.

10. Weight gains per stage were exponential over the complete range of development from N4 to female, at a rate of 0.73 µg per µg per stage. One could divide this into linear phases: (1) N4 to C2, 0.55 µg per µg per stage, and (2) C3 to C6, .76 µg per µg per stage.

11. The length-weight relationship between C1 through C6 was $W = 4.13\ L^{3.28}$. Weight was added at a greater rate per unit length in the older copepodite stages. From C4 through C6, the relationship was $W = 2.00\ L^{3.92}$.

12. The time rate of weight change is constant over a large fraction of the total developmental stages. From N4 to C5, the relationship is $W_t = W_o\ e^{0.176\ t}$. Weight gains between egg and N3, and C5 to C6 are much slower. C5 add weight at the rate of 0.024 µg per µg per day. The rate of weight gain by C5 is slow because development into female is slow. As previously mentioned, this could result because gonads are maturing. Females do gain the predicted amount of weight based on the weight-stage regression. It just takes them longer to achieve this weight.

CHAPTER V. REPRODUCTION

INTRODUCTION

Reproduction is another basic part of any life history study. Studies on Calanus marshallae reproductive biology were initiated in order to better understand why eggs were most abundant three to five miles from shore during upwelling. It was clear from the field data that this was a zone of maximum egg abundance because females were most abundant there. But at times, large numbers of females were found here with few eggs present, and vice versa. Occasionally, females were abundant many miles to seaward, but no eggs were found. Therefore, I carried out some laboratory studies to learn about the egg laying process. Also, since cohorts were known to be produced in the field, I needed to find out what environmental effects could greatly enhance egg production, thereby helping to generate a cohort.

Food was guessed to be the dominant factor in producing variation in egg production. Therefore, the response of daily egg production to both food quantity and food quality was investigated. The effects of temperature and size of mother on egg production were also studied. Daily egg laying rates among females collected in winter, spring and summer months were compared to determine if females were more fecund at one time than another. The egg laying of a sympatric congener, Calanus pacificus, was also studied and compared to C. marshallae. Finally, laboratory-measured fecundity rates were compared to finite birth rates calculated for the field population of C. marshallae.

Because natural selection operates in part by differential reproductive success, studies of reproduction are of considerable interest to population ecologists. Four basic dichotomies must be addressed before one can describe the type of reproductive pattern which has evolved:

(1) Does the organism lay many eggs or few?

(2) Does it reproduce early in life or late?

(3) Does it reproduce a few times or many times?

(4) Does the organism expend a great amount of energy in reproducing, or a small amount?

Answers to these questions allow a description of an individuals reproductive strategy. The answers for Calanus marshallae are found in this chapter.

REPRODUCTION - LABORATORY MEASUREMENTS

METHODS

Female Calanus marshallae were obtained with a 0.5 m diameter, 0.24 mm mesh plankton net towed at various stations within five miles from shore off Newport, Oregon. Towing times never exceeded two to three minutes and towing speeds were set by the slowest possible speed which the research vessel could sustain, usually less than two knots. The catch was poured into five-gallon cylindrical insulated coolers and transported by automobile to the Oregon State University campus in Corvallis, a distance of 50 miles inland. Upon arrival at campus, females were immediately sorted from the plankton catch and

kept individually in 400 ml of seawater in 600 ml beakers. The time between capture and sorting never exceeded five hours, and was usually completed within three hours. All work was carried out in a constant temperature walk-in cold room. When sorting, care was taken to select only those females which seemed healthy. Females which swam erratically, had broken antennules, missing furcal setae or other obvious injuries were not used in any experiment. After being transferred to the experimental containers, the females were fed either a mixture of the diatom Thalassiosira fluviatilis and the flagellate Isochrysis galbana, or T. fluviatilis alone, depending upon the experimental plan. The copepods were allowed to adjust to their new lives in this greatly reduced ocean and to the new food, for 24-48 hours, before being used in an experiment.

I began my Calanus laboratory work in May 1976 with the initial purpose of determining if C. marshallae could be maintained in the laboratory with any success. Various food types were tried and containers of different volumes were tried. Much of this work was done in a casual and qualitative manner. A great deal of time was expended in culturing eight clones of phytoplankton. I experimented with the diatoms Thalassiosira fluviatilis, T. pseudonana, T. aestevalis, T. nordenskoldii, Skeletonema costatum and Ditylum brithgwelli, the flagellates Isochrysis galbana, Pseudoisochrysis sp., and Rhodomonas sp., and the dinoflagellate Amphidinium sp.. I chose T. fluviatilis as my primary food. It occurs as single cells of about 13 µm diameter. I preferred to use this diatom because (1) it is easy to maintain in culture, (2) it remains in suspension without the need

for continuous stirring, (3) it is intermediate in size so can be grazed upon by all life cycle stages, (4) it has been used in so many studies of copepod growth and fecundity that it has almost become a standard food, and (5) Calanus does well on it by all criteria. This was later confirmed in several experiments comparing egg laying rates among females fed three diatom species.

The 600 ml beakers were chosen because a large supply of them was on hand from previous laboratory work done at Oregon State University. The Calanus did not seem to behave peculiarly in these containers. Individuals seldom to never swam erratically; instead, they exhibited the stereotyped behavior of swimming up to near the surface, slowly sinking through the eight cm water column, then bouncing off the bottom toward the surface again. When starved, the animals would feed along the bottom of the beaker, reworking and probably reingesting their own fecal pellets. When fed adequate amounts of food, they remained in the water column.

Three aspects of reproduction were studied. First, the effect of food concentration on egg laying was studied during the summer of 1977 and spring-summer 1978. Second, seasonal differences were investigated between January and September 1978. Third, fecundity of Calanus pacificus females was studied in March 1978. This was done because there were no C. marshallae off Oregon at that time.

All measurements of egg laying rates were taken on individual females. The number of eggs laid was determined by a daily census. A standard run lasted eight days. The water in each beaker was poured through a 110 µm nylon screen and the females, their eggs and

fecal pellets were rinsed from the screen into a plastic dish. The female was immediately returned to her beaker and the eggs counted. The fecal pellets were counted then discarded. All of the egg data are listed in the appendix.

During the measurements of daily egg laying rates at various food concentrations, water and food were completely renewed daily. Therefore each day's measurements began at a known concentration of fresh food. These measurements also lasted eight days. Calanus marshallae females were fed only Thalassiosira fluviatilis during these experiments. In order to assure that the diatoms were always growing in log-phase, cultures were started weekly. Thus, the C. marshallae females were given plants which were between three and 10 days old.

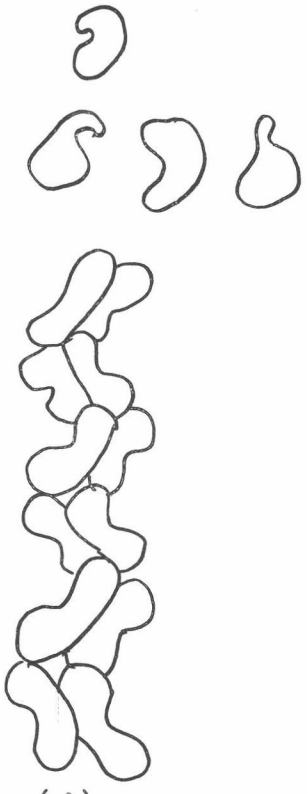
During the measurements of egg laying rates under conditions of unlimited food, females were daily fed mixtures of Thalassiosira fluviatilis and Isochrysis galbana. The concentration of the diatom was measured but that of the flagellate was not measured. The water in the beakers was changed every two to three days. Only one-half of the volume was renewed at these times.

For all of the measurements, concentrations of Thalassiosira fluviatilis were known from either (1) Fuchs-Rosenthal Counting Chamber using a compound microscope (summer 1977), or (2) a Model B Coulter Counter (all 1978 measurements). In addition to the egg laying work, grazing rates of individual females were measured during many of the 1978 experiments. The Coulter Counter was used to make the measurements of filtration and ingestion rates.

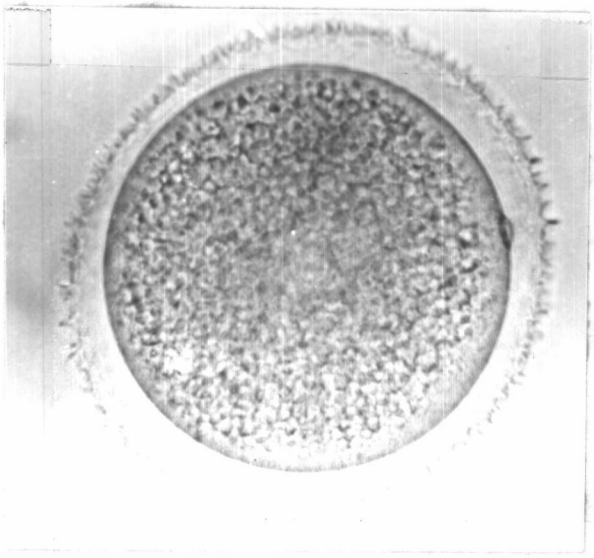
RESULTS

EGG LAYING AND EGG HATCHING. From time to time while changing the water in beakers and making egg counts, I would find a female laying a batch of eggs. When these fortuitous events occurred, I observed the process of egg laying, the changes in appearance of the eggs during development, the egg hatching process, and the total time required for a clutch of eggs to hatch.

A clutch of eggs is laid within one to two minutes. Eggs come from either one or both oviducts and are extruded in chains. While being laid, the eggs have a variety of shapes including kidney-shaped, tear drop with a hook at the narrow end, or pear shaped (Figure 42). Within one minute of laying, the chains separate and the eggs become spherical. At this point, they have a diameter of 180 µm. After 10 minutes, an outer membrane (= fertilization membrane ?) begins to lift off from the egg surface (Figure 42b). Twenty to thirty minutes after being laid, this outermost of three membranes separates from the egg, and the total egg diameter becomes 220 µm. The three membranes are shown in Figure 42c. The outer one is reticulated, while the inner two are smooth. The eggs of Calanus marshallae resemble the eggs of a Calanus from Tromso, Norway pictured in Marshall and Orr (1955, p. 7, Figure 2b). I showed photographs of the C. marshallae eggs to Dr. S. Marshall on 24 September 1976. She verified that the C. marshallae eggs looked exactly like the Tromso Calanus eggs and further remarked that the Tromso Calanus was C. glacialis. The eggs of C. marshallae and C. glacialis both have this peculiar outer



(A)



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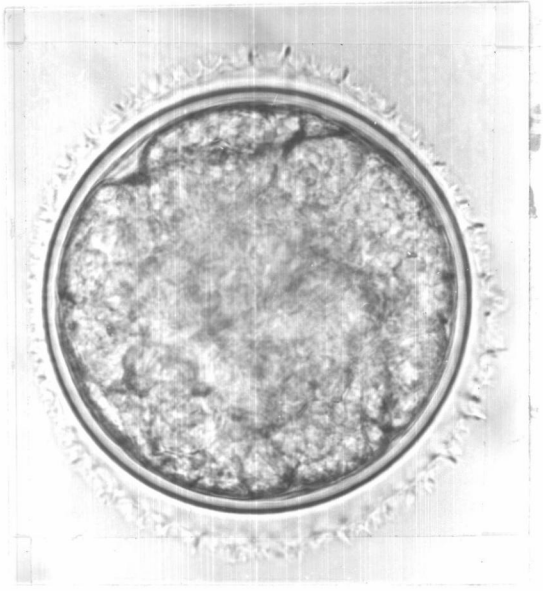

(C)

Figure 42. The eggs of Calanus marshallae. (a) eggs that have just been laid before becoming round, (b) an egg 15 minutes old showing the outer membrane as it just begins to lift away from the inner membranes, and (c) an older egg showing the three membranes and a developing nauplius within.

reticulated membrane. The eggs of C. finmarchicus, C. helgolandicus, and C. pacificus have two membranes, and lack the outer reticulated one.

At about the same time that this outer membrane has completely lifted from the egg, two clear circular objects, approximately 40 µm in diameter, appear near the center of the egg. They persist until the egg is about 45-50 minutes old. These objects are presumably the male and female pronuclei pictured in Marshall and Orr (1955, p. 43, Figure 20d). Within 55-65 minutes of laying, the first cleavage begins. The second cleavage begins an hour later, and by two hours and 30 minutes,the eggs are at the eight-cell stage. No other cleavages were followed. Egg development progresses from looking like a golf ball to a structureless sphere. Within a few hours of hatching (exact time not determined), a grey cloud of matter coalesces within the egg. This soon differentiates into a nauplius. The nauplius can be identified as such within about one hour of hatching.

When the nauplius is about to hatch, the limbs begin to twitch. The egg membranes swell to a diameter of 0.24 mm and the innermost membrane bulges, cracking the second membrane. The inner membrane continues to swell and soon pops through a slit in one side of the outermost reticulated membrane. The outer membranes then peel down over the enlarged inner membrane until they lie in a crumpled mass at the base of the innermost membrane. The inner membrane now has the appearance of a very thin-walled bubble about to pop. The inner membrane which contains the nauplius soon frees itself from the outer

membrane. Immediately, the outermost membrane assumes its original spherical shape with the second membranecrumpled up within it. Figure 43 shows the nauplius within its bubble, the egg membranes from which the bubble emerged, and a complete egg just beginning to swell and free itself of the outer two membranes. Also pictured is an egg which has not yet begun to swell.

The bubble has now reached a diameter of 0.28 to 0.30 mm which equates to a 4.6 fold increase in volume from the 180 µm diameter egg (not including the outer membrane). The nauplius begins to swell, and the limbs, which were folded dorsally, begin to unfold. After the limbs are positioned latero-posteriorly, the nauplius next appears to test its musculature. Then, with a single forward arcing slice of the antennules, the bubble is pierced and the nauplius darts off, leaving the fragmented membrane in its wake. The time from the bubble being freed from its confining membranes to the swimming away of the nauplius ranged from 5 min 40 sec to 7 min 50 sec. The total time required for a complete clutch of eggs to hatch ranged from less than one hour to 2 hrs 15 minutes. The mean of seven observations was 1 hr 28 min.

The final hatching of the nauplius from its thin membrane is by mechanical means. But because the eggs swell and membranes burst as the egg begins to hatch, it is certainly safe to conclude that the hatching process is initiated by uptake of water. The remaining question is whether this uptake process is active, or osmotic. I hypothesize that for Calanus marshallae the process is osmotic and is triggered by the release from the nauplius of a small pellet of uric

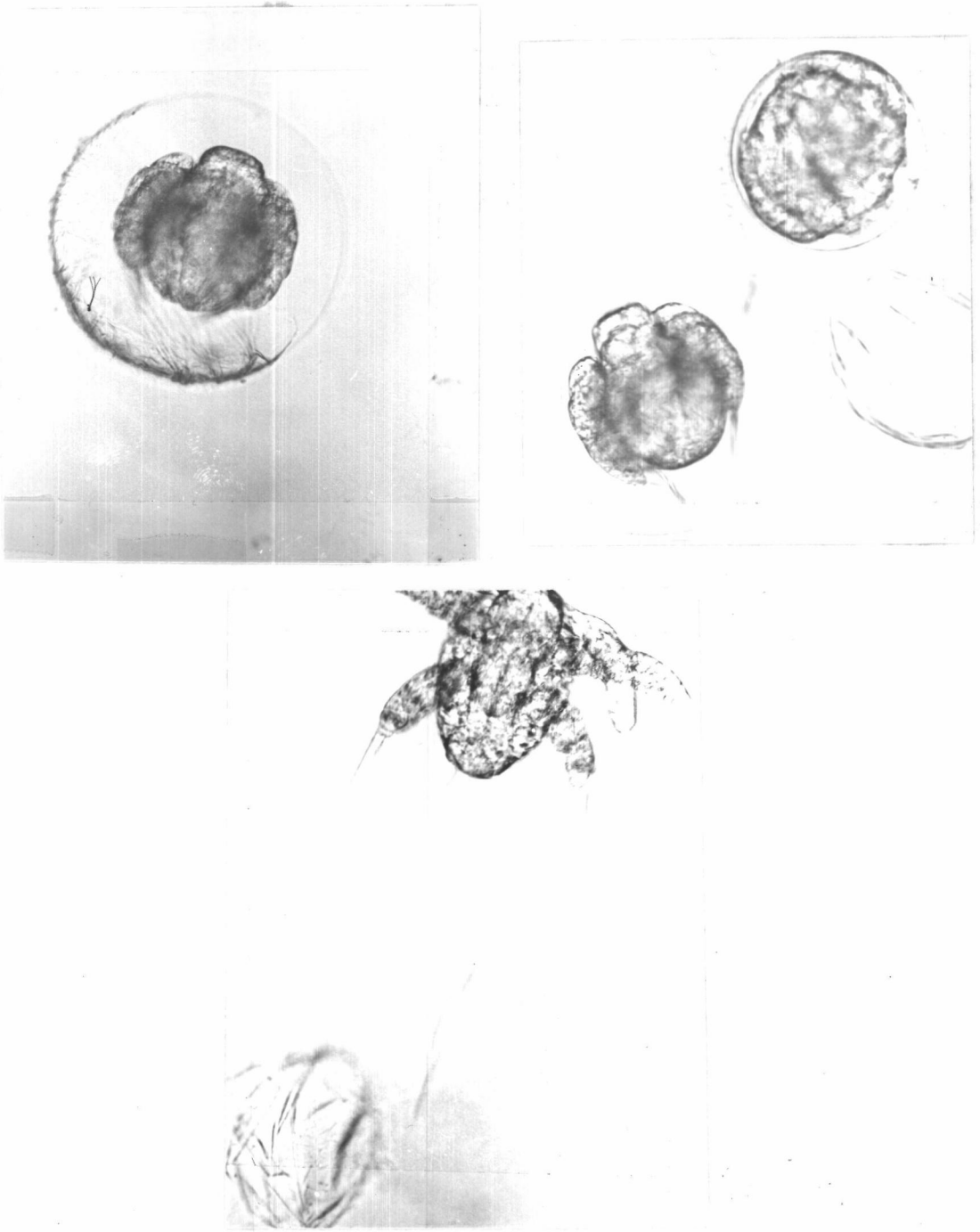

Figure 43. Examples of hatching Calanus marshallae eggs.

acid. This waste product would have accumulated from the 40 hours of metabolizing which elapsed while the egg was developing. The pellet would increase the osmality within the inner membrane thus allowing additional water to enter across the membrane. This hypothesis was not tested.

Unfertilized females which were grown up in the laboratory also laid eggs. On one occasion only, I saw one female lay a clutch of 30 apparently normal eggs. They were kidney-shaped when laid but became round within a few minutes. At the time when I expected to see the reticulated membrane lift away from the egg surface, the outer membrane ruptured, spilling the grey matter. All eggs ruptured within a few minutes of each other. It is because of this observation that I hypothesized that the outermost membrane is a fertilization membrane.

EGG DEVELOPMENT TIME. The time from egg laying to egg hatching is the egg development time. It is more precisely defined by McLaren (1966) as the time between the laying of a clutch of eggs and the hatching of the median egg. Very careful observations must be made to make this precise determination because one does not know which is the median egg until the entire clutch has hatched. My data are less precise. Hatching times were taken to be the time when most of the eggs were hatching. Usually the bulk of eggs did hatch within 30 minutes of each other, but there were always a few forerunners and a few stragglers.

The egg development time (D) at several temperatures (T) is shown in Figure 44. The temperature range over which the data were taken was not great. I did not expand my observations because

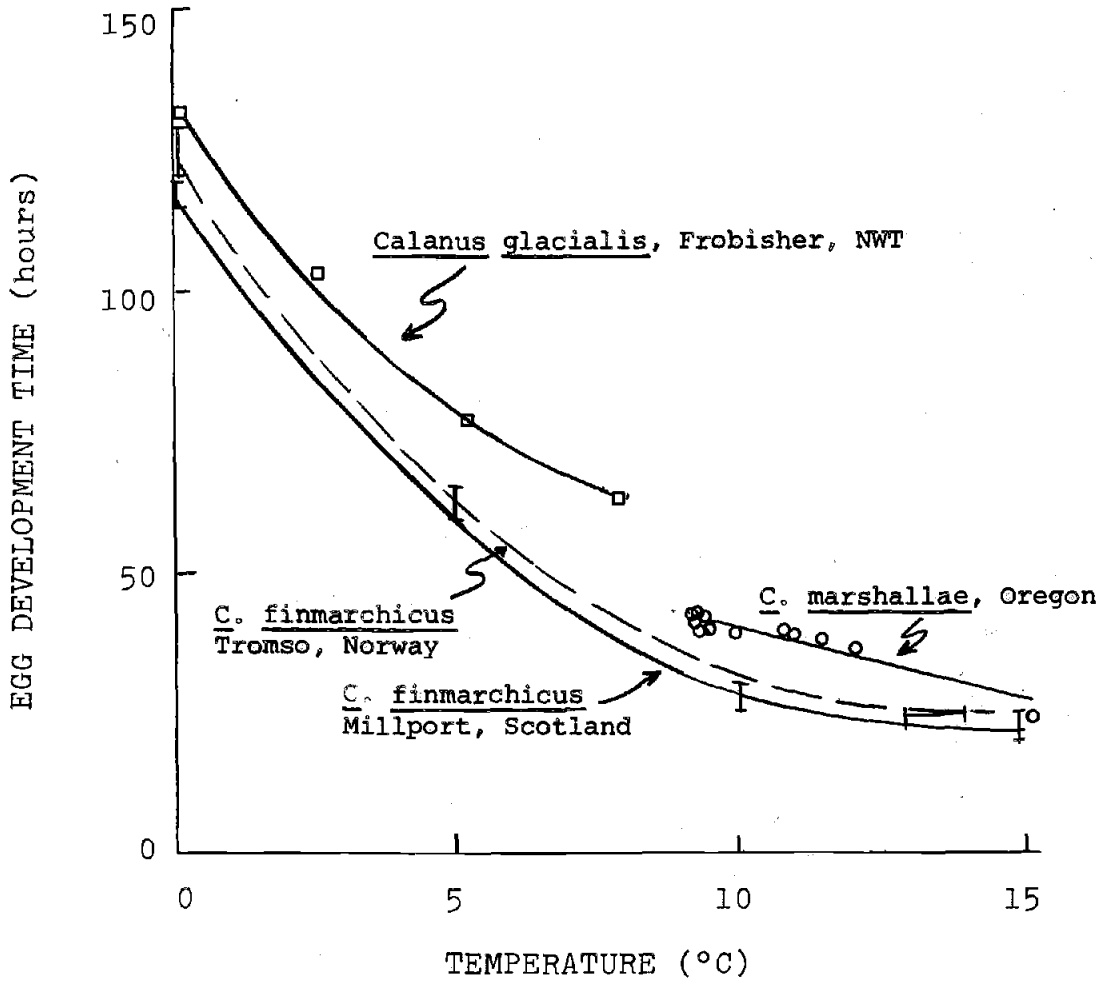

Figure 44. Egg development time as a function of temperature for three Calanus species.

Calanus marshallae does not lay eggs, even exist, at temperatures beyond the range of about 7° to 15°C. The egg development time at 15°C is not exactly known. In two experiments, all eggs hatched within 24 hours. Figure 44 shows a clear effect of temperature on egg development rates. Eggs develop faster at higher temperatures than at low temperatures. Such relationships are usually fit by power functions, but for C. marshallae, such a function did not describe the data as well as a simple linear regression. The power function, assuming development at 15°C was 23 hours, is $D = 713\ T^{-1.24}$ ($r = -0.93$), whereas the linear function was $D = 74.3 - 3.32\ T$ ($r = -0.97$). The power function did not describe the data as well because the egg hatching data did not span a wide enough temperature range.

AVERAGE CLUTCH SIZE. The egg laying of 32 females was studied under conditions of unlimited food supply. The concentration of Thalassiosira fluviatilis in these experiments ranged from 3500 to 8000 cells ml^{-1}. These food levels are shown to produce maximum egg laying rates in a following section of this dissertation. The data discussed here are from females collected in January, June, August 1977 and May, June, August and September 1978. All experiments were run at 10°C.

All of the daily egg counts are pooled in a histogram in Figure 45. There is a pronounced central tendency and there are a large number of days when no eggs were produced. The overall mean number of eggs was 23.9 eggs $female^{-1}$ day^{-1}. The median observation, including the zero class, was 25 eggs. The large number of zero

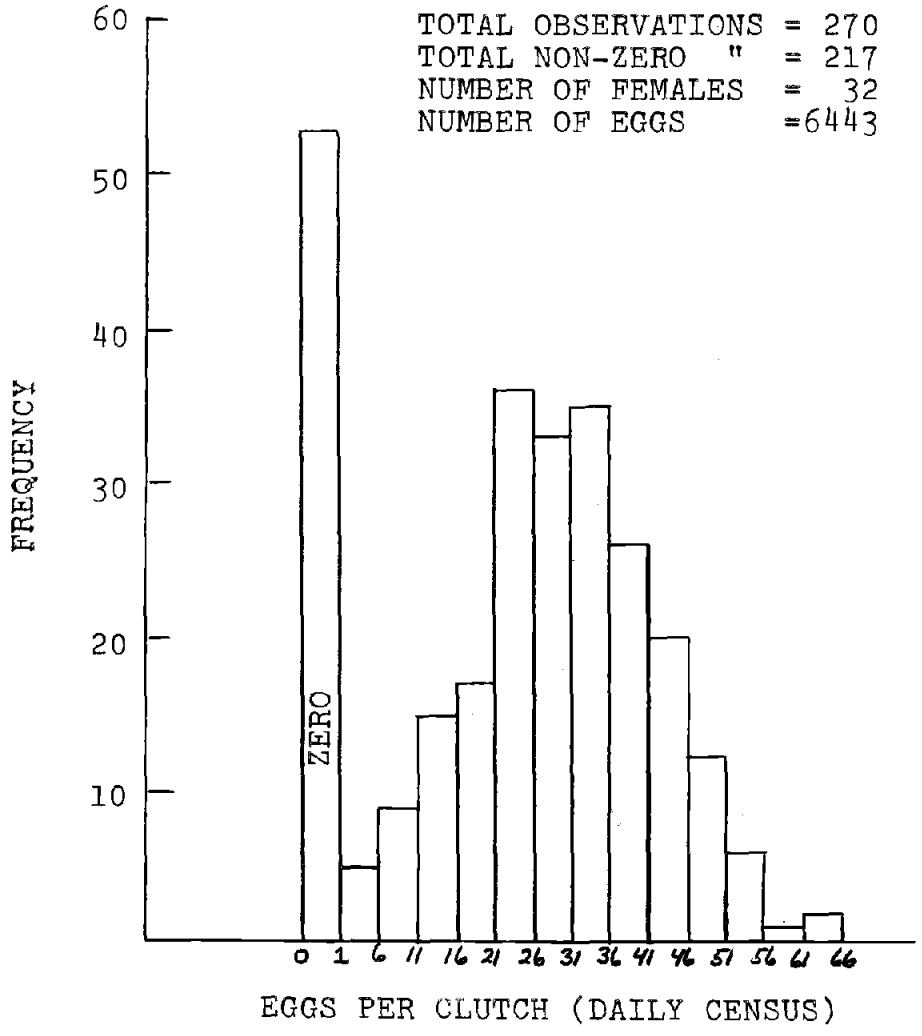

Figure 45. Frequency distribution of eggs per female per clutch for Calanus marshallae from measurements made under conditions of excess food (3500 to 8000 cells per ml) of the diatom Thalassiosira fluviatilis

observations came about because females do not lay a clutch every 24 hours. The frequency distribution of number of clutches laid per day is: 53 observations of no clutches laid, 201 observations of one clutch and 8 observations of two clutches being laid in a single day. Female Calanus marshallae usually lay one clutch per day, but on the average, over all females, there were 217 clutches laid in 270 female-days, or 0.80 clutches per day. The inverse is 1.24 days per clutch or 30 hours between laying, on the average. When a clutch is laid, the mean number of eggs is 29.7 eggs per female.

SEASONAL DIFFERENCES IN CLUTCH SIZE. Seasonal differences in eggs per clutch between the various experimental dates were investigated by calculating all possihle pairs of independent t-tests. It is clear from Figure 45 that the eggs per day data are not normally distributed because of the large peak of zero eggs per day. Therefore, these data cannot be examined using parametric test statistics. The eggs per clutch data can be examined if one assumes that zero eggs is not a clutch. This assumption removes the large tail, making the data distinctly normal. Therefore, only the eggs per clutch data are examined for differences between experimental dates.

Egg laying on seven dates is compared in Table 15. The t-values and other descriptive statistics are shown in the table. The pooled sample variance for all dates was calculated from least squares one-way analysis of variance formulas, and used to calculate the individual t-tests. Since multiple comparisons are being made, there is the danger that spurious differences will arise. This is because in a group of j means, there are $j(j - 1)/2$ potential differences.

Table 15. Descriptive statistics concerning seasonality of egg production. n is the number of clutches laid by all females during the measurement period. Differences in egg laying between sampling dates were investigated by calculating all possible pairs of t-statistics. Those results are shown below.

DATES	♀	n	MEAN	VARIANCE	CODE
6-19 JAN 1977 (10°C)	5	54	24.94	137.83	1
23-30 JUNE " "	4	26	27.42	175.45	2
15-22 AUG " "	1	6	27.50	357.10	
21-29 MAY 1978 "	4	32	39.16	98.07	3
27 JUNE-9 JULY "	4	28	29.64	161.13	4
" " "	3	23	33.09	123.63	5
7-10 AUG 1978 "	4	14	32.21	58.80	6
7-14 SEPT " "	7	34	27.15	86.74	7
15-22 AUG 1977 (15°C)	5	27	25.82	192.16	

t-values for each code pair

	1	2	3	4	5	6	7
1	----						
2	0.85	----					
3	5.74 *	3.86 *	----				
4	1.67	0.63	3.26 *	----			
5	2.83	1.61	2.13	1.02	----		
6	2.19	1.24	2.33	0.69	0.26	----	
7	0.93	0.09	5.08 *	0.89	2.18	1.80	----

The two-sided significance level, $\alpha/2$, must be adjusted so that only the largest t-values will lead to rejection of the null hypothesis. I chose the $\alpha/2 = 0.025$ level. This was adjusted according to the approach suggested by Bonferroni (Neter and Wasserman, 1974). My data have $(7 \times 6)/2 = 21$ possible comparisons and the adjusted α level is $\alpha = 0.05/21 \times 2, = 0.9988$. I interpolated the t-tables. The critical t-value was $t = 3.03$ (204 degrees of freedom). Significant differences are indicated by a * in the table.

For the most part, there are no differences between sampling dates. Females collected in May 1978 differed from females collected in January and June 1977, and June and September 1978. There were no other differences. Thus, for most times of the year, it is justifiable to use the overall average of 29.7 eggs per female per clutch.

FOOD TYPE - FECUNDITY RELATIONSHIPS. Egg laying as a function of different diatom species was studied in July 1977 and May-July 1978 under conditions of excess food. These experiments were conducted by Julie Ambler (School of Oceanography, Oregon State University) at the same time as, and in much the same manner, as my fecundity measurements. A detailed discussion of her work is in preparation (J. Ambler, personal communication, Deparment of Oceanography, Texas A & M Univ.). A brief summary is given below.

The data are presented in Table 16. Of four diatoms tested, females fed Thalassiosira fluviatilis always produced the highest average daily eggs, although the differences were not statistically significant. A fifth diatom species, T. angstii (=Coscinodiscus angstii) produced a higher egg laying rate on one occasion (2 July 78)

Table 16. Daily egg production of female *Calanus marshallae* fed different species of diatoms offered in excess quantities. The diatom *Thalassiosira fluviatilis* usually produced the highest egg laying rates.

JULY 1977	EGGS DAY^{-1}	95% CI
Skeletonema costatum	12.4	4.13
Chaetoceros didymus	12.0	4.37
Thalassiosira fluviatilis	22.0	6.03
10 and 20 MAY 1978		
Thalassiosira fluviatilis	29.6	1.8
" "	24.2	4.3
" "	29.8	7.7
" "	30.7	1.7
25 JUNE 1978		
Ditylum brightwelli	20.3	7.1
" "	18.3	7.0
" "	14.1	6.5
Thalassiosira angstii	31.1	11.4
2 JULY 1978		
Thalassiosira angstii	34.1	3.5
T. fluviatilis	24.3	5.2
Skeletonema costatum	22.8	8.6
" "	23.4	6.6

but the same rate on 25 June 1978 (compare to Table 15). One can conclude from this work that T. fluviatilis is nutritionally adequate. For pragmatic reasons, I believe it to be a superior food to others tested: it is very easy to culture compared to the others, and it remains in suspension without continuous stirring. This latter quality greatly simplifies experimental work.

TEMPERATURE - FECUNDITY RELATIONSHIPS. One set of experiments was run in August 1977 to examine the effect of elevating temperature to 15°C on egg laying rates. This temperature was chosen because it is just above the upper limit at which Calanus marshallae occur in the field. The descriptive statistics are shown in Table 15. Using the Bonferroni approach, the mean number of eggs per clutch, 25.8 per female, was only significantly different from the May 1978 experiment. Furthermore, the average number of eggs per clutch at 15°C was the same as for clutches from a single control female collected from the field at the same time and place but maintained at 10°C. I conclude that there are no obvious effects of temperature on egg production over the range of 10° to 15°C. Even though copepodites growing at 15°C had low survivorship in the laboratory, the wild adults are not obviously affected by this temperature. This would be adaptive for the adults in the Oregon upwelling zone because there are times when surface waters offshore warm to 15° or 16°C. These temperatures may be lethal to juveniles but do not harm the breeding stock.

FEMALE BODY LENGTH - FECUNDITY RELATIONSHIPS. Since there were, at most, small differences in fecundity between seasons, examination of differences in clutch size among females of different total lengths

is probably unnecessary. I proceeded anyway and looked at the regression of average number of eggs per clutch on female body length. The null hypothesis is that large females have the same clutch size as small females. The relationship is shown in Figure 46. The slope of the regression line was slightly negative but was not different from zero ($r = -0.0093$, 24 degrees of freedom). A test statistic is not necessary. I conclude that clutch size is not a function of female body length.

FOOD CONCENTRATION - FECUNDITY RELATIONSHIPS. The effect of food concentration on egg laying rates was measured on 57 individual females. Eggs in these experiments were censused daily for eight days, giving 456 female-days of data. Females were collected from the field between May and September 1977 and 1978. At that time, I assumed that there were no differences in egg laying between seasons. This has now been confirmed for nearly all times of the year which have been tested. Therefore, it is valid to treat data from different seasons and years as one experiment. Since the May 1978 females did lay a significantly greater number of eggs, they were not included in the following analyses.

The results are shown in Figure 47. There is a clear effect of food concentration on egg production. Egg production increases hyperbolically, reaching a maximum at a food concentration of about 3500 cells per ml of Thalassiosira fluviatilis, of about 24 eggs per day. The data were first fitted to a curvilinear function of the Ivlev type (Ivlev, 1966 for example). I fit the data using ordinary least squares methods. The equation , $E = E_{max} (1 - e^{-\alpha P})$, where

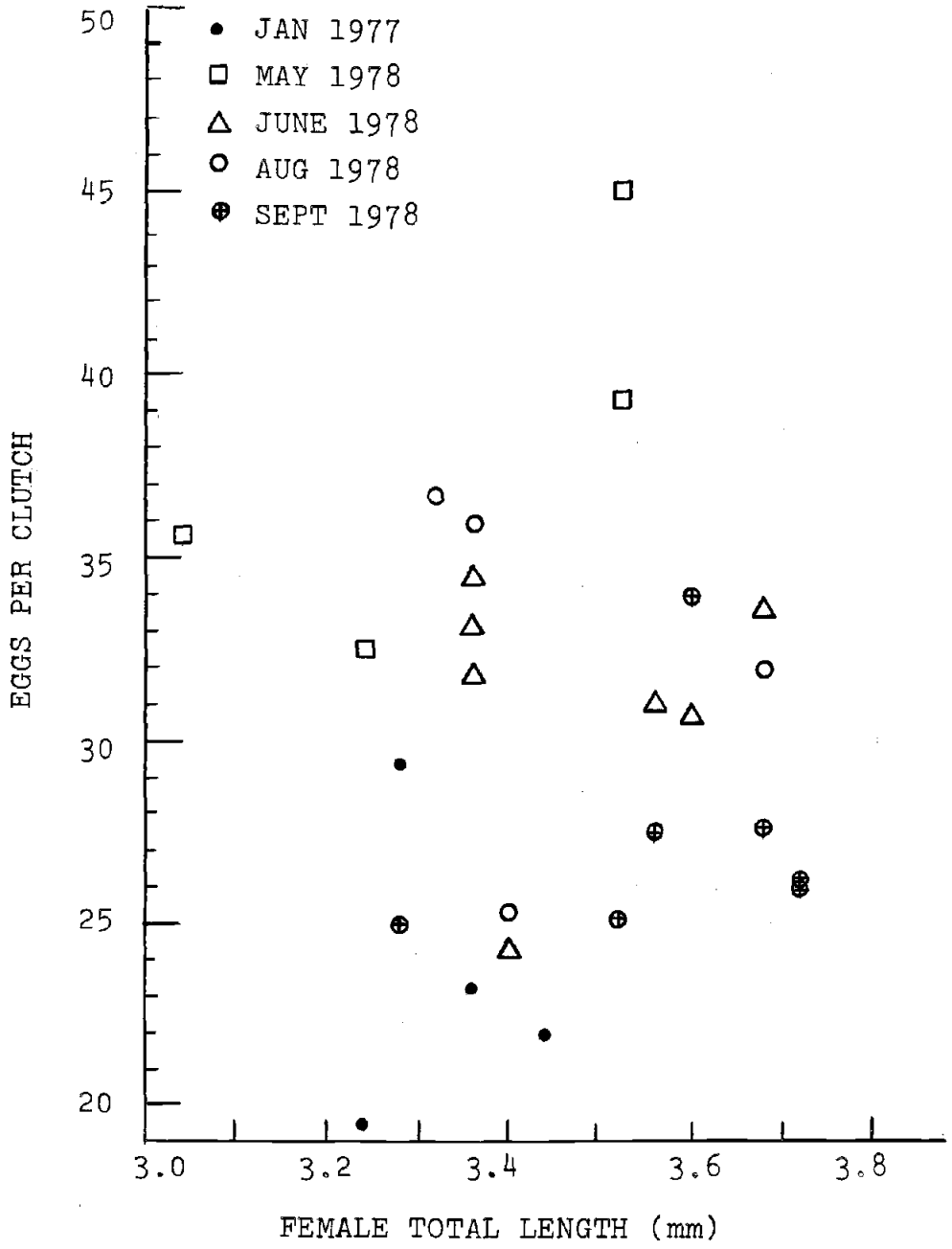

Figure 46. A scatter diagram showing the relationship between eggs per clutch and total length of mother, for Calanus marshallae. The two were not related ($r = -0.0093$).

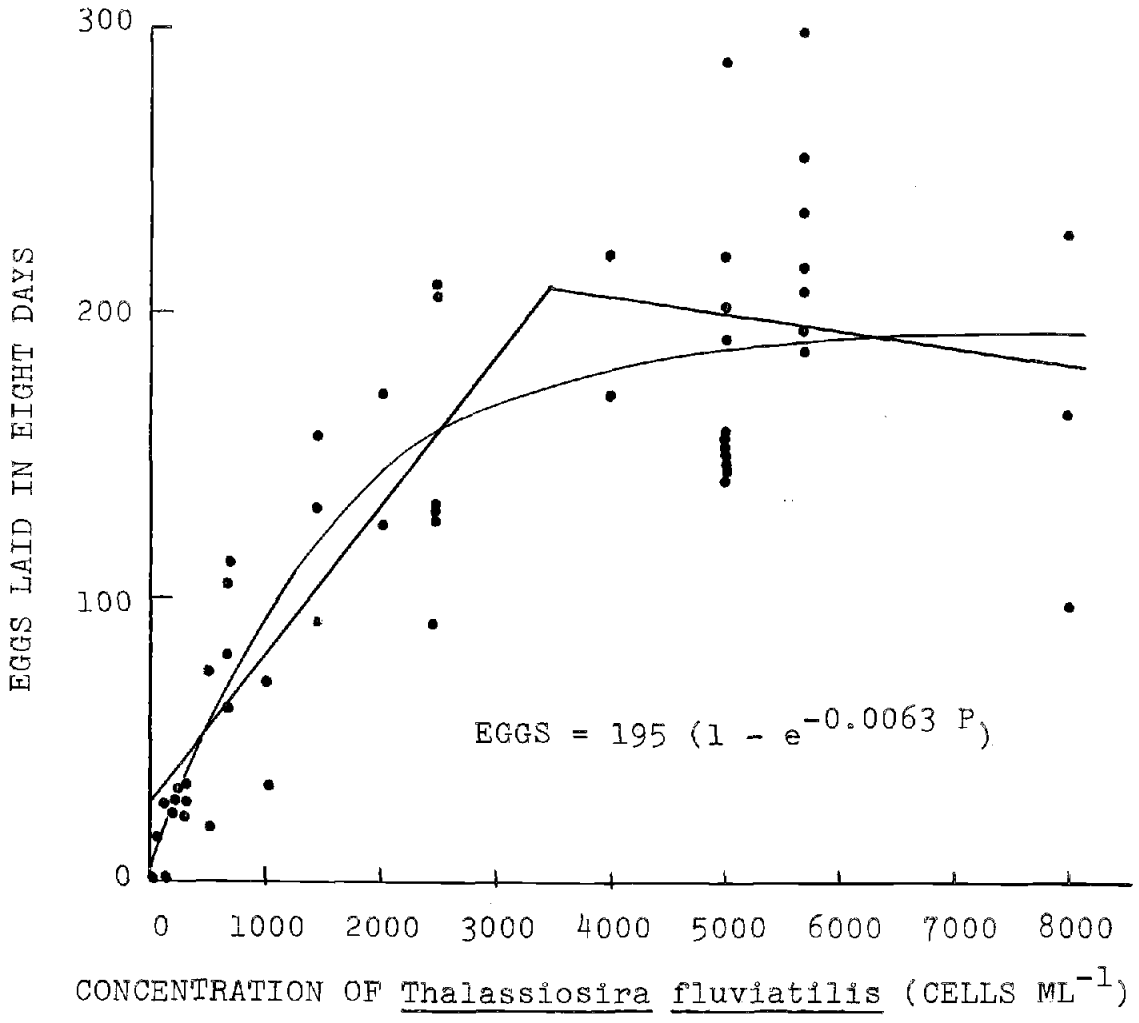

Figure 47. The relationship between number of eggs laid and food concentration for female Calanus marshallae. Maximum egg laying rates occur at 3500 cells per ml of the diatom Thalassiosira fluviatilis. This is equivalent to about 450 µg carbon per liter.

E = total number of eggs laid in eight days

E_{max} = maximum number of eggs laid in eight days

α = constant of proportionality

P = plant concentration in cells per ml

was transformed to

$$\log_e (E_{max}-E) = \log_e (E_{max}) - \alpha P$$

which is a linear equation of the form

$$y = b - mx .$$

A minor problem arose with this transformation. I could not regress the egg data from the experiments where food was in concentrations in excess of about 4000 cells per ml because some of the data had values that were larger than the E_{max}, thus giving a negative number. Since the logarithm of a negative number if undefined, I could not proceed. To overcome this difficulty, I averaged the 23 observations from food levels of 4000 cells per ml and greater, arbitrairly set E_{max} at three eggs greater than this number, and continued the regression using as data, 192 eggs per eight days, at food levels of 4000, 5000, and 8000 cells per ml. No serious problems arise with this modification since the portion of the curve which has the greatest influence on the overall shape is that part where food concentrations are much less than 4000 cells per ml. A pooling of the "high food" data is justified because it has been shown that there is no difference between females, between seasons and between female body length.

The egg laying-food concentration data were also fit with two separate linear functions. The straight lines are also drawn on Figure 47. The regression equations are $y = 14.94 + 0.0608\ x$

($r = 0.88$) for the steep ascending line, and $y = 215.21 - 0.0042\ x$ ($r = -0.0931$) for the plateau. The slope of the plateau line did not differ from zero ($F_{1,22} = 0.184$).

There are no theoretical reasons to help one decide which model is the more correct. One can view the number of eggs produced per clutch as a continuous function of the amount of food available. The rationale come from the fact that daily energy intake is partioned into respiration (catabolism) and growth (anabolism). Most of the daily energy intake is expended on respiration and maintenance. Whatever is left over will go into anabolism, which in the case of female copepods equates to egg production. As more food is digested, increasingly greater amounts of energy will be available for reproduction, up to a maximum level set by the maximum potential output of the ovaries.

ENERGETICS OF EGG PRODUCTION. It is possible to study the energetics of egg production because the rates at which female Calanus marshallae ingest food (energy intake) were measured at the same time as the rates of daily egg production, at various food levels. The ingestion rate vs. food concentration relationship is shown in Figure 48. Between plant concentrations of 300 to 3500 cells per ml, ingestion rate increases linearly. The regression equation was $y = 1147.7 + 2.51\ x$ ($r = 0.97$). Above approximately 3500 cells per ml, the ingestion rate is constant. The plateau portion was $y = 11,677.7 - 0.28\ x$ ($r = -0.28$). The slope of this line did not differ from zero. The mean of the Y observations over the range of 3500 to 8000 cells per ml was 10,923.5 cells per hour ingested. In carbon equivalents, this is 1.37 µg carbon ingested per hour or

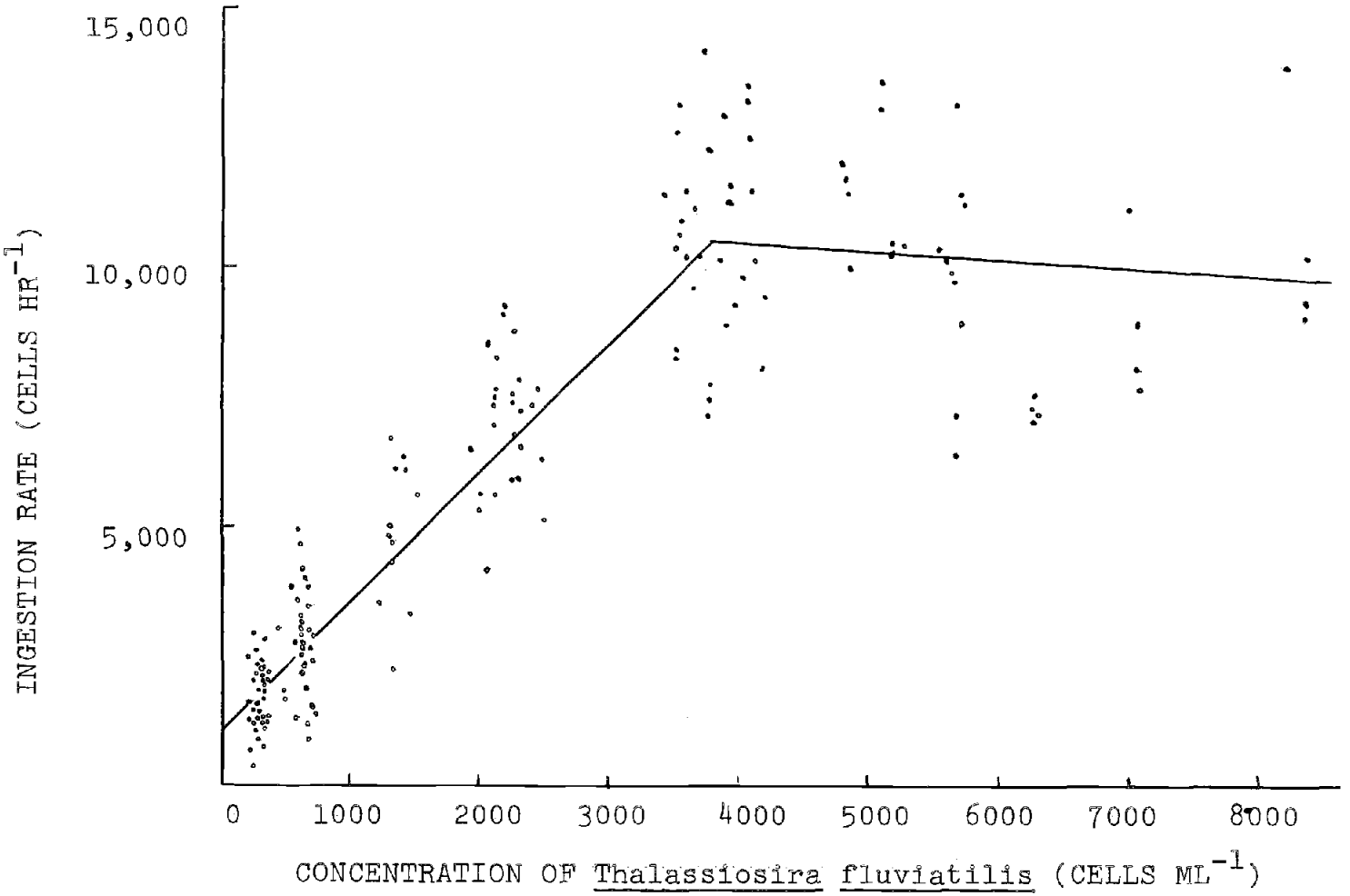

Figure 48. The relationship between ingestion rate of female Calanus marshallae and concentration of the diatom Thalassiosira fluviatilis. The data are best described by two straight lines. Maximum ingestion rates occurred above 3700 cells per ml.

32.8 µg carbon per day. This ingestion rate is achieved at plant concentrations in excess of 3700-3800 cells per ml. Referring back to Figure 47, the maximum egg laying rates for C. marshallae also occurred at this plant concentration.

The gross efficiency of egg production can be calculated because average daily energy intake is known (from the ingestion data) and daily egg production is known. The ratio of weight of eggs per day to weight of food ingested daily is the gross efficiency of egg production. The weight of eggs produced per day is 23.9 eggs day^{-1} x 0.75 µg dry weight egg^{-1} x 0.4 µg carbon per µg dry weight = 7.2 µg carbon as eggs per day. Daily energy intake was 32.8 µg carbon per day. The gross efficiency of egg production is then 7.2 / 32.8 = 22.0 %.

The coefficient of daily egg production was calculated by comparing weight produced as eggs per day and the weight of an average female. The coefficient is (17.9 µg dry weight of eggs / 260 µg dry weight per female) = 0.069. If females put all of their growth into egg production then the coefficient of daily egg production should equal the coefficient of daily growth calculated in Chapter IV. The female growth coefficient is 0.024 µg μg^{-1} day^{-1}. This means that a female should produce at least 0.024 x 260 = 6.2 µg dry weight per female per day. However, nearly three times this weight is produced per day as eggs. Perhaps it is not appropriate to compare the C5 to C6 growth coefficient to the coefficient of daily egg production. Growth rate during this interval may be slow because processes other than growth of somatic tissues are taking place: the sex organs are maturing at this time. The true female growth coefficient must lie

somewhere between the N4 to C5 rate of 0.18 and the C5 to C6 rate of 0.024. The egg production coefficient falls within this range. Landry (1978) found a similar result. Production of eggs by Acartia clausii tended to be higher that the observed growth of C5 under the same conditions. The greatest differences were seen at 15°C. Female growth rate (fecundity) was about twice as great as pre-adult rates.

REPRODUCTIVE EFFORT. At an average rate of 23.9 eggs per day, a female Calanus marshallae is producing 6.9 % of her body weight per day as eggs. Compared to other marine copepods, this value is very low. Landry (1978) found Acartia clausii to produce eggs at a rate of 50 % of their body weight per day at temperatures of 10°, 15° and 20°C. Checkley (1978) got a rate of 37 % of female body weight per day for Paracalanus parvus at 18°C. Johnson (J.K. Johnson, School of Oceanography, Oregon State University) calculated that Acartia californiensis produces about 50 % of the female body weight per day as eggs. Another estuarine copepod, Eurytemora affinis produces eggs at a maximum daily rate of 40 % of female body weight (my calculations from Heinle and Flemer, 1975). These calculations are for April and May in the Patuxtent Estuary when water temperatures ranged from 13° to 25°C. During February and March when temperatures were only 4° to 8°C, the reproductive effort was reduced to only 5 to 10 % of female body weight per day. Reproductive effort of Calanus pacificus was calculated from my own data. Females produce about 11 % of their body weight per day as eggs. Female Euterpina acutifrons, a pelagic marine harpacticoid copepod, expend 37 % of their body weight per day as eggs (Zurlini, Ferrari and Nassogne, 1978).

In conclusion, existing data support a hypothesis that smaller copepods put an overwhelmingly greater effort into egg production than do larger copepods. Curiously, most produce the same number of eggs per day, between 20 and 30 per female.

EGG LAYING IN OTHER CALANUS SPECIES. In March 1978, I set out to collect additional Calanus marshallae in order to continue by investigation of seasonality of egg production. Large numbers of females were taken but they were all Calanus pacificus. Since my laboratory was set up to run an experiment, I measured egg laying rates of this copepod instead of C. marshallae. Egg laying was studied for 23 days at 10°C. I measured daily egg production of three individual females fed excess amounts of Thalassiosira decipiens for a few days, followed by T. fluviatilis, T. pseudonana, and then T. fluviatilis again.

The results are shown in Table 17. Over the first 18 days, a phenomenal number of eggs were laid compared to C. marshallae. The mean egg production of C. pacificus was 78.8 eggs per female per day, and 58.2 eggs per clutch. A clutch was laid every 17.8 hours on the average.

Paffenhoffer (1970) studied Calanus helgolandicus (=C. pacificus) from San Diego, California. Five field-collected females laid an average of 49.3 eggs per day over a 46 day measurement period. The difference between San Diego and Oregon females is probably real although statistical testing is not possible.

At the other end of the spectrum are the data of Marshall and Orr (1952) on Calanus finmarchicus, from Millport, Scotland. In one

Table 17. Egg laying by female Calanus pacificus in March 1978. The effect of food type was compared in this experiment.

				Thalassiosira descipiens				
♀	EGGS	DAYS	A	B	C	D	E	F
1	627	7.83	10	0.78	80.1	62.7	1459	186.3
2	551	7.83	10	0.78	70.4	55.1	1194	152.5
3	336	4.83	6	0.81	69.6	56.0	796	164.8

				Thalassiosira fluviatilis				
♀	EGGS	DAYS	A	B	C	D	E	F
1	395	4.97	7	0.71	79.5	56.4	917	184.5
2	478	4.97	8	0.62	96.2	59.8	799	160.8
3	380	4.97	7	0.71	76.5	54.3	805	162.0

				Thalassiosira pseudonana				
♀	EGGS	DAYS	A	B	C	D	E	F
1	431	5.01	7	0.72	86.0	61.6	843	168.3
2	385	5.01	6	0.84	76.8	64.2	643	128.3
3	373	5.01	7	0.72	74.5	53.3	598	119.4

				Thalassiosira fluviatilis				
♀	EGGS	DAYS	A	B	C	D	E	F
1	478	5.01	7	0.72	95.4	68.3	868	173.3
2	201	5.01	4	1.25	40.1	50.3	606	121.0
3	296	5.01	6	0.84	59.1	49.3	684	136.5

A = number of clutches of eggs laid
B = number of days per clutch
C = number of eggs laid per day per female
D = number of eggs laid per clutch
E = number of fecal pellets
F = number of fecal pellets per female per day

experiment which ran for seven days, egg production as a function of food concentration was studied. The functional response was curvilinear with a maximum egg production rate of 21 eggs per female per day. This is very similar to my results for C. marshallae.

DISCUSSION

EGG CANNIBALISM. An assumption for all of my egg laying measurements is that the mother does not eat her own eggs. Females had the opportunity to eat their eggs because both were present in the same beaker. However, the eggs are more dense than seawater and sink to the bottom immediately upon being laid. Therefore, they are not readily available. As stated in the methods section of this chapter, well-fed females seemed to remain in the water column most of the time.

To test the assumption that well-fed females do not eat their eggs, I compared the histogram of clutch sizes (Figure 45) which represent a random sample of eggs of all ages (called Group I), to a histogram of clutch sizes of batches of eggs that were known to be less than 2.5 hours old (called Group II). This latter histogram includes eggs that had just been laid, or had cleaved to the two, four, or eight cell stage. The hypothesis under test is that the average clutch sizes calculated from the two histograms is the same. I would expect the alternate hypothesis, that mean clutch size of all eggs is less than mean clutch size of newly-laid eggs, to be true if the females cannibalize their own eggs. Because my census interval was always 24 hours, the females in Group I would have had up to

21.5 hours to feed on their own eggs, whereas those in Group II would have had at most 2.5 hours to feed on their own eggs.

The histogram of sizes of clutches which were less than 2.5 hours old is shown in Figure 49. The observations come from all laboratory data collected between May 1976 and September 1978, a total of 50 observations. The average clutch size was 30.2 $\pm$ 3.91 (95 % confidence interval). This is not statistically significantly different from the average clutch size of 29.7 eggs per clutch laid by well-fed females. I conclude that well-fed females do not eat their own eggs and that my data are free of that sort of bias.

Starved Calanus marshallae on the other hand, do eat their own eggs. This was verified in an experiment conducted in August 1978, after I had completed all experimental work on the effects of food concentration on egg production. In these egg cannibalism experiments, I offered eggs to females which had been underfed for several days. Experiments ran for 24 hours. I gave each female her own eggs for these tests. Since it is possible to age eggs, one can differentiate between the experimental eggs and eggs which a female may have laid over the course of a single day's measurements.

The results of the cannibalism experiment are shown in Table 18. There can be no doubt that starved females eat their eggs. I conclude from this set of experiments that my egg laying data from food concentrations less than at least 650 cells per ml underestimate the true egg laying rates. The data from food concentrations between 650 and 3500 cells per ml may be underestimated as well.

Because of cannibalism, I cannot exactly quantify the effect of

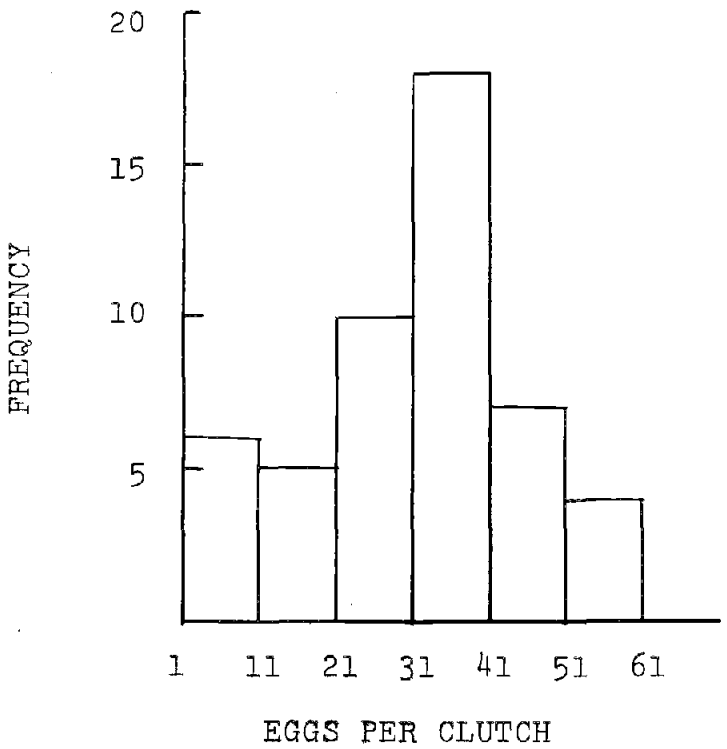

Figure 49. Histogram of clutch sizes of eggs that were 0 - 2.5 hours old.

Table 18. Results of the egg cannibalism experiments.

Date	Eggs Eaten	/ Eggs Offered	% Eaten	Food Level (Cells ml^{-1})
28 June 1978	9	30	30.0	585
"	21	30	70.0	"
29 June 1978	23	35	65.7	500
"	21	31	67.7	"
"	22	52	42.3	"
30 June 1978	21	30	70.0	"
"	23	31	74.2	"
"	33	49	67.3	"
16 June 1978	18	22	81.8	301
"	32	33	97.0	"
14 June 1978	27	30	90.0	293
13 June 1978	34	44	77.3	285
Totals	284	417	68.1	

food concentration on egg production. This does not nullify my egg laying data however. Two data points cannot be challenged. First, well-fed females lay 29.7 eggs per clutch, and second, unfed females lay no eggs. Evidence for this latter fact is presented next.

It is known from six experimental females that eggs are not laid if the females are not fed. One cannot say that this observation arose because the females ate all of their eggs for the following reasons: First, in the cannibalism experiment, out of 12 trials, no female ever ate all of the eggs offered. Even if the females which were unfed had laid eggs and later proceeded to eat them, at least a few eggs would have been present at the census. Second, out of 48 female-days of data taken under starved conditions, the probability of a clutch being laid within two hours of the daily census is fairly high. This probability can be estimated. Assume (1) a continuous 48 day time series and (2) on the average a clutch is laid every 30 hours and (3) a census interval of 24 hours. A clutch will be laid at the same time as the census was made, every 120 hours. For every five census events, four egg laying events will take place. Out of 1156 hours (48 female-days x 24 hours), 1156 / 120 or 9.6 events would occur simultaneously. The probability of my observing the two events simultaneously is then 9 out of 48 trials, or 0.188. This probability is a minimum estimate because I did not take into account the duration of the two types of events. The calculation will suffice however. In 48 trials, I never saw a clutch of eggs from any of the six females. I therefore conclude that starved females lay no eggs.

A histogram of clutch sizes of females fed 100 to 3000 cells per ml of Thalassiosira fluviatilis is shown in Figure 50. In nearly half of the observations (114 / 244 = 46.7 %), no clutch was laid within the 24 hour census interval. There is no central tendency whatsoever, and the data are clearly distributed non-normally. A different process is operating here, compared to that producing the histogram of clutch sizes of well-fed females. Either cannibalism or food quantity is controlling apparent clutch size.

To further explore the effect of food concentration on egg production, I plotted the number of clutches laid in eight days against food concentration. This will give an indication of the effects of food quantity alone, since it is highly probable that even if cannibalism is rampant, mothers will never find and eat all of their progeny. The data are shown in Figure 51. Females maintained at food concentrations ranging from 0 to 640 cells per ml laid significantly fewer clutches than females maintained at concentrations of 2000 to 8000 cells per ml (2.9 vs. 6.8 clutches per eight days, $t = 9.05$, 58 degrees of freedom). The number of clutches laid reaches a maximum at plant concentrations near 2000 cells per ml of Thalassiosira fluviatilis. If these clutches contained the average number of eggs (30 per clutch) before being cannibalized, then maximum egg laying rates could be occurring at 2000 cells per ml!

The fecal pellet data support the tentative conclusion that egg laying rates could be at a maximum at food concentrations of 2000 cells per ml. The relationship between egestion rate (fecal pellet production) and food concentration is shown in Figure 52. The data are

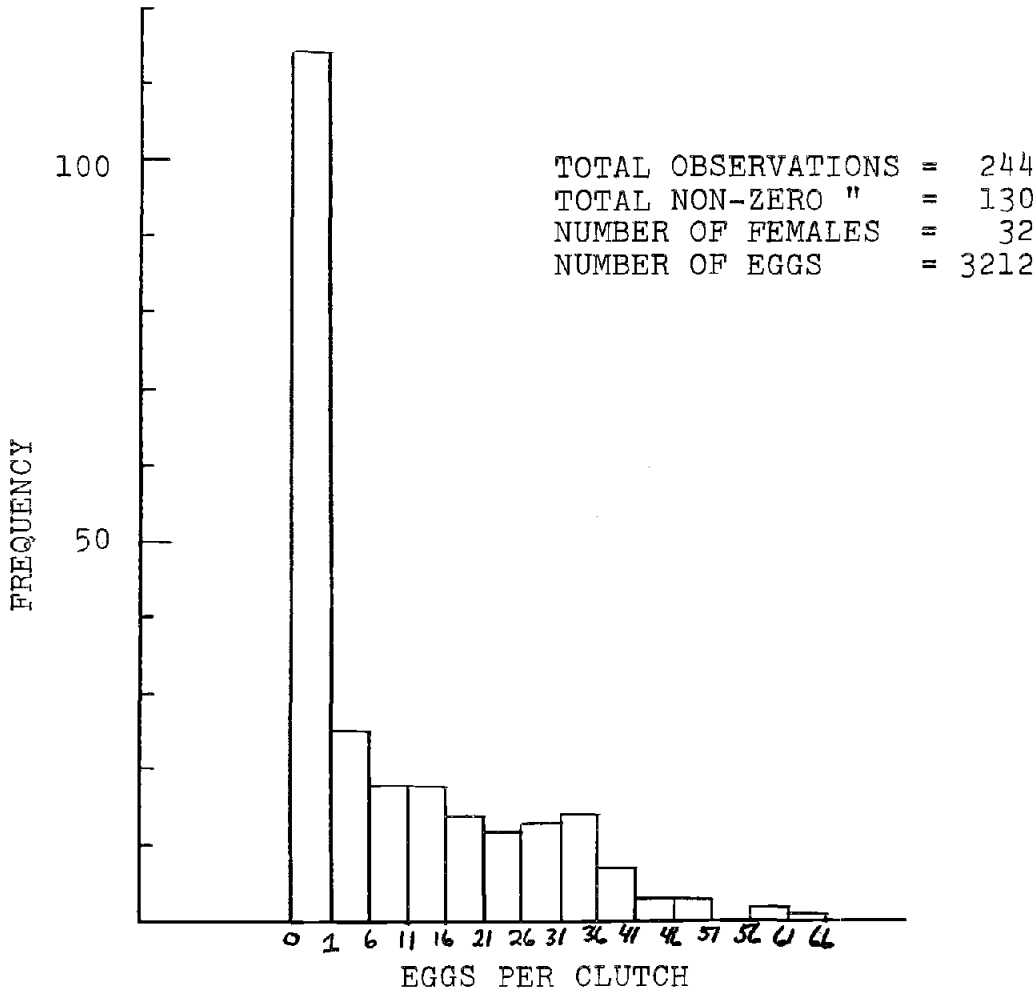

Figure 50. Clutch sizes of female Calanus marshallae fed between 100 and 3000 cells per ml of the diatom Thalassiosira fluviatilis.

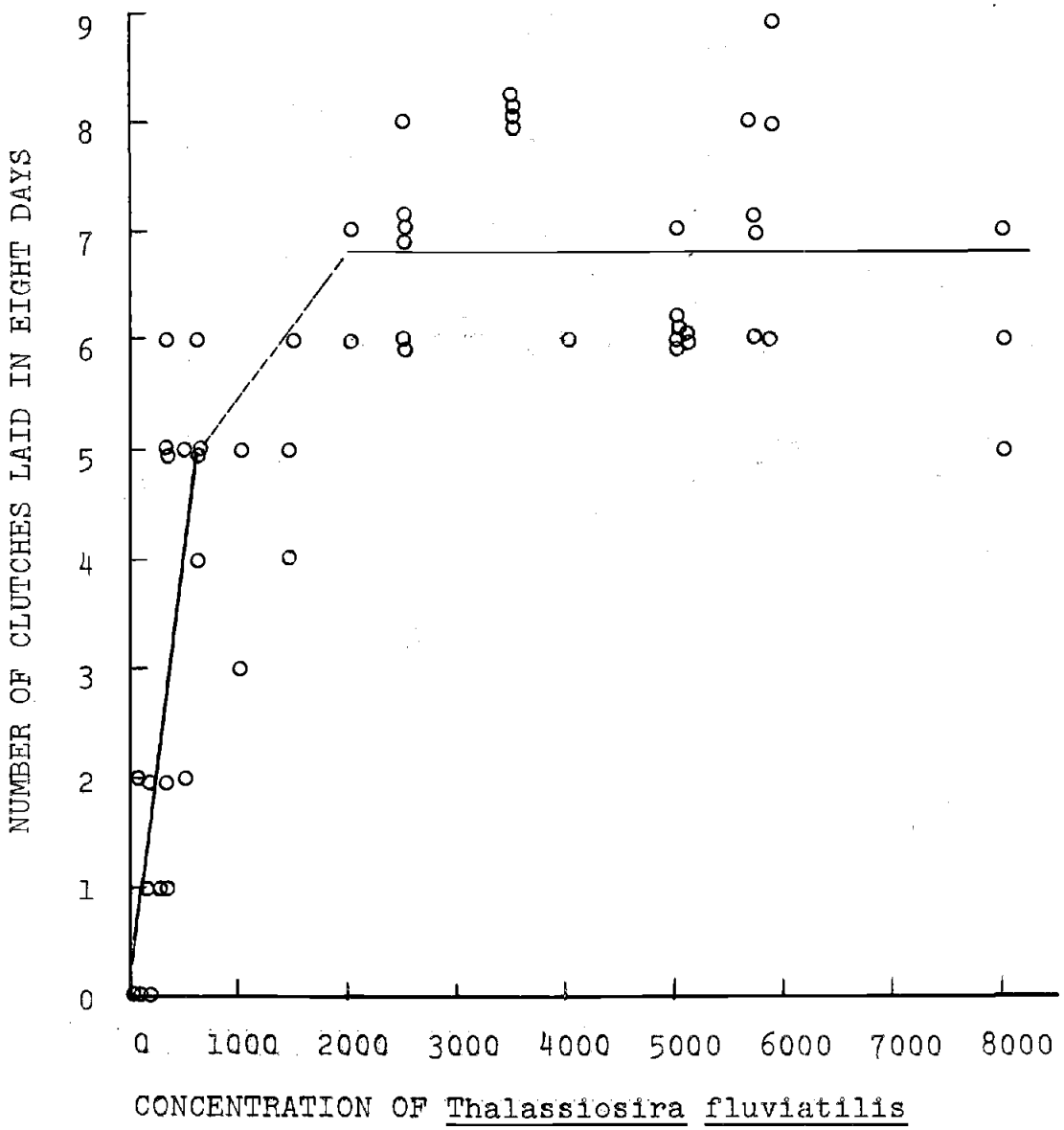

Figure 51. The relationship between the number of clutches of eggs laid by female Calanus marshaldae in eight days, and concentration of Thalassiosira fluviatilis. The number of clutches laid reaches a maximum at 2000 cells per ml.

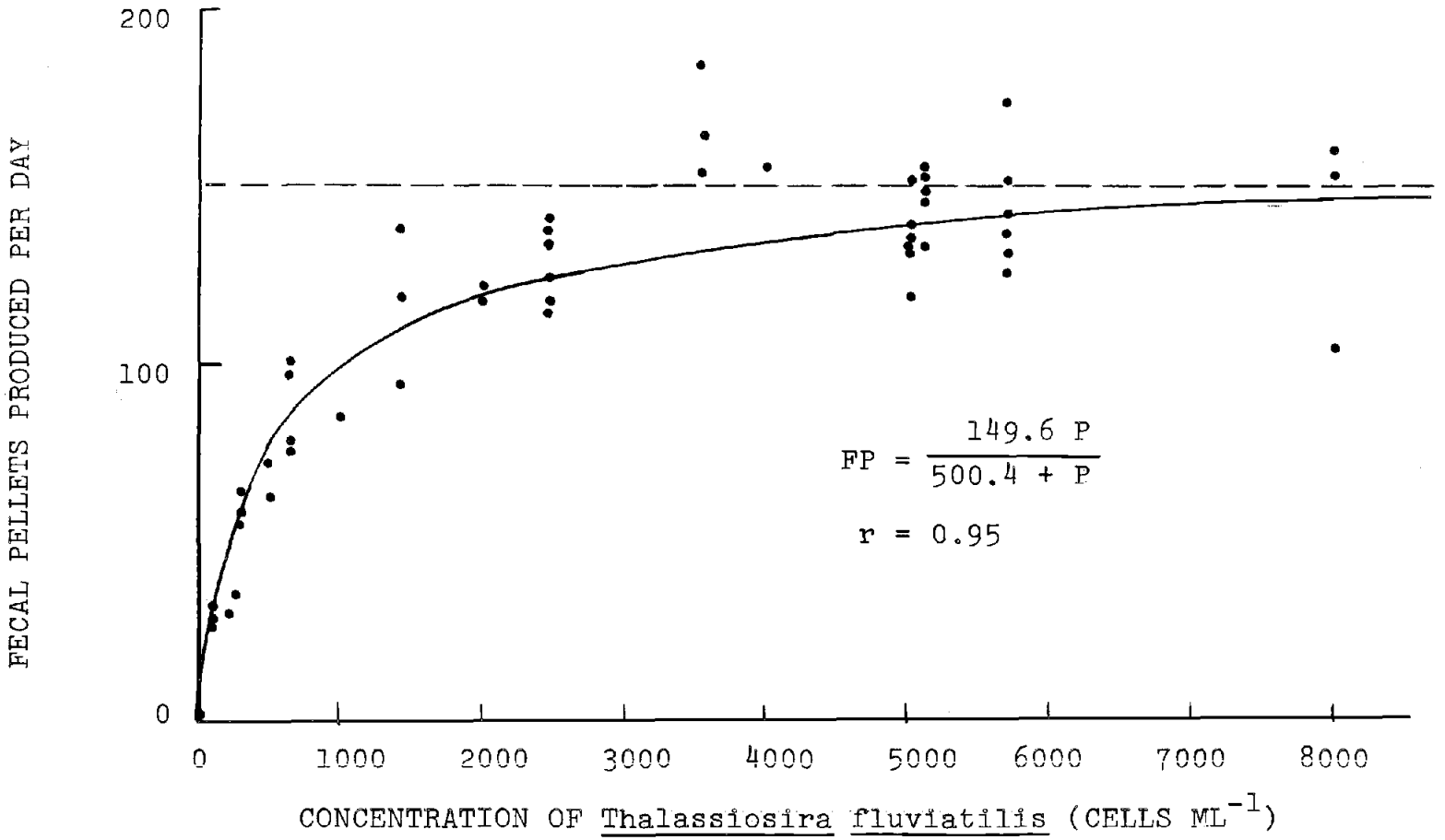

Figure 52. The relationship between fecal pellet (FP) production and plant concentration (P). Fecal pellet production is 80 % saturated at 2000 cells per ml of Thalassiosira fluviatilis.

best described by the Michaelis-Menton function, Fecal Pellets = 149.6 P / (500.4 + P), r = 0.95, where P is plant concentration. At plant concentrations of 1600 cells per ml, 75 % of the maximum egestion rate is achieved, at 2000 cells per ml, 80 % and at 3500 cells per ml, 87 % has been achieved. It is possible that at plant concentrations of approximately 2000 cells per ml, the egestion process is "saturated". That is, food is moving through the gut at rates very near the maximum rate. Above these food levels, even though up to twice as many plant cells are ingested per hour, there is only a small increase in the number of fecal pellets passing through the gut. At higher food levels, the fecal pellets are measureably larger. The maximum rate of 149.6 pellets per day equates to one pellet per 9.6 minutes.

Since food is moving through the gut at near-maximum rates at 2000 cells per ml, it seems reasonable to speculate that the net energy gained from feeding is also near its maximum at this food level. I further speculate that the relationship between net energy gained and food concentration would look like the fecal pellet vs. food level relationship. This would suggest that assimilation efficiency is high at 2000 cells per ml and drops at higher food levels. Perhaps the egg data would also show the same relationship if it were not for cannibalism.

Many unanswered questions have been raised here. More experimental data are needed to answer them, particularly egg laying data at 2000 cells per ml, and 2500 cells per ml, in experiments where cannibalism is guarded against. We cannot progress further in our

in our understanding of egg production energetics until the true and unbiased fecundity rates are known at several cell concentrations between 2000 and 3500 cells per ml.

Of all published works on the effects of food concentration on egg production of pelagic marine copepods (Raymont and Gross, 1942; Marshall and Orr, 1952; Corkett and McLaren, 1969; Valentin, 1972; Gaudy, 1974; Dagg, 1977; Iwasaki, Katoh and Fujiyama, 1977; Parrish and Wilson, 1978; Checkley, 1978), only one worker tried to deal with the problem of cannibalism. Checkley corrected his egg counts upward by a "cannibalism factor". That factor was calculated under the assumptions (1) that eggs are fed upon at the same rate as phytoplankton, (2) that the eggs are randomly distributed throughout the beaker, and (3) that eggs are produced constantly.

Cannibalism notwithstanding, the five data sets which are most complete (Marshall and Orr, Valentin, Iwasaki et. al., Checkley, this dissertation), all show a curvilinear relationship with zero eggs at zero food and a maximum in egg production at some intermediate food level above which eggs are not produced at a greater rate. These two data points may be connected by a curve or a straight line. Due to the different levels of cannibalism which affect these data sets, the true maximum egg production may occur at a lower food concentration than the data would suggest.

Checkley is the only other worker to compare ingestion rates to egg laying rates. His result was the same as mine: maximum egg production apparently occurs at the same plant concentration as maximum ingestion rate. However, because of the high probability of

cannibalism in my experiments, maximum egg laying rates likely occur at food levels much lower that those which produce maximum ingestion rates. It would appear that Calanus marshallae females are more efficient at producing eggs than Paracalanus parvus females.

REPRODUCTION - FIELD OBSERVATIONS

METHODS

Egg production in the field was studied from the 8 July to 13 August 1977 vertically stratified pump samples. Egg laying rates were calculated in two ways. In the first method, egg and female abundance profiles at each station were integrated by the trapezoid method. This converts abundance estimates from number per cubic meter to number of individuals within a square meter water column extending from 1 m to the deepest depth sampled. Numbers per square meter were summed over all stations on a date, giving a single abundance estimate for eggs and females on each date. In the second method, abundance estimates (no. m^{-3}) at all depths and stations along a transect were summed, yielding an index of total abundance of eggs and females. For both methods, the ratio of eggs per female was calculated.

RESULTS

EGG LAYING RATES. The total number of eggs and females seen on each sampling data and the ratio of eggs:females, are shown in Table 19. The ratio averaged from the square meter data was 62.8 and from the m^{-3} data, 56.4 eggs per female. To simplify things, I pooled the 16

Table 19. Abundance of eggs (E) and females (F) along the 1977 transect lines, and the ratio, eggs:females, calculated by two methods. The overall average number of eggs per female is shown below the table.

	NUMBER M^{-3} SUMMED			NUMBER BENEATH M^2		
	EGGS	FEMALES	E/F	EGGS	FEMALES	E/F
8 July 1977	194,874	13,610	14.3	896,344	73,126	12.3
15 July	327,550	1,877	174.5	1,613,010	19,833	81.3
21 July	28,728	885	32.5	107,806	9,109	11.8
24 July	176,515	3,576	49.4	680,237	26,268	25.9
26 July	68,719	520	132.1	300,717	1,215	247.5
29 July	321,037	6,773	47.4	1,408,813	40,401	34.9
4 August	30,254	597	50.7	156,599	4,393	35.6
13 August	350	286	1.2	2,586	1,554	1.7

(1) OVERALL AVERAGE
EGGS/FEMALE = 59.6 eggs female^{-1}

(2) AVERAGE w/o
15,26 July = 26.5 eggs female^{-1}

dates which gave an average of 59.6 eggs per female. This is not a rate. On any sampling date, one will sample some eggs that were laid on that day and some which were laid on the previous day. Since an average female lays a clutch every 30 hours and that clutch will not hatch for 40 hours, eggs seen in the field on a given day represent at least two clutches for each female present. A simple input-output model gives a more precise determination. It is known from laboratory observations that eggs are laid (input) with a time constant of 1.25 days per clutch, and hatch (output) with a time constant of 1.67 days per clutch. In steady state, the time constant for addition of eggs is 1.67 - 1.25 = 0.42 days per clutch. Therefore, on any given day, the egg:female ratio needs to be multiplied by 0.42. The inverse is 2.38 clutches per day. The finite birth rate is then,

$$B = \left(\frac{\text{EGGS}}{\text{FEMALES}}\right)\left(0.42\right)$$

Based on the overall average number of eggs per female, birth rates are 59.6/2.38 = 25.0 eggs per day. This compares extremely well with the measured laboratory rate of 23.9 eggs per day. The egg abundances on 15 and 26 July are very high and grossly overestimate expected daily egg production. If one assumes that these estimates are incorrect because females were undersampled and exclude them from the overall average, then the finite birth rate becomes 26.5/2.38 = 11.1 eggs per day. This is assumed to be the minimum estimate of field egg laying rates.

The finite birth rate assumes that all females seen in the field lay eggs every 30 hours and that there is no egg mortality. These

assumptions are discussed next.

OVARY RIPENESS. The first assumption was tested by examining the state of ovary ripeness in field-collected females. Females which have fully developed ovaries with large eggs filling their oviducts are defined to be ripe by Marshall and Orr (1960) and expected to lay eggs on schedule. Females lacking fully developed ovaries have not laid eggs in their life time yet, and those with developed ovaries but with no large eggs in their ovaries cannot be expected to lay eggs soon. These females are unripe and semi-ripe respectively, after Marshall and Orr (1960). I found that it was easy to score "ripe" and "unripe" females, but the "semiripe" state represented a broad spectrum of ovary development. Therefore, I only classified females into three categories: ripe, unripe, and other. I examined females from transects taken on 24, 26, 29 July and 4, and 13 August 1977. The result was that virtually all females at all depths within five to seven miles of the coast were ripe. This was the geographical region where most females were found. I conclude that the first assumption listed above is a reasonable one.

Further support for my contention that females found in the nearshore zone are all ripe comes from laboratory observations. Egg laying of at least 60 females was studied from May 1976 to September 1978. All laid eggs within 24 to 48 hours of being brought into the laboratory. Therefore, all were ripe.

The time between molting to adult female and the laying of the first eggs is quite long. Marshall and Orr (1955) report that the "unripe" state persists in C. finmarchicus for many days. Twelve

unfertilized females brought into the laboratory as C5 laid unfertile eggs only after a lag of 7 to 20 days. In another experiment, field-collected females with attached spermatophores were maintained separately in the laboratory. Marshall and Orr reported that usually a period of up to two weeks elapsed before these females began laying eggs.

I tried to determine for Calanus marshallae the lag between molting into female from C5, and the laying of the first eggs. I was unable to measure this directly with unfertilized females because unfertile eggs rotted within an hour of being laid. Females from the field never had spermatophores attached so I could not repeat that experiment either. Therefore, I scored my laboratory-raised females for ovary ripeness, and looked at percent of females having ripe ovaries vs. age of female. Experimental groups were studied by a census made every five to seven days. Each female's age was only known to a precision of $\pm$ 2.5 to $\pm$ 3.5 days, which is half the census interval. This is because each female could have molted on any day within the census interval. The result is shown in Figure 53. A few females were ripe on the day that they molted, but half of the females in a given sample were not ripe until about a week after molting from C5. The conclusion which I draw from all of the above considerations on ovary ripeness is that female Calanus marshallae in the nearshore zone are ripe when they arrive there, and that up to one week has elapsed since they molted from the fifth copepodite.

EGG MORTALITY. The second assumption listed at the top of the previous page is also testable. It is known that field egg laying

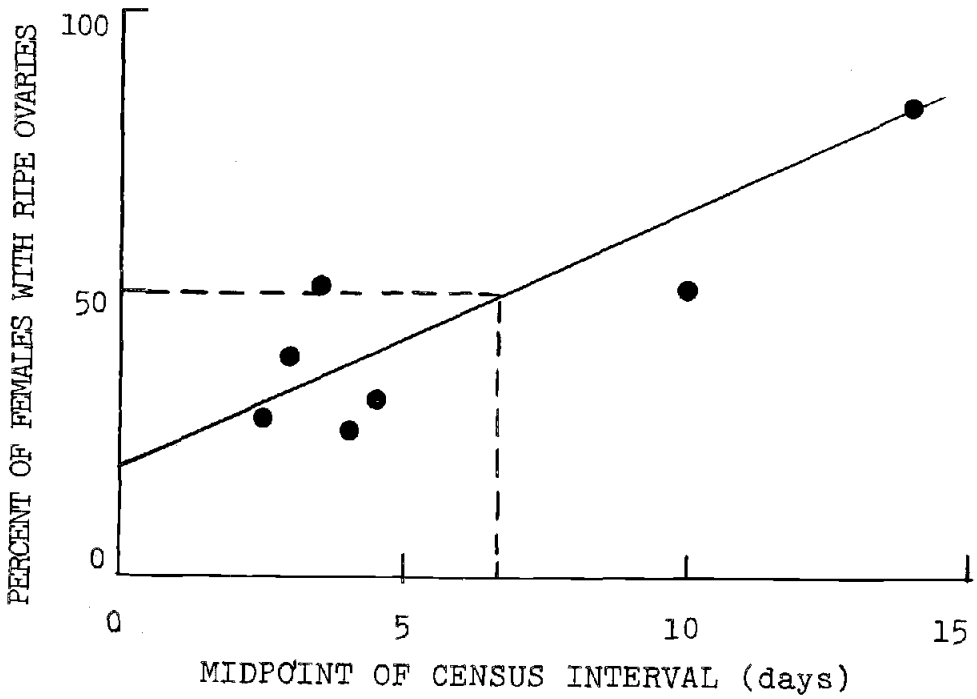

Figure 53. Ovary ripeness of laboratory-raised females. Half of the population was ripe 6.8 days after molting from C5. Almost 20% were ripe on the same day that they molted. The maximum error of these estimates is about ± 2-3 days.

rates are very close to maximum egg laying rates observed in the laboratory. Field rates are highly variable but the average is somewhere between 11.1 and 25.0 eggs per day. Laboratory rates were 23.9 eggs per day averaged over all seasons, and 27.4 eggs per day for five females studied from June and August 1977. It would seem then that egg mortality ranges from zero to perhaps 50 %. Many more estimates of daily egg production in the field are needed however, to study egg mortality from these kind of data.

Another approach suggests that mortalities may be even higher. Egg abundances on one particular cruise were compared to N3 and N4 abundances on the following cruise. The sampling interval between cruises ranges from six to nine days. The proportion of the population which would have reached N3 and N4 six to nine days from egg hatching was estimated from the laboratory development time data (Figure 29). The number of (N3 + N4) which resulted from the eggs laid on the previous cruise was calculated then compared to the number of eggs. The results are shown in Table 20. On the average, 90 % of the eggs do not reach the third nauplius stage. Unfortunately, it is not possible to know if the deaths are evenly distributed over the six to nine day interval between eggs and N3, or if deaths are at one stage, either eggs, N1 or N2. This is because I usually did not count N1 or N2 stages from the field samples. They are about the same size as Pseudocalanus N3 and N4. Pseudocalanus nauplii are so overwhelmingly abundant nearshore (up to 50-100 per liter) that I did not have the patience to separate the Calanus N1 or N2. The Calanus marshallae N3 were difficult enough to separate. My impression at the

Table 20. Estimates of egg mortality from field samples.

DATE		TIME INTERVAL	PROPORTION OF EACH STAGE		NUMBER OF EACH STAGE PER M^2		TOTAL NAUPLII	TOTAL EGGS	EGG MORTALITY
EGGS	NAUPLII	(DAYS)	N3	N4	N3	N4	(M^2)	(M^2)	(%)
8 July	15 July	7	.73	.27	91,996	20,985	112,981	896,344	87.0
15 July	21 July	6	.83	.17	4,524	3,976	8,500	1,613,010	99.5
21 July	29 July	8	.65	.35	20,045	16,720	36,765	107,806	66.0
29 July	4 August	6	.83	.17	9,254	510	9,764	1,408,813	99.3
4 Aug	13 August	9	.56	.44	416	87	503	156,599	99.7

AVERAGE EGG MORTALITY = 90.0

time was that there were many less N1 and N2 than N3. Recall that it was shown in Chapter IV that these first two stages have a duration of only 0.9 days each and that N3 have a duration of 6.8 days. In steady state, one would expect to see (0.9 + 0.9) / 6.8 = 0.26 as many (N1 + N2) as N3, or roughly four times as many N3.

Whether this 90 % mortality is at egg stage alone, or N1 and N2, my study clearly demonstrates that mortality is extremely heavy in these first three life cycle stages. After 3.5 days of development (i.e., 3.5/64 days or 5.5 % of the total development), 90 % of the mortality has taken place. Only two individuals per female per day survive the egg stage to begin the 60 day period to adulthood.

EGG SINKING RATES. The eggs of many marine copepods are known to be more dense than seawater. In the field, Calanus marshallae eggs are abundant between 1 and 10 m, never deeper. I needed to know the sinking rate of eggs to better understand this observed distribution pattern.

Sinking rates were measured in the laboratory using filtered sea water of 33.8 $^{o}/_{oo}$ salinity and 10°C. Sinking rates were measured in a simple settling chamber. I placed a clear glass ungraduated cylinder inside an 800 ml tall-form beaker. Both were filled with sea water and allowed to stand for one day before running an experiment. Eggs were introduced singly with a pipette, just below the water surface and near the center of the water column of the inner cylinder. I timed the fall of individual eggs with a stopwatch as they fell through a 5 cm distance. The eggs fell approximately 3 cm before passing through the standard measurement distance. I measured

the descents of 68 eggs. The results are shown in Figure 54. The eggs sank at a mean rate of 36.0 m day^{-1}.

Eggs that are as dense as this should not be found only within the 1 to 10 m layer of the water column. At a rate of 36.0 m per day, they could fall to 60 m depth (36 m per day x 1.67 days to hatch). Some process is acting to keep the eggs near the surface. There are at least two possible explanations:

1. Predator Control Hypothesis. Eggs are laid at the surface and only sink a few meters before being eaten. This hypothesis requires the females to migrate to the surface and lay eggs. Since females are never found at the surface during the day, they would have to move to 1 m at night and spawn there.
2. Vertical Upwelling Transport Hypothesis. Eggs are laid at any time and anywhere in the water column that females are located. Since the main spawning center is in the region of maximum upward vertical velocity, the eggs are simply carried upward. Therefore, as a first approximation, since eggs do not appear to sink in the field, their sinking rate may be taken to equal the upward velocity rate. The 36.0 m per day sinking rate compares moderately well to vertical velocities computed by Halpern (1976). He calculated vertical velocities of 2 x 10^{-2} cm sec^{-1}, which is 17.3 m per day. This is fair agreement.

LONGEVITY OF FEMALES. In order to calculate the number of eggs which a female lays in her lifetime and the net reproductive rate, one

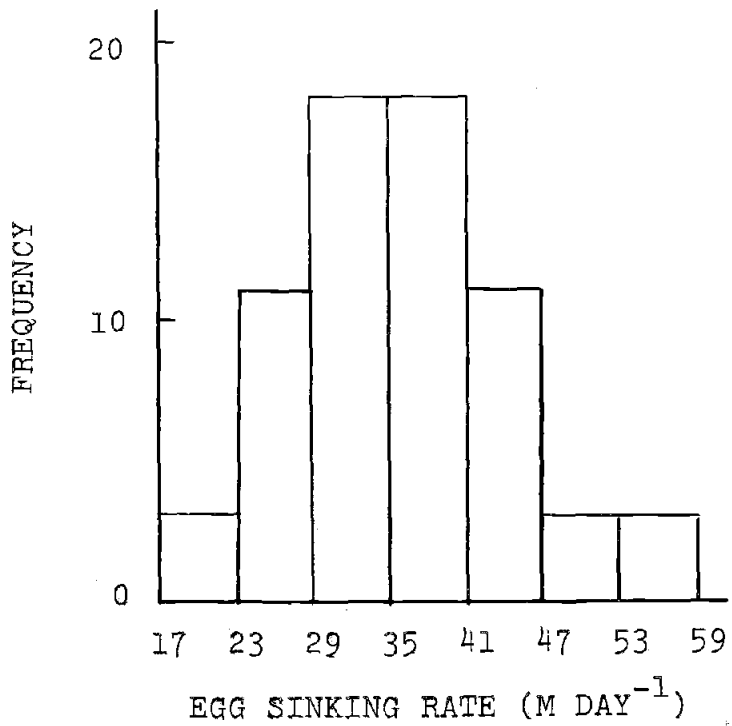

Figure 54. Laboratory measured sinking rates of Calanus marshallae eggs. The mean rate was 36.0 m day^{-1}.

needs to know how long a female lives in the field, on the average. I used the method of Green (1976) to calculate the average longevity of adult females. Methods like this one use laboratory development time data and average abundance of C5 in the field to calculate the number of C5 which will recruit into adulthood, and compares this to the difference in abundance of females between two successive sampling dates. The computational formulas are

$$\Delta A = (N_{♀,t_1} - N_{♀,t_2}) + \left[\frac{\bar{N}_{C5}}{D_{C5}} T\right]$$

where

ΔA = change in adult (female) abundance

$N_{♀,t_1}$ = abundance of females on the first sampling date

$N_{♀,t_2}$ = abundance of females on the second sampling date

$\bar{N}C_5$ = mean number of C5 between the two sampling dates

D_{C5} = C5 stage duration in the laboratory

T = time interval (days) between sampling dates

and

$$L = \frac{\bar{N}_{♀}}{\Delta A} T$$

where

L = longevity of females

$\bar{N}_{♀}$ = mean number of ♀ between the two sampling dates.

The calculations are in Table 21. One estimate gave a negative longevity. This is a sampling artifact which came about because there was a large increase in female abundance on 29 July 1977 unaccounted for by recruitment from C5. Therefore, this estimate cannot be used

Table 21. The calculation of recruitment into female from C5, and longevity of females for the 1977 data. N is the abundance in number beneath a square meter water column summed over all stations along a transect. R is the number of daily recruits from C5 to female. Other symbols are defined in the text.

DATE	T	$N_{♀}$	$\overline{N}_{♀}$	N_{C5}	$\overline{N}_{C5}$	D_{c5}	R	$N_{♀1}-N_{♀2}$	ΔA	LONGEVITY
8 July 1977		73126		11076						
	7		46480		11568	20.9	3874	53293	57167	5.7 days
15 July		19833		12060						
	6		14471		26005	20.9	7466	10724	18190	4.8 days
21 July		9109		39950						
	8		24755		31092	20.9	11901	-31292	-19391	(-10.2 days)
29 July		40401		22234						
	6		22397		18237	20.9	5236	36008	41244	3.3 days
4 Aug		4393		14239						
	9		3251		25110	20.9	10813	2839	13652	2.3 days
13 Aug		1554		35981						
								MEAN LONGEVITY =		4.0 days

to calculate female longevity. The mean longevity in 1977 based on four estimates, was 4.0 days. In further calculations, I am assuming that this is the usual life span of reproductive females.

As a check on this calculation, I computed mean longevity for the year 1970 from samples collected off Newport, Oregon described earlier in this dissertation. The results are shown in Table 22. Adults were again found to be shortlived in the field, surviving 6.5 days on the average.

NET REPRODUCTIVE RATE. Population biologists define the average total number of eggs that a female lays during her lifetime as the net reproductive rate (Ro). It is given by

$$R_o = \sum_{x=1}^{x=\infty} l_x b_x \Delta x$$

l_x = the probability that a female will be alive at age x

b_x = the number of eggs per female at age x

x = time (days)

The fecundity and female longevity are known. The probability of an egg surviving to become a female is low and needs to be estimated. This is done next.

Table 23 shows the abundance data from 1977 for each stage. These are number of individuals beneath a square meter summed over all stations and dates. Note that the abundances of each stage, except eggs, are about equal to each other. The other column of numbers is the daily recruitment to the next successive stage, and is obtained by dividing the abundace of each stage by stage duration which is known from laboratory measurements. Daily recruitment between stages is

Table 22. The calculation of recruitment into female from C5, and longevity of females for the 1970 data. Symbols are defined in Table 21 and in the text. The longevity estimate enclosed in ( ) was not used in calculation of mean longevity. Abundances are number per m3.

DATE	T	$N_{♀}$	$\overline{N}_{♀}$	N_{C5}	$\overline{N}_{C5}$	R	$N_{♀1}-N_{♀2}$	ΔA	LONGEVITY
4 June 1970		12.4		9.8					
	19		17.4		9.8	8.9	-10.0	- 1.1	Negative
23 June		22.4		9.9					
	9		15.2		8.8	3.8	14.5	18.3	7.5 days
2 July		7.9		7.7					
	14		9.9		8.3	5.6	- 3.9	1.7	(81.5 days)
16 July		11.8		8.8					
	13		8.0		6.2	3.9	7.6	11.5	9.0 days
29 July		4.2		3.6					
	15		2.5		3.8	2.7	3.5	6.2	6.0 days
13 Aug		0.7		3.9					
	10		5.2		10.0	4.8	- 8.9	- 4.1	Negative
23 Aug		9.6		16.1					
	19		6.5		11.8	10.7	6.2	16.9	7.3 days
11 Sept		3.4		7.4					
	14		3.5		27.9	18.7	- 0.1	18.6	2.6 days
25 Sept		3.5		48.4					
							MEAN LONGEVITY =		6.5 days

Table 23. Abundances of Calanus marshallae life history stages summed over all stations and dates in 1977. Also shown is the number of recruits, obtained by dividing abundances by duration of each stage, which move to the next developmental stage per day.

	OVERALL ABUNDANCE NO PER M^2	ABUNDANCE / STAGE DURATION
EGGS	4,182,572	2,521,620
N3	185,547	27,286
N4	156,532	32,610
N5	120,145	35,337
N6	90,134	34,667
C1	136,959	31,851
C2	179,482	39,018
C3	300,552	44,199
C4	254,845	41,104
C5	135,540	6,485
FEMALE	149,511	37,378
MALE	8,413	

equal from N3 to C1. The C2 to C4 stages have more recruits. This is because there was a strong abundance peak of C2-C4 between 8 and 21 July which biases these data upward, compared to the other data. Had we been able to sample for at least an additional month, the C2-C4 data may have averaged out to be the same as the N3-C1. Even though cohorts do move through the Calanus marshallae population, stage-specific abundances over the six-week sampling interval in 1977 average out to be about the same. This happens in part because mortality from N3 to C5 is so low. Assuming steady state, the probability of an egg reaching adulthood is the ratio females:eggs or (149,511/4,182,572) = 0.036. The net reproductive rate can now be estimated. The calculation shown below assumes that females decline exponentially from day 64 to infinity with median longevity of 4 days. Daily female mortality (m) is calculated from

$$S = e^{-mD}$$

where survivorship (S) is 0.5 and median duration (D) is 4 days, giving

$$\frac{\log_e 0.5}{4} = -m, = 0.173 .$$

Finite survivorship is then

$$e^{-m} = 0.84 \text{ and}$$

and the finite death rate is (1 - 0.84) or 0.16 per day. This is the rate at which females survivorship declines per day. R_o is calculated below, for a 20 day time period.

DAYS SINCE EGGS WERE LAID	l_x	b_x	$l_x b_x$	$\Sigma l_x b_x$
0	1.00	0.0	0.0	0.00
°	°	°	°	
63	.043	0.0	0.0	0.00
64	.036	23.9	0.86	0.86

65	.030	23.9	0.72	1.58
66	.025	23.9	0.61	2.19
.	.	23.9	.	.
.	.	23.9	.	.
.	.	23.9	.	.
83	.0015	23.9	.035	5.35

The meaning of the R_o value is that once an egg develops into a female, that female will produce 5.4 offspring which will reach adulthood. Given an average sex ratio (males/males+females) of 0.95, calculated from Table 23, a female will produce 5.1 daughters and 0.3 sons which will become adults.

This reproductive rate agrees with what is known about the annual cycle of Calanus marshallae abundance, shown in Figure 4. Numbers do not increase dramatically during the February-September population developmental period. Total numbers of C. marshallae increase by no more than three to five fold. The population dynamics are like this because (1) egg mortality is so high and (2) females are short lived.

SUMMARY AND CONCLUSIONS

1. Eggs are laid every 30 hours in clutches of 29.7 eggs per female. The eggs have three membranes like those of the closely related Calanus glacialis. The outermost membrane is unusual because it is rigid and reticulated. The eggs hatch after 40 h at 10°C.
2. Seasonal differences in daily egg production were slight. With the exception of some super-fecund females collected in May 1978 which laid 39.2 eggs per day, females collected in January and June through September did have clutch sizes significantly

different from the overall average of 29.7 eggs per clutch.

3. Food type did not greatly affect egg production. Of five diatoms tested, all produced statistically similar results.

4. Temperature over the range 10 to 15°C had no effect on egg laying.

5. There was no tendancy for large females to lay more eggs. This was shown for females whose body weights ranged from 187 to 302 µg dry weight. It would seem that there is no reproductive advantage in achieving a larger size. This result agrees with a finding in Chapter IV: size of daughter was not influenced by size of mother.

6. Egg production is influenced by food concentration. Starved females produce no eggs. Females fed Thalassiosira fluviatilis in concentrations above 3500 cells per ml lay eggs at the maximum rate of 30 eggs per clutch.

7. Maximum ingestion rates also occurred at about 3500 cells per ml.

8. The gross efficiency of egg production is 22.0 %.

9. An average female produces 6.9 % of her body weight per day as eggs. This rate is nearly three times greater than the female growth rate assumed from the C5 to female growth coefficient. A reproductive effort of 6.9 % is very low compared to most other marine copepods.

10. Calanus pacificus, which normally lives farther offshore than C. marshallae, occassionally is a dominant in continental shelf waters. Females collected in March 1978 were extremely fecund, laying 58 eggs per clutch and laying a clutch every 18 hours on the average.

11. Starved females cannibalize their own eggs therefore my egg production vs food concentration relationship is biased. The egg counts

from food levels below 3500 cells per ml need to be adjusted upward. At food concentrations between 2000 and 3000 cells per ml, females laid the same number of clutches in eight days as females fed food in excess of 3500 cells per ml. Therefore, maximum egg laying rates could be occurring at food levels as low as 2000 cells per ml.

12. Estimates of egg laying rates in the field ranged from 11.1 to 25.0 eggs per female per day.

13. Only 10 % of all eggs produced per day survive to the third nauplius stage, 3.5 days after being laid. It is not known if mortality is concentrated at egg, N1 or N2 stage.

14. Eggs sink in the laboratory at a rate of 36.0 m per day.

15. Females lived only 4.0 days on the average in July-August 1977 and 6.5 days between June-September 1970.

16. Net reproductive rate is 5.1 female offspring per female. This rate is in accord with the annual cycle of Calanus marshallae abundance: numbers do not increase dramatically during the February-September growing season.

CHAPTER VI. GENERAL DISCUSSION

POPULATION RETENTION MECHANISMS

Calanus marshallae has a complex of behavioral and life history adaptations which enable it to inhabit the Oregon upwelling system. A cyclic mechanism by which the population is retained within the upwelling zone, as suggested by Peterson, Miller and Hutchinson (1979), was given in the introduction to this dissertation. There are four different phases of the mechanism during the 64 day period of development from egg to adult. These are:

1. Eggs are laid between one and five miles from shore.
2. A small percentage of them become nauplii which develop at a distance of one mile from shore.
3. The copepodite stages have their centers of abundance at increasingly greater distances from shore as development progresses.
4. Females return nearshore where eggs are laid, beginning the cycle once again.

The time schedule of these four phases is:

1. Phase One: Eggs, N1, N2 = 3.5 days
2. Phase Two: N3 to N6 = 15 days
3. Phase Three: C1 to adult = 45.5 days
4. Phase Four: Adult = 4 to 6.5 days

ONSHORE - OFFSHORE TRANSPORT RATES

EARLY DEVELOPMENT: EGGS, N1, N2. Eggs are found from one to five miles from shore but are most abundant three to five miles from shore. The first two naupliar stages were not enumerated so I have no knowledge of their distribution.

NAUPLIAR DEVELOPMENT: N3 to N6. These stages are usually only abundant one to three miles from shore. Since eggs are most abundant three to five miles from shore, it was hypothesized by Peterson, Miller and Hutchinson (1979) that the early developmental stages are transported landward after the eggs hatch. An alternate hypothesis has been suggested to be my Bruce Frost (Department of Oceanography, University of Washington). Since only 10 % of the eggs laid will survive to the third nauplius, it is possible that few to none of the eggs laid at three and five miles from shore survive, and that all of the nauplii at one mile from shore originated from eggs which were laid one mile from shore. There are always enough eggs found at one mile to account for the number of N3. This is a more parsimonious hypothesis because it suggests a simpler circulation system operating between the very nearshore zone (one to two miles from shore) and more offshore zones. It is no longer necessary to explain how nauplii are transported into the very nearshore zone and how young copepodites are transported out of it. This hypothesis supports the view that the zone from a mile to two or three miles from shore is moderately isolated with little transport into or out of it.

If this newer hypothesis is true, all naupliar stages should be

found only at the one-mile station. If the original hypothesis is true, there should be a naupliar age-gradient with younger stages farther offshore than the older naupliar stages. The data are equivocal. Referring to Figures 10-19 and the appendix, it is seen that in some transects the N3 are farther to sea than N4-N6 and in other cases, all naupliar stages are one mile from shore. More sampling is needed to allow a choice between the two hypotheses.

COPEPODITE DEVELOPMENT: C1 to C5. Through some undiscovered mechanism, the first copepodite stage is shifted farther seaward than the sixth nauplius. There has to be an ontogenetic change in behavior between N6 and C1. Older copepodites are found in turn at increasingly greater distances seaward.

Because of the development time data which I generated, the rates at which animals are transported offshore can be calculated and compared to transport rates from direct measurements by moored current meters. Animal transport rates can be calculated from (1) the offshore distance that a stage was transported from some beginning point, and (2) the time elapsed since that stage left the starting point. Time is the laboratory measured development time between the two developmental stages in question. To evaluate this, I examined the net offshore transport of the fourth copepodite stage.

The starting point was taken to be one mile from shore and the beginning stage, N6. I looked at both the 1973 and 1977 data sets. The offshore position of the C4 population center during 1973 was determined by inspection of Figures 20-23. The 1977 dat were more rigorously analyzed because station and depth coverage was much more

extensive. The distances which the abundance centers were offset offshore was calculated by first converting all abundance estimates to numbers beneath a square meter water column. For each developmental stage on a date, I summed the abundances at all stations, then converted the data into percent of a stage at each station. Percent vs. distance from shore was plotted and the area beneath these curves was calculated by the trapezoid method. The area-midpoint was taken to be the distance from shore where the population was centered. This is the same calculation used to study cohort development. It is adequate if both the offshore and onshore extents of the distributions of the stage in question are known. We were not always successful in reaching the offshore extent of the population on all cruises. Therefore, the population area-midpoints are closer to shore than they should be for those cruises.

The results are shown in Table 24. One clear conclusion is that the location of the C4 population center is a function of the state of the upwelling. During active upwelling (29 July, 15, 16 August 1973; 4 August 1977), C4 were much farther seaward than during the relaxed upwelling periods seen on all other dates. We did not sample far enough seaward during active upwelling to find the offshore limit of the Calanus marshallae population. This supports the view that active upwelling spreads copepod populations zonally and that relaxed upwelling compresses them.

A total of 18.3 days elapsed in the laboratory between the development of the median individual from N6 to C4. The daily average transport rates over this developmental period is 0.4 km per day during

Table 24. Offshore transport rates of the fourth copepodite stage of Calanus marshallae from a point 1.5 km from shore to the listed location of the offshore population center of abundance. Compare these average daily transport rates to transports known from direct current measurements shown in the lower portion of this table.

DATE	LOCATION OF POPULATION CENTER	AVERAGE DAILY TRANSPORT RATE
29 July 1973	> 14.5 km	> 0.79 km day^{-1}
15 August	> 14.5	> 0.79
16 August	14.5	0.79
12 September	6.5	0.36
15 July 1977	6.3	0.34
21 July	7.6	0.42
29 July	> 14.5	> 0.79
4 August	> 14.5	> 0.79
13 August	6.3	0.34

TRANSPORT RATES FROM DIRECT CURRENT MEASUREMENTS

Halpern et. al. DEPTH	Offshore Transport km per day	Pillsbury et. al. DEPTH	Onshore Transport km per day
1 m	5.1	20 m	2.9
3 m	7.8	40 m	3.8
8 m	3.8	60 m	2.2
10 m	2.4	80 m	1.0
14 m	0.04		
16 m	0.47		
18 m	0.31		

relaxed upwelling and 0.8 km per day during active upwelling. An overall average would be on the order of 0.5 km per day, perhaps a bit higher. The only valid estimates of offshore transport come from the N6 to C4 calculation. This is because once the C4 stage is reached, the animals begin diel vertical migration. Therefore, they no longer spend 24 hours per day in the same general water parcel. Since they reside at depth during some unknown fraction of a day, their offshore transport is greatly reduced.

These N6 to C4 transport estimates compare well with rates known from direct current measurements. The velocities averaged from the moored current meters are shown in Table 24. All measurements are from current moored in 100 m water depth along 45°14' N latitude off Sand Lake, Oregon. The 1 m to 18 m measurements are from Halpern, Holbrook and Reynolds (1974) and the 20 m to 80 m measurements from Pillsbury, Bottero, Still and Gilbert (1974). The measurements were carried out between 5 July and 28 August 1973 and 30 June and 28 August 1973 respectively. The velocities shown in the table are averages for this two month interval. I am assuming that they are typical for an upwelling season. The averages include both active and relaxed events.

Agreement between measured offshore velocities and rates at which Calanus marshallae C4 are transported offshore is excellent at some depths. If the early copepodites spend most of the 24 hour day between 10 and 18 m, they would experience an average net offshore transport of 0.8 km per day. These stages could roam between 5 and 30 m and still realize a net daily offshore transport of about 0.8 km per day. Agreement would be poor if Calanus resided between 1 m and 10 m.

Transport rates are extremely high in these upper layers, averaging 5 km per day. Examination of the data in Figures 10-19, 20-23, and in the appendix reveals that the depths of maximum abundance in fact range between 5 and 30 m, and that 10-20 m is the depth zone most frequently occupied.

ADULT PHASE. Females are always found deeper in the water column and closer to shore than the C5, although the separation of stages is not always great. The differences between the location of the two population centers is compared in Table 25. The mean net distance shoreward which females are transported from the offshore position of C5is 6.4 km. Water beneath 20 m is moving landward at 2-4 km per day. If these females move out of the upper 20 m to any place below this depth, they will arrive at the main egg laying center within 2 to 4 days. In fact, the only way that females can arrive back nearshore and complete the 60-70 day dircuit is by leaving the upper 20 m. This necessitates a change in behavior compared to the C4 and C5 stages. The behavior change must be that females cease diel vertical migration, or at least, reside at depth during more hours of the 24-hour day than C4 or C5.

VERTICAL TRANSPORT RATES

Estimates of vertical velocities were calculated from sinking rates of Calanus marshallae eggs. In the laboratory, eggs sink at a mean rate of 36.0 m per day. In the field, eggs should be abundant to 60 m because they are in the water column 1.6 days before hatching. However, eggs are never abundant below 10 m depth. Two

Table 25. Net transport of female Calanus marshallae from the offshore location of the C5 population center to the nearshore location of females.

DATE	C5 CENTER	FEMALE CENTER	NET TRANSPORT
29 July 1973	> 16.1 km	4.8 km	> 11.3 km
15 August	> 16.1	3.2 km	> 12.9
16 August	> 16.1	8.1	> 8.0
12 September	11.3	8.1	3.2
15 July 1977	10.6	5.3	5.3
21 July	8.7	8.2	0.5
29 July	> 13.5	6.3	> 7.2
4 August	> 18.1	11.3	> 6.8
13 August	9.5	7.1	2.4
		MEAN TRANSPORT	= 6.4 km

explanations are possible: (1) Either all eggs which fall below 10 m are eaten or (2) upward transport of upwelling water keeps the eggs above 10 m. There is fair agreement between egg sinking rate (36.0 m per day) and vertical upwelling velocities (17.3 m per day) calculated by Halpern (1976).

ALONGSHORE TRANSPORT RATES

The dominant flow of water is to the south during the upwelling season. Alongshore velocities range from 10-30 cm per sec (8.6 to 26 km per day) between 0 and 50 m, with the highest velocities at the sea surface.

Zooplankton are transported south with this flow and will be lost from the system if there is no mechanism for return to the north. There are several possible ways to reduce southward advection. First, the very nearshore zone is characterized by little net alongshore flow, although flow may be strong toward either north or south at velocities of 30-50 cm per sec (Peterson, Miller and Hutchinson, 1979). Second, over the continental shelf there is a northward flowing countercurrent at 80 m water depth, seven miles from shore,deepening to 120 m at 15 miles from shore. Third, during November through March or April, all of the shelf waters are flowing northward.

For the zooplankton there must be a balanced budget, i.e., little net southward transport over an annual period. If net transport were southward, in time the entire stock would be washed out of the system. If the north-south and/or east-west transport rates do not balance, then one must invoke a large pool of Calanus marshallae individuals

hundreds of miles to the north of the Washington-Oregon upwelling zone, which are brought into the system as expatriots.

Some first-order calculations suggest that the problem of losses to the south is not serious for Calanus marshallae. Assume that on the average there is no southward transport during development of the naupliar stages. The C1 through C4 stages realize the greatest transport. In the 18.3 day developmental period, southward transport is 315 km or 190 miles (18.3 days x 20 cm sec^{-1}). The C4 and C5 stages show diel vertical migrations on some nights. This greatly reduces the extent of their offshore transport and will reduce their southward transport as well. When they are found at depth during the daytime, their depth range is 70-100 m. This corresponds to the position of the northward-flowing countercurrent. Assuming that the C4 and C5 reside at depth during the day for 16 h and in the upper 20 m for 8 h at night, their net daily transport would be 2.7 km per day northward (16 h x 5 cm sec^{-1}) - 5.8 km per day southward (8 h x 20 cm sec^{-1}) = 3.1 km per day to the south. A total of 27 days pass as C4 and C5 develop. They are transported 84 km (50 miles) southward during this time. Females return shoreward to spawn. Their southward transport is at most a few miles because they only live for four days on the average.

Total transport during development of the summer generation is then on the order of 250 miles southward. Two generations pass (May and July) during the time of the year when upwelling circulation dominates over the shelf. This gives a total transport of 500 miles for the Calanus marshallae population. The first generation of the

year takes place in January or February when flow is northward over the shelf. Nothing is known about the distribution of developmental stages during winter-spring so transports cannot be calculated. But, if all stages experience northward transport during the 65 day developmental period, then transport rates need only be about 15 cm per sec to achieve an annual net transport of zero (15 cm sec^{-1} x 65 days = 845 km or 507 miles). Therefore, it is possible that losses to the south on an annual basis are not a problem for Calanus marshallae.

THE ROLE OF DIEL VERTICAL MIGRATION

I think that the key to understanding both offshore-onshore and alongshore balance in transport of the Calanus marshallae population is diel vertical migration. Older copepodites, particularly the long-lived C5, must reside at depths greater than 50 m for a large fraction of the day in order to avoid being carried out of the coastal upwelling zone. Calanus marshallae, like many zooplankton species, do perform diel vertical migrations. The classical pattern for continental shelf waters shows individuals moving into near-surface waters at night where they feed, and returning to 80-100 m depths where they reside during the day. Peterson, Miller and Hutchinson (1979) review the literature and show that this phenomenon is by no means regular nor predictable and, therefore, not the least bit "classical". Our data and most other published data from other geographical areas are equivocal on this matter. What is classical is that people continue to believe that vertical migration is regular and predictable. Calanus marshallae will migrate on some

nights but not others. It is obvious from most of the 1977 transects that the stages that migrate, C4 and C5, are abundant between the surface and 20 m during the day. Only once, on 29 July 1977, were C4 and C5 seen exclusively at depth during the day. In the 1973 transects, C4 and C5 were seen at both the surface and at depths of 70 to 100 m on most dates. The role of vertical migration in aiding population retention in the upwelling zone is clear, but it is not clear how Calanus marshallae take advantage of it. The data base is at present insufficient to allow careful study of the problem. The reason why Calanus migrate on some nights but not others remains one of the great puzzles of 20th century planktology in my opinion. An understanding of vertical migration is a missing link in our knowledge of Calanus marshallae life history and ecology.

LIFE HISTORY STRATEGY

A life history study is a research viewpoint that combines studies of reproduction, growth and mortality in an ecological setting. Through an organism's interaction with its biological and physical environment, these three basic life history components become coadapted.

I hypothesize that a major selective force which has shaped the life history of Calanus marshallae is high mortality of eggs, N1 and N2. High mortality is seen in the field abundance data. As a result of this high mortality, development is rapid in early stages. The eggs of many Calanus species, including C. marshallae, hatch up to three times faster than those of other neritic copepods (see McLaren,

1966). Also, the first two naupliar stages of C. marshallae develop extremely rapidly. Selection may have acted to minimize time spent in these three stages because of the high probability of death here.

High mortality or uncertain survival of eggs and/or early naupliar stages should lead to the evolution of iteroparity (Murphy, 1968). The logical reason for this is that if an individual female lays a few eggs every day for many days, enough of them will survive in the long run for that female to gain representation in the next generation. Calanus marshallae females are iteroparous. They lay a clutch of 30 eggs every 30 hours on the average, for up to two months in the laboratory. The adults may not lay eggs for up to one week after she has molted into this terminal stage. Reproductive effort is very low. Only 7 % of a female's body weight is produced as eggs each day. The eggs must be yolky because it is known that the third nauplius can survive for 10 days without feeding. I consider this to be a form of parental care.

I further hypothesize that because of intense selection for rapid development to N3, this stage has a special status. My laboratory experiments have shown that development progresses only as far as N3 if no food is available. It was also shown that N3 is one of the longest-lived stages. Its stage duration of 6.8 days is equaled by C4 and exceeded only by C5. Also, nearly all of the variance in development time within each stage among families comes at the N3 stage. There must be a plausible explanation for this. Selection must act to get an individual to N3 as quickly as possible without regard for its ability to develop and grow on its own. It is known

to have enough lipid reserves to carry it for 10 days without feeding. This is much longer than the normal one-week term of development. It may be that the N3 stage is where the digestive system and musculature for feeding develop. Major physiological events such as these might contribute to a high variance in development time in this stage.

An unexplained attribute of Calanus marshallae life history is the short adult life span in the field. Current life history theory (Stearns, 1976) does not deal with the contingency of high juvenile mortality and short adult life span. There can be little doubt that the life span is short: they survived only 4.0 days in 1977 and 6.5 days in 1970 compared to at least 70 days in the laboratory. If such a high death rate of adults is usual, there should be selection for a greatly increased reproductive effort, or at least for the evolution of some new behavior which reduces female mortality rates. There may be some trade-off operating. The most important factors governing the life history strategy of C. marshallae may be high egg mortality and the selective advantage of a yolky egg.

An alternative (and speculative) hypothesis is that Calanus marshallae may not be completely adapted to the upwelling zone. This would be because of the problem of being advected out of the system in the alongshore direction. For a boreal neritic copepod, the coastal upwelling zone may only extend from Cape Flattery, Washington south to Cape Mendocino, California, a distance of 600 miles. A faunal boundary exists at Cape Mendocino (Fleminger, 1964) south of which boreal species do not survive. We don't know what happens to zooplankton north of Washington State, but it is known that the upwelling

season is short, lasting at most two months (Bakun, 1973). Therefore, from the viewpoint of a Calanus marshallae individual, the upwelling zone may be only 600 miles long. Earlier, I showed that net alongshore transport could be zero over an annual period, but that southward transport during the spring and summer generations could total 500 miles. I now suggest that Calanus marshallae could be advected out of the system because mortality rates greatly increase south of Cape Mendocino. Individuals may not get a chance to return northward during the winter.

The implication of this is that Calanus marshallae individuals may not be able to become adapted to the upwelling zone because they pass through the system in two generations. They may not be returned frequently enough or far enough north during winter. Intense selection could occur as individuals pass through the system but those individuals which had the most adapted gene complex do not get another opportunity to test those genes. They run the gauntlet but once. If I am correct, then Calanus marshallae may be a preadapted expatriot.

Additional field sampling is needed farther north and to the south, as well as during the winter months, before some of these speculations can be critically examined.

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BIBLIOGRAPHY

Bakun, A. 1973. Coastal upwelling indices; west coast of North America, 1946-1971. U.S. Dept. Commer., NOAA Tech. Rep. NMFS SSRF-671, 103 p.

Bigelow, H.B. 1924. Plankton of the offshore waters of the Gulf of Maine. Bull. U.S. Bureau of Fisheries, 40 (Part II):1-509.

Binet, D. 1977. Cycles biologiques et migrations ontogeniques chez quelques copepodes pelagiques des eaux ivoiriennes. Cah. O.R.S.T. O.M., ser Oceanogr. 15:111-138.

Binet, D. and E. Suisse de Sainte Claire. 1975. Le copepode planktonique Calanoides carinatus: repartition et cycle biologique au large de la cote d'ivoire. Cah. O.R.S.T.O.M., ser Oceanogr. 13: 15-30.

Checkley, D.M. 1978. The egg production of a marine, planktonic copepod in relation to its food supply. Ph.D. Thesis, University of California, San Diego.

Corkett, C.J. and I.A. McLaren. 1969. Egg production and oil storage by the copepod Pseudocalanus in the laboratory. J. Exp. Mar. Biol. Ecol. 3:90-105.

Cushing, D.H. and D.S. Tungate. 1963. The identification of a Calanus patch. J. Mar. Biol. Ass. U.K. 43:327-337.

Dagg, M. 1977. Some effects of patchy food environments on copepods. Limnol. Oceanogr. 22:99-107.

Daniel, W.W. 1978. Applied nonparametric statistics. Houghton Mifflin Co., Boston, 503 p.

Fleminger, A. 1964. Distributional atlas of calanoid copepods in the California Current region, Pt. 1. Calif. Coop. Ocean. Fish. Invest., Atlas no. 7, 213 p.

Fleminger, A. and K. Hulsemann. 1977. Geographical range and taxonomic divergence in north Atlantic Calanus (C. helgolandicus, C. finmarchicus and C. glacialis). Mar. Biol. 40:233-248.

Frost, B.W. 1974. Calanus marshallae, a new species of calanoid closely allied to the sibling species C. finmarchicus and C. glacialis. Mar. Biol. 26:77-99.

Gaudy, R. 1974. Feeding of four species of pelagic copepods under experimental conditions. Mar. Biol. 25:125-141.

Green, J.D. 1976. Population dynamics and production of the calanoid copepod Calamoecia lucasi in a northern New Zealand lake. Arch. Hydrobiol. Suppl. 50. 4:313-400.

Guillard, R.R.L. and J.H. Ryther. 1962. Studies on marine planktonic diatoms. 1. Can. J. Microbiol. 8:229-239.

Halpern, D. 1976. Structure of a coastal upwelling event observed off Oregon during July 1973. Deap-Sea Res. 23:495-508.

Halpern, D. J.R.Holbrook and R.M.Reynolds. 1974. A compilation of wind, current, and temperature measurements: Oregon, July and August 1973. Coastal Upwelling Ecosystem Analysis Technical Report 6, Ref M74-73, Department of Oceanography, University of Washington, 190 p.

Harris, R.P. and G.-A.Paffenhoffer. 1976. Feeding, growth and reproduction of the marine planktonic copepod Temora longicornis Muller. J. Mar. Biol. Ass. U.K. 56:675-690.

Heinle, D.R. 1969. Temperature and zooplankton. Ches. Sci. 10:186-209.

Heinle, D.R. and D.A.Flemer. 1975. Carbon requirements of a population of the estuarine copepod Eurytemora affinis. Mar. Biol. 31: 235-247.

Heip, C. and N.Smol. 1976. Influence of temperature on the reproductive potential of two brackish-water harpacticoids (Crustacea: Copepoda). Mar. Biol. 35:327-334.

Hirche, H.J. 1978. On the occurrence of a diapause in marine calanoid copepods. Intnl. Council Explor. Sea, C.M. 1978/L:21, 10 p. Unpublished Manuscript.

Ivlev, V.S. 1966. The biological productivity of waters. J. Fish. Res. Bd. Canada, 23:1727-1759.

Iwasaki, H. H.Katoh, and T.Fujiyama. 1977. Cultivation of marine copepod Acartia clausii Giesbrecht -I. Factors affecting the generation time and egg production. Bull. Plankton Soc. Japan, 24:55-61.

Johnson, J.K. 1974. The dynamics of an isolated population of Acartia tonsa Dana (Copepoda) in Yaquina Bay, Oregon. M.S. Thesis, Oregon State University, 97 p.

Landry, M.R. 1975. The relationship between temperature and development of life stages of the marine copepod Acartia clausii Giesbrecht. Limnol. Oceanogr. 20:854-857.

Landry, M.R. 1976. Population dynamics of the planktonic marine copepod Acartia clausii Giesbrecht, in a small temperate lagoon, Ph.D. Thesis, University of Washington, 200 p.

Landry, M.R. 1978. Population dynamics and production of a planktonic marine copepod Acartia clausii, in a small temperate lagoon on San Juan Island, Washington. Int. Revue. ges. Hydrobiol. 63:77-119

Marshall, S.M. and A.P.Orr. 1952. On the biology of Calanus finmarchicus VII: Factors affecting egg production. J. Mar. Biol. Ass. U.K. 30:527-547.

Marshall, S.M. and A.P.Orr. 1955. The biology of a marine copepod. Oliver and Boyd. Edinburgh, 188 p.

Marshall, S.M. and A.P.Orr. 1960. On the biology of Calanus finmarchicus XI: Observations on vertical migration, especially in female Calanus. J. Mar. Biol. Ass. U.K. 39:135-147.

McLaren, I.A. 1966. Predicting development rate of copepod eggs. Biol. Bull. 131:457-469.

McLaren, I.A. 1974. Demographic strategy of vertical migration by a marine copepod. Am. Natur. 108:91-102.

McLaren, I.A. 1978. Generation lengths of some temperate marine copepods: estimation, prediction and implications. J. Fish. Res. Bd. Canada 35:1330-1342.

Miller, C.B., J.K.Johnson and D.R.Heinle. 1977. Growth rules in the marine copepod genus Acartia. Limnol. Oceanogr. 22:326-335.

Mullin, M.M. and E.R.Brooks. 1967. Laboratory culture, growth rate and feeding of a planktonic marine copepod. Limnol. Oceanogr. 12:657-666.

Mullin, M.M. and E.R.Brooks. 1970. Growth and metabolism of two planktonic marine copepods as influenced by temperature and type of food. in J.H.Steele (ed.), Marine Food Chains, Univ. of California Press, 552 p.

Murphy, G.I. 1968. Pattern in life history and environment. Am Natur. 102:390-404.

Neter, J. and W.Wasserman. 1974. Applied linear statistical models. Richard D. Irwin, Inc. Homewood, Ill. 842 p.

Nichols, A.G. 1933. On the biology of Calanus finmarchicus III. Vertical distribution and diurnal migration in the Clyde Sea area. J. Mar. Biol. Ass. U.K. 19:139-164.

Pace, S.D. 1978. Distribution, abundance and rates of fecundity and growth of Acartia tonsa Dana and Acartia californiensis Trinast (Copepoda). M.A. Thesis, San Jose State University, 113 p.

Paffenhoffer, G.-A. 1970. Cultivation of Calanus helgolandicus under controlled conditions. Helgolander wiss. Meeresunters.20:346-359.

Paffenhoffer, G.-A. 1976. Feeding, growth and food conversion of the marine planktonic copepod Calanus helgolandicus. Limnol. Oceanogr. 21:39-50.

Paffenhoffer, G.-A. and R.P.Harris. 1976. Feeding, growth and reproduction of the marine planktonic copepod Pseudocalanus elongatus Boeck. J. Mar. Biol. Ass. U.K. 56:327-344.

Parrish, K.K. and D.F.Wilson. 1978. Fecundity studies on Acartia tonsa (Copepoda: Calanoida) in standardized culture. Mar. Biol. 46:65-81.

Parsons, T. and J.D.H.Strickland. 1972. A practical handbook of seawater analysis. Fish. Res. Bd. Canada, Bull. 167, 310 p.

Pearcy, W.G., H.V.Lorz and W.Peterson. 1979. Comparison of the feeding habits of migratory and non-migratory Stenobrachius leucopsarus (Myctophidae). Mar. Biol. 51:1-8.

Peterson, W.T. and C.B.Miller. 1975. Year-to-year variations in the planktology of the Oregon upwelling zone. Fish. Bull. 73:642-653.

Peterson, W.T. and C.B.Miller. 1976. Zooplankton along the continental shelf off Newport, Oregon, 1969-1972: Distribution, abundance, seasonal cycle and year-to-year variations. Oregon State Univ., Sea Grant College Program Publication No. ORESU-T-76-002, 111p.

Peterson, W.T. and C.B.Miller. 1977. Seasonal cycle of zooplankton abundance and species composition along the central Oregon coast. Fish. Bull. 75:717-724.

Peterson, W.T., C.B.Miller and A.Hutchinson. 1979. Zonation and maintenance of copepod populations in the Oregon upwelling zone. Deep-Sea Res. 26 A:467-494.

Pillsbury, R.D., J.S.Bottero, R.E.Still, and W.E.Gilbert. 1974. A compilation of observations from moored current meters. VII. Oregon continental shelf, July-August 1973. Data Report 58. School of Oceanography, Oregon State University.

Raymont, J.E.G. and F.Gross. 1942. On the feeding and breeding of Calanus finmarchicus under laboratory conditions.Proc. Roy. Soc. Edinburgh, B, 61:267-287.

Smith, R.L. 1974. A description of current, wind, sea level variations during coastal upwelling off the Oregon coast, July-August 1972. J. Geophys. Res. 79:435-443.

Stearns, S.C. 1976. Life-history tactics: A review of the ideas. Quart. Rev. Biol. 51:3-47.

Strathmann, R.R. 1967. Estimating the organic carbon content of phytoplankton from cell volumn or plasma volume. Limnol. Oceanogr. 12:411-418.

Valentin, J. 1972. La ponte et les oeufs chez les copepodes du golfe de Marseille: cycle annuel et etude experimentale. Tethys 4:349-390.

Wiborg, K.F. 1954. Investigations on zooplankton in coastal and offshore waters of western and northwestern Norway. Fiskeridirektoratets Skrifter, Serie Havundersokelser 11:1-246.

Zurlini, G., I.Ferrari and A.Nassogne. 1978. Reproduction and growth of Euterpina acutifrons (Copepoda: Harpacticoida) under experimental conditions. Mar. Biol. 46:59-64.