LIFE HISTORY AND VERTICAL MIGRATION OF THE PELAGIC SHRIMP *SERGESTES SIMILIS* OFF THE SOUTHERN CALIFORNIA COAST

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ABSTRACT

Sergestes similis in the southern California eddy was observed with respect to reproduction, daily and ontogenetic vertical migrations, growth, and longevity. The period of highest spawning activity occurs between late December and early April, but small pulses of spawning are occasionally observed in late spring and summer. The release of eggs takes place close to shore above the continental slope, and then the eggs sink to 200 m or deeper. Nauplius larvae ascend and protozoeal and zoeal larvae stay mostly above 100 m. The daily vertical migration becomes evident after the second protozoeal stage. Adults are abundant between 50 and 200 m at night and 250 and 600 m in the daytime.

The spawning activity of *S. similis* becomes highest during the period when the vertical thickness of the optimum temperature zone (10°-15°C) is the greatest. The authors speculate that the local population off the southern California coast may be joined by the subarctic population. It is possible that multiple spawnings occur from females of the southern California population.

The lifespan of *S. similis* is 2.0-2.5 years for females and about 1.5 years for males. Sexual maturity is reached at about 1 year in both sexes. Females reproduce in two successive spawning seasons, and males seem to accomplish multiple fertilizations. Growth trends are similar to those reported for *S. similis* off Oregon. Growth rates are described using growth curves fitted by the von Bertalanffy and logistic equations.

Sergestes similis Hansen is the most abundant oceanic, pelagic shrimp in the North Pacific Drift, lat. 40°-50°N. This subarctic and transitional species occurs mainly in waters where temperature ranges between 3° and 13°C. Its distribution extends from Japan to the coast of North America as far south as lat. 27°N (Pearcy and Forss 1969; Omori et al. 1972).

In the cooler part of the California Current, *S. similis* composes a substantial fraction of all micronekton. The adults perform extensive vertical migrations, living between 250 and 600 m in the daytime and ascending to 50-200 m depths at night. According to Barham (1963) and Clarke,[3] *S. similis* is consistently associated with the lower component of a sonic scattering layer off southern California.

Sergestes similis sheds eggs in the sea. From

eggs hatch the first of four naupliar stages (N1-N4), which go on to develop three protozoeal stages (PZ1-PZ3), and two zoeal stages (Z1, Z2) before entering postlarval stages (PL) (Omori 1979).

Sergestes similis plays an important role in the dynamics of northern Pacific oceanic ecosystems. As an adult, it feeds mainly on copepods and euphausiids and is, in turn, preyed upon by squids, mesopelagic fishes, rockfishes, albacore, basking shark, and baleen whales (Pereyra et al. 1969; Judkins and Fleminger 1972; Omori et al. 1972; Mutoh and Omori 1978). In certain areas there is a strong possibility that the enormous standing stock can be exploited by commercial fisheries (Omori 1974).

In spite of the great importance of this species, little is known about its life history, especially its reproduction, development, and growth. Although the distribution and daily vertical migration of adult *S. similis* off the coasts of California and Oregon have been studied (Barham 1963; Clarke, see footnote 3; Pearcy and Forss 1966; Davies and Barham 1969; Pearcy et al. 1977), no work has been done on the biology of larval and early postlarval stages. Details of the spawning season and lifespan of the species have not yet been confirmed. Barham (1957) stated that *S. similis* in Monterey Bay, Calif., reached maturity at age 1 yr and dis-

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appeared after spawning. He found that the two size-groups, which spawned in December-January and June-July, respectively, showed the same developmental history but 6 mo out of phase with each other. On the other hand, *S. similis* off the Oregon coast spawned during most of the year but predominantly during the winter and spring, with the individuals living for about 1 yr (Pearcy and Forss 1969). Genthe (1969) determined that the lifespan for the southern California population is 2 yr and that the maximum breeding activity occurs in the early summer and fall. The disagreement in these conclusions is mainly due to two factors: first, the difficulty of sampling a nonrandomly distributed population which moves both horizontally and vertically with time and spatial location; and second, the lack of knowledge about the developmental biology of the larval stages of *S. similis*. Knowledge of the development and growth of larvae and juveniles of *S. similis* has been severely restricted by the difficulties of maintaining this oceanic species under laboratory conditions. Recently, however, Omori (1979) has successfully reared this species from the egg to the eighth postlarval stage. This success prompted us to examine the life history of *S. similis* off southern California and to provide further biological information about its population dynamics.

The present study deals with the reproduction, growth, longevity, and both daily and ontogenetic vertical migrations of *S. similis*. The study area is the southern California eddy, which is bounded on the north by Point Conception, lat. 34°N, and on the south by about lat. 30°N. The east-west extent of the eddy is about 250 km. This region is the southernmost in which *S. similis* is abundant. The sluggish, cyclonic circulation of this eddy, defining a singular water mass, permits substantial autonomy for the resident population. Complex topography, including a scattering of islands, basins, and canyons in the area, appears to provide substantial swarming grounds for *S. similis*. Because the majority of the population resides in an area such as the southern California eddy, which Brinton (1976) has described as "hydrographically restricted," data on the life history of *S. similis* may be measured more easily than in other oceanic areas.

MATERIALS AND METHODS

In the present study, data on occurrence of the larvae and early postlarvae were determined from examination of California Cooperative Oceanic Fisheries Investigations (CalCOFI) samples.

Samples were obtained from selected stations in CalCOFI cruise 6401 (January-February 1964). Stratified plankton sampling was carried out along three parallel transects: Line 60, Line 90, and Line 100 (Figure 1). The samples were collected by oblique tow to various depths of water with a standard CalCOFI net of 1-m diameter and 0.55-mm mesh openings (Ahlstrom 1948). The mesh size of the cod end and the 40-cm section in front of it was 0.25 mm. Opening-closing net series were obtained to depths of approximately 100 m at three stations and 450 m at one other station on Line 60, and to depths of 400-600 m at all stations on Line 90. Sampling was carried out at whatever time of day the ship arrived on station. Both day and night series, to approximately 600 m depth, were obtained at all station on Line 100. In the present study the samples obtained from the usual habitat of *S. similis*, i.e., above 400 m depth, were examined (Table 1). At each station, usually two to six nets were towed in each of two or three series of tows. The opening and closing of the nets were messenger-activated, using a Leavitt-type device, and a flowmeter was mounted within the mouth of each net. A net filtered an average volume of about 600 m³/tow. A trace of depth vs. time was made during the course of a tow by a recorder attached near the bottom net. For a detailed description of the sampling procedure and the analysis of depth recorder traces, see Brinton (1967).

The spawning season of *S. similis* was determined by examining CalCOFI standard oblique haul samples obtained at Stn. 90.37 from January 1951 to December 1954. Station 90.37, lat. 33°11'N, long. 118°37'W, was selected because it was located near the center of *S. similis* larval distribution in CalCOFI 6401. Sampling was not conducted in October and December 1952, May, September, and November 1953, and June and September 1954, but sampling from a nearby station, 90.35, was done in May 1953. Details of this sampling method are described by Ahlstrom (1948) and Fleminger (1964). The net was towed obliquely between the surface and a depth of about 140 m while the ship proceeded at a speed of about 2 kn. As explained later, this sampling depth covered the entire vertical distribution of protozoeal and zoeal stages of *S. similis*. Because free eggs and nauplii of *S. similis* are <0.5 mm, they were not retained by the CalCOFI net. Specimens of protozoeal stages were retained by the fine meshes
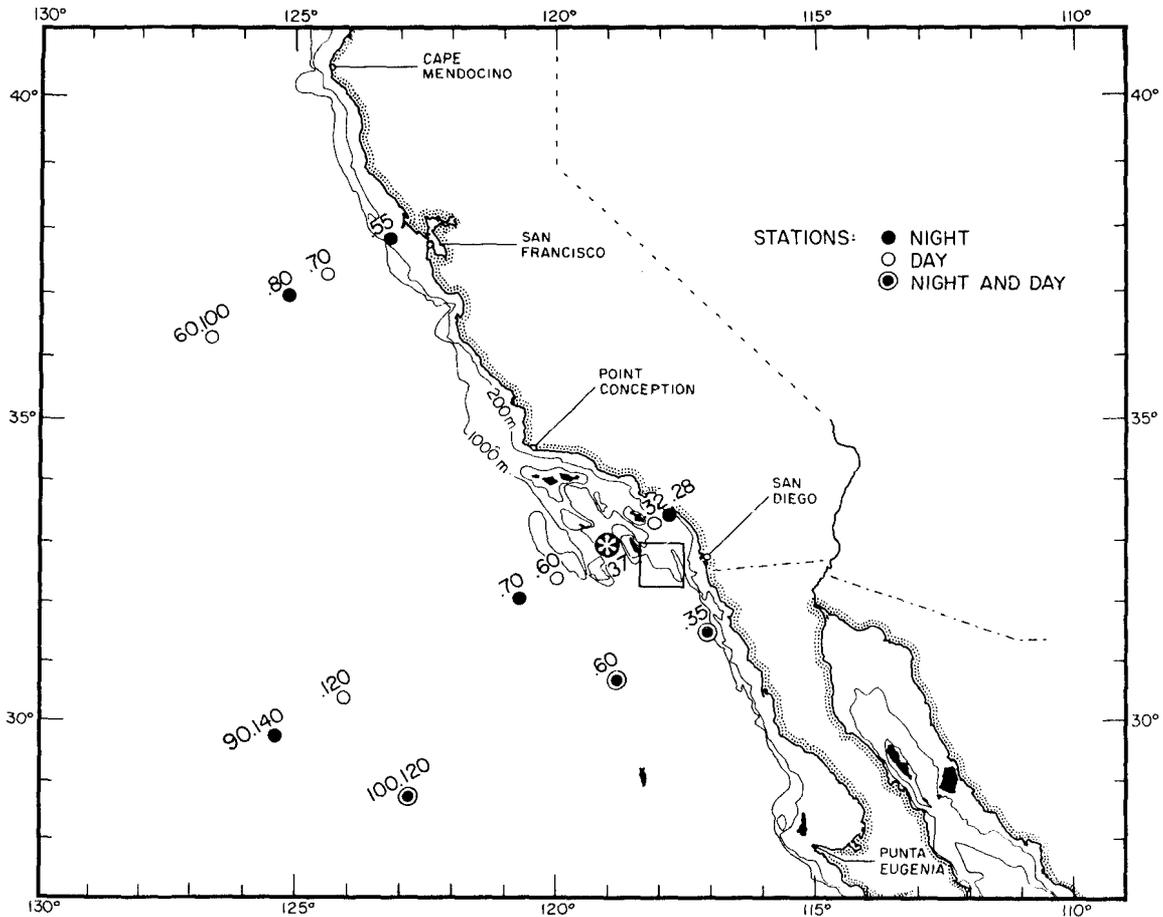
FIGURE 1.—Sampling stations for *Sergestes similis* off southern California. Circles indicate stations sampled by stratified opening-closing oblique net hauls with CalCOFI net (CalCOFI 6401, January-February 1964). Line 60 (Stn. 60.55, 60.70, 60.80, and 60.100) extending southwestward from Pt. Reyes, Calif.; Line 90 (Stn. 90.28, 90.32, 90.37, 90.60, 90.70, 90.120, and 90.140) extending southwestward from Dana Pt., Calif.; and Line 100 (Stn. 100.35, 100.60, and 100.120) extending southwestward from Punta Banda, Baja California. Number 37 (flowered circle) marks Stn. 90.37 at which monthly CalCOFI standard oblique haul samples were obtained. The square indicates the area of IKMT trawls.

TABLE 1.—Summary of data from stratified plankton sampling off southern California with standard CalCOFI net (CalCOFI cruise 6401, January-February 1964).

Station	Period	Depths covered by series of tows	Number of stratified samples	Date	Towing times including 2-3 series of tows	Light condition
60.55	Night	0-108	3	31 Jan.	2316-0056	Dark
60.70	Day	0-450	10	1 Feb.	1241-1455	Clear
60.80	Night	0-72	4	1 Feb.	2024-2044	Dark
60.100	Day	0-108	6	2 Feb.	0829-1003	Clear
90.28	Night	0-80	4	6 Feb.	0342-0407	Clear, ½ moon
90.32	Day	0-140	8	6 Feb.	0854-1052	Clear
90.60	Day	0-373	8	7 Feb.	1053-1346	Clear
90.70	Night	0-100	5	7 Feb.	2044-2149	Dark
90.120	Day	0-490	8	9 Feb.	1345-1640	60-90% clouds
90.140	Night	0-132	6	9 Feb.	2330-2356	Dark
100.35	Night	0-236	7	16 Feb.	2242-0106	Dark
	Day	0-400	9	17 Feb.	0715-0903	Clear
100.60	Night	0-260	8	16 Feb.	0041-0300	Dark
	Day	0-355	9	16 Feb.	0930-1140	95% clouds
100.120	Night	0-185	6	14 Feb.	0203-0538	Dark
	Day	0-500	8	14 Feb.	1051-1302	60% clouds

of the posterior part of the net and were thus counted as being indicative of their general occurrence.

Juvenile and adult *S. similis* were collected by a 6-ft (1.8-m) Isaacs-Kidd Midwater Trawl (IKMT), having mesh width of 2 mm, on the continental slope of the San Diego Trough, Calif., at five occasions in 1976 and 1977. Sampling was done at night and daytime by releasing the cable at 50m/min until the net reached a desired depth and then retrieving. Ship speed was 4 kn while the net was sinking, and 2 kn during the retrieval. Usually the biomass of shrimp was large when the net was towed at the depths of 50-200 m at night and 250-600 m in the daytime. To fill in gaps where sampling was sparse and to provide more information on reproduction and growth of *S. similis*, six IKMT collections from the SIO (Scripps Institution of Oceanography) Invertebrate Collection were examined. These samples were all collected by 10-ft IKMT with mesh width of 5 mm between lat. 32°28'N and 33°15'N and long. 117°29'W and 118°38'W (Table 2).

TABLE 2.—Summary of data from sergestid sampling with Isaacs-Kidd Midwater Trawl off southern California. Six-foot IKMT with 2-mm mesh size; 10-ft trawl with 5-mm mesh size.

Date	Local time	Location Lat.	Long.	Estimated depth of haul (m)	IKMT (ft)
26 Jan. 1977	1915-1935	32°44'N,	117°30'W	0-200	6
3 Mar. 1977	1810-1836	32°43'N,	117°29'W	0-250	6
12 Apr. 1972	2206-2345	33°15'N,	118°38'W	0-500	10
21 Apr. 1977	0332-0414	32°47'?	117°29'W	0-300	6
21 June 1953	1601-1937	32°37'N,	118°10'W	0-1,490	10
27 July 1973	1725-2320	32°28'N,	117°58'W	0-800	10
19 Aug. 1976	1800-1830	32°4'N,	117°29'W	0-300	6
24 Aug. 1954	2400-0400	32°0'N,	117°35'W	0-549	10
28 Oct. 1972	1800-1900	3. 45'N,	117°30'W	0-500	10
29 Oct. 1976	2000-2100	33°10'N,	118 20'W	0-350	6
8 Nov. 1975	1600-?	32°36'N,	117°20'W	0-500	10

An aliquot of ¼ to 1/32 of each CalCOFI sample was examined, and the number of individuals of each developmental stage from the first protozoeal stage to the second zoeal stage was counted. Postlarvae having a body length (BL) <5.0 mm (stages I-VI) were classified together as early postlarvae. In order to increase accuracy, if the initial aliquot contained only two or fewer individuals of any particular stage, a second aliquot of equal size was examined for specimens of that stage. All counts were then standardized for 1,000 m³ of water filtered by the net. An estimate of the total number of individuals of each stage beneath 1 m² of sea surface was made using the equation,

$$n = \frac{N}{1000} \times d$$

where n is number of individuals per square meter, N is the number of individuals/1,000 m³, and d is the depth of the stratum sampled. Data on physical and chemical environments were obtained from "Oceanic observations of the Pacific" 1951-53 (Scripps Institution of Oceanography 1963, 1965a, b) and "CalCOFI cruise 6401 data report" (Scripps Institution of Oceanography[4]).

In January and March 1977, a small number of healthy females carrying well-developed eggs in their ovaries were removed from the IKMT collection to be used for spawning and rearing experiments. They were transferred immediately after sampling to chilled filtered seawater in large containers and were brought back to the laboratory. The spawning of eggs was observed individually. The sinking speed of the eggs over a 70-cm distance was measured at 10° and 14°C in a constant temperature room using a graduated glass cylinder of 70-mm diameter. Seawater used for the experiment was obtained at the station where ovigerous females were collected. It was filtered through Millipore[5] filters HA (0.45 µm). Salinity was 33.72‰.

The remaining specimens in the IKMT collections were preserved in 5% Formalin-seawater. Most specimens of *S. similis* having carapace lengths (CL) >5.0 mm were sorted, counted, and sexed. The carapace length from the tip of the rostrum to the posterior margin of the carapace at the dorsal midline was measured to the nearest 0.5 mm.

Change through time in the carapace length-frequency histograms of *S. similis* was graphically analyzed using probability paper (Harding 1949; Cassie 1954). In order to compare the growth trends of the *S. similis* population off southern California with trends in other waters, previous data on the size-frequency distribution of *S. similis* reported by Genthe (1969), Pearcy and Forss (1969), Omori et al. (1972), and Mutoh and Omori (1978) were reanalyzed to obtain average or modal carapace lengths[6] for the populations at

[6]BL/CL regression of *Sergestes similis* (>5.5 mm CL) are as follows:

different sampling dates and locations. The von Bertalanffy and logistic equations were used to fit these growth data.

RESULTS

Daily and Ontogenetic Vertical Migrations of Larvae and Early Postlarvae

Coastal upwelling is generally weak in southern California during the winter (Bakun 1973). This is consistent with the data on environmental properties at the sampling stations (Figure 2). The thermocline remained at about 75 m at all stations on Line 60 with the mixed layer temperature ranging from 11.5°C inshore to 14.0°C offshore. Salinity was usually <33.30‰ in water above 75-m depth. On Line 90, except for the two outermost stations, the thermocline was at 30-50 m and the temperature within the mixed layer was >13.5°C. Salinity was >33.20‰ at all depths. On Line 100 the thermocline was at about 50 m at Stn. 100.35 and 100.60. Temperature within the mixed layer was about 15°C, and salinity was >33.50‰. The position of the oxycline coincided with that of the thermocline at nearly all stations. Generally, the oxygen level at depths below the mixed layer increased going seaward.

The main population of *S. similis* larvae was always between the surface and 100-m levels, and they occurred in greater abundance at stations on the continental slope (Figure 3). The population density was highest at Stn. 90.32 (101 individuals/m²). The larvae did not occur at Stn. 90.120, 90.140, and 100.120. In these southern offshore stations the temperature above 100 m was >16°C. The temperature-salinity curves characterized the water mass as eastern North Pacific Central water, where *S. similis* has never been found. In this water mass, the "ortmanni type" larvae (the *Sergestes corniculum* group, see Yaldwyn 1957 and Omori 1974) were commonly distributed.

The vertical distributions of larvae and early postlarvae from eight stations where they were abundant shows that the larvae were scattered

from 20 to 100 m during the daytime (Figures 4, 5). On Line 90, the distribution pattern did not coincide well between the stations closest to shore (Stn. 90.28 and 90.32) and the offshore stations (Stn. 90.60 and 90.70). At Stn. 90.60 in the daytime, the larvae were widely distributed throughout the 0-110 m layer, but larvae occurred only between 44 and 88 m at Stn. 90.32 during the day. The greatest population density observed was within the 66-88 m layer at Stn. 90.32 (about 3,500 individuals/1,000 m³). Nighttime larval distribution was between 20 and 90 m at Stn. 90.70, but again, it was below 40 m at the closest inshore station. A similar inshore and offshore assemblage was observed along Line 100, although the vertical distribution of the larvae was expanded more widely. At Stn. 100.35 the larvae were most abundant between 50 and 100 m in the daytime and 0 and 80 m layer at night. On the other hand, at Stn. 100.60 the main population in the daytime occurred between 20 and 120 m, while at night the distribution ranged from the surface to 140 m with considerable numbers in the 0-40 m layer. At both stations, there was a clear daily vertical migration of the main population of zoeal and postlarval stages.

With the present sampling method, there was some doubt whether the same population was measured by day and night tows. However, as indicated in Figures 4 and 5, the estimates of abundance beneath 1 m² of sea surface did not differ appreciably between day and night at the two closest stations on Lines 60 and 90 and between day and night tows at the same station on Line 100. It can be said, at the least, that the avoidance of nets by larvae in the daytime was no greater than at night.

When abundance vs. depth is combined and averaged for each larval stage at each station, the extent of daily vertical migration becomes clear. The first protozoeal stage shows at least a restricted daily vertical migration (Figure 6). The larvae gradually increase their range of vertical distribution with growth while gradually inhabiting deeper water. Thus, the main population of early postlarva (40-45 m at night and 70-75 m in the daytime) shows a deeper distribution than earlier larval stages.

Eggs of *S. similis* (about 0.3 mm in diameter) were slightly heavier than the density of the experimental water; the difference in sinking rates was not significant at the 5% level between 10° and 14°C under laboratory conditions (Table 3).

BL = 3.15 + 2.85 CL for females,
BL = 2.55 + 3.11 CL for males (Omori et al. 1972).
The regression for juveniles with carapace length 5.5 mm or less is:
BL = 3.08 CL.
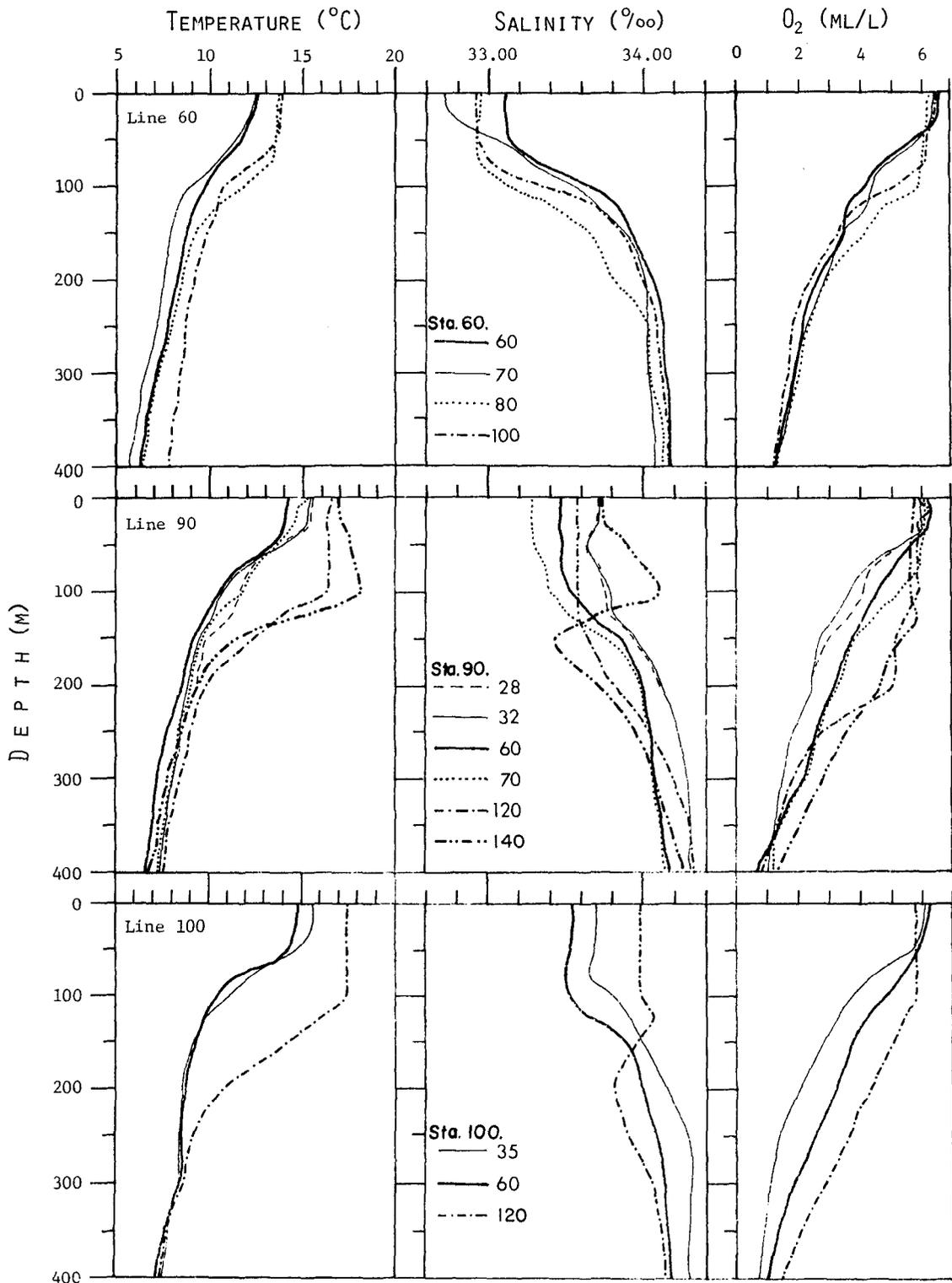
FIGURE 2.—Vertical profiles of temperature, salinity, and oxygen on CalCOFI Lines 60, 90, and 100, January-February 1964, off southern California.
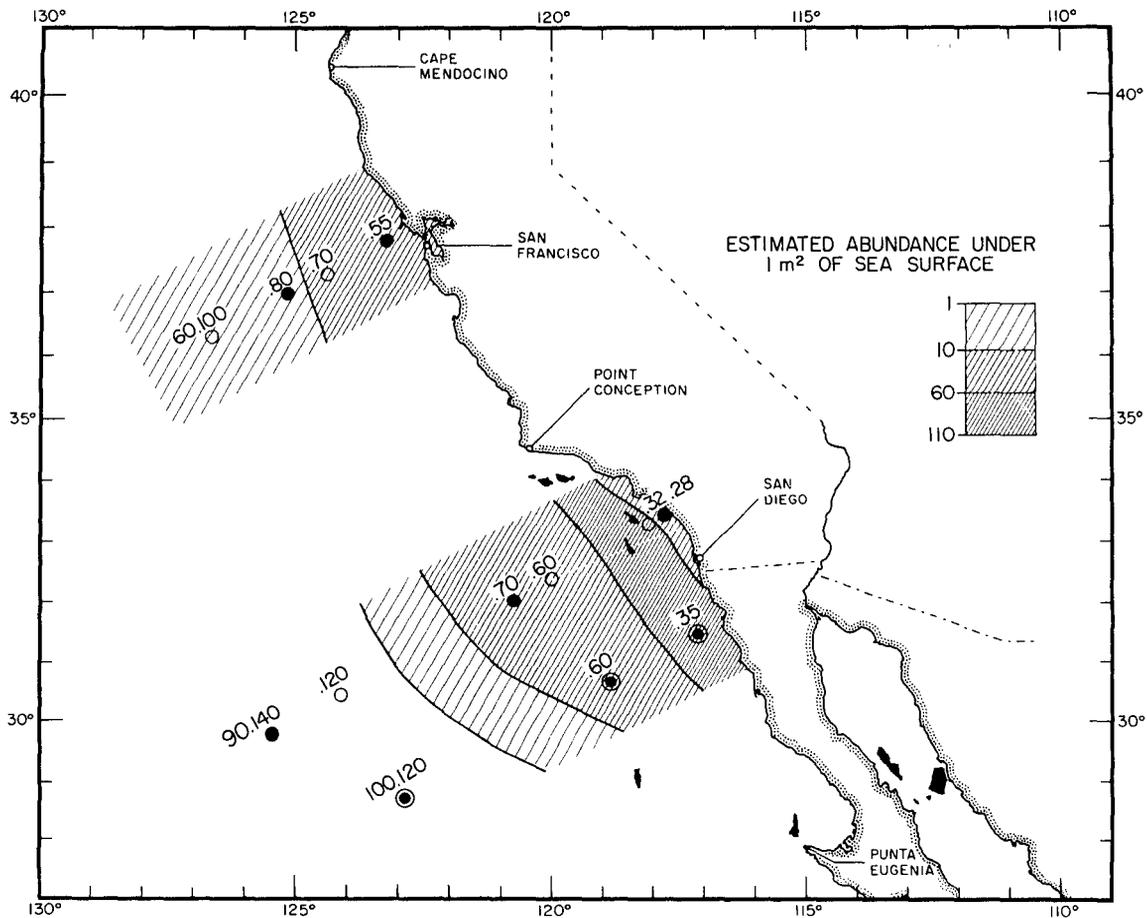
FIGURE 3.—Distribution and abundance of *Sergestes similis* larvae from January to February 1964. Estimated abundance is expressed as number of individuals beneath 1 m² of sea surface in depths between 0 and 100 m.

TABLE 3.—Experimental data on sinking velocity of eggs of *Sergestes similis* in water of salinity 33.72‰. Difference in sinking rates is not significant at the 5% level.

| Temperature (°C) | Replicates | Sinking velocity (m/h) | | |
		Average	SD	Range
10	9	1.45	0.44	0.91-2.19
14	9	1.81	0.52	1.04-2.99

Spawning Season

The highest spawning of *S. similis* took place from late December to early April. Protozoea larvae occurred most abundantly between January and April at Stn. 90.37 (Figure 7), but were not found in samples collected in November and December. During 1951-54, a number of PZ2 and PZ3 appeared each year between January and July, but the occurrence of PZ1 was restricted to January-April, except for August 1952 and July 1954. Although one-third of the autumn months were not represented by samples, these months were scattered enough to make the data significant. Seasonal abundance of zoeal stages duplicated that of PZ1. Early postlarvae were found in plankton from February to early July. Considerable numbers of PZ1 and PZ2 (<1.3 mm BL) apparently passed through the mesh of the CalCOFI net, as their measured population densities were almost always lower than those measured for PZ3.

The optimum temperature range for larval development is 10°-15°C (Omori 1979), and the highest temperature at which adult *S. similis* occur is 13°C. Thus, the best temperature for the larvae is close to the upper temperature limit of the adult's habitat. Furthermore, comparison of the reproductive activity of *S. similis* with physical and

NO. OF INDIVIDUALS / 1000 m³
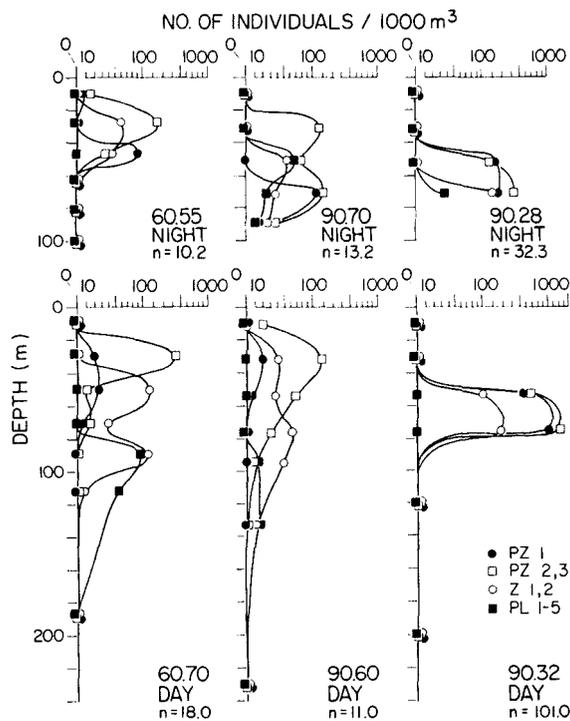
FIGURE 4.—Vertical distribution of larvae and postlarvae of *Sergestes similis* on CalCOFI Lines 60 and 90 off southern California. PZ, protozoeal stages; Z, zoeal stages; PL, postlarval stages. Estimated total number of larvae beneath 1 m² of sea surface indicated by n.

stratum of optimum temperatures for larvae was thickest. It decreased before colder water was brought in by coastal upwelling which was normally most intense from May to August (see Bakun 1973). A seasonal minimum, or cessation, of spawning occurred during the summer and autumn when the upper layer was covered by unfavorably warm temperatures ($>15°C$).

Growth

Because of the smaller mesh size, the 6-ft IKMT retained a larger proportion of small shrimp than did the 10-ft IKMT (Figure 8). While specimens of 4 mm CL occurred in the smaller net, few <7 mm were retained in the larger net.

Well-defined progressions of size-frequency modes gave indications of average growth rates for certain cohorts, although we sometimes encountered difficulties in interpreting these trends due to inadequate sampling, and possibly to extended spawning of the species. One 1975 cohort (12.0-14.5 mm CL) and two conspicuous 1976 cohorts (5.0-11.0 mm CL) were seen in females collected in August 1976 (Figure 8A). The former cohort was not found in the following two samplings. The large-sized 1976 cohort (mean modal length, 8.4 mm CL in August) reached 9.9 mm CL in October, 10.5 mm CL in January, and 11.8 mm CL in March 1977. Growth of the small-sized cohort was traceable until April 1977, when the shrimp attained an average carapace length of 10.4 mm. Recruitment of postlarvae <6.0 mm CL (1977 cohort) was intense in April. The histogram for March showed only a single mode of males, and it is not possible to

chemical environmental data indicates that there is a relationship between temperature and spawning season (Figure 7). Spawning activity was highest during the period when the vertical

NO. OF INDIVIDUALS / 1000 m³
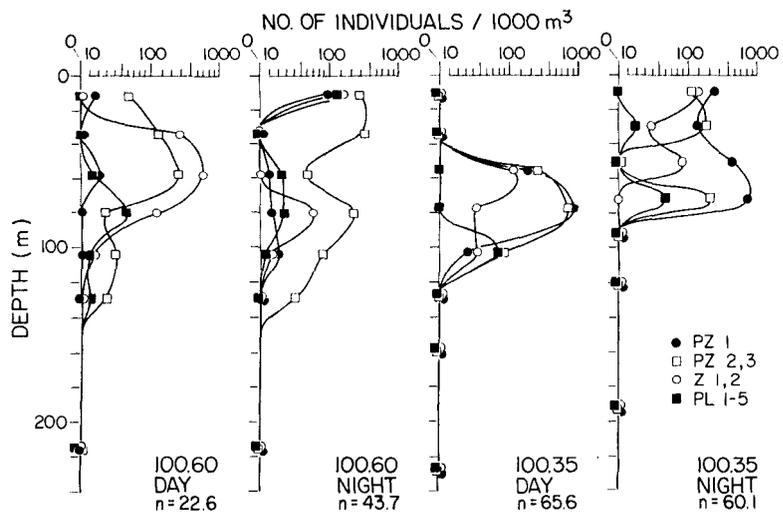
FIGURE 5.—Vertical distribution of larvae and postlarvae of *Sergestes similis* at CalCOFI Stn. 100.35 and 100.60 off southern California. Estimated total number of larvae beneath 1 m² of sea surface indicated by n.

RELATIVE ABUNDANCE (%)
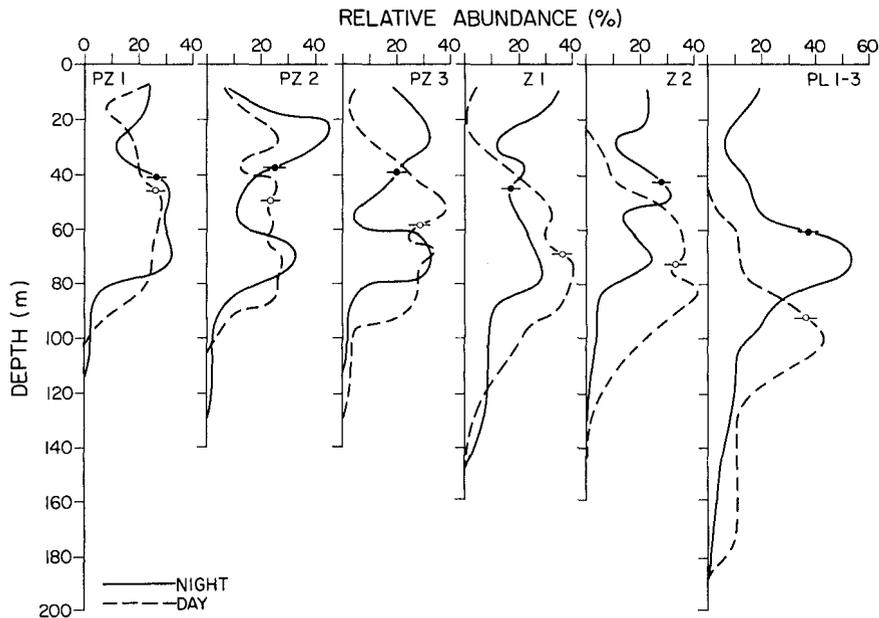
FIGURE 6.—Vertical distribution of larvae and postlarvae of *Sergestes similis* off southern California. Abundance vs. depth at all sampling stations was combined and averaged. Horizontal line indicates the depth at which the cumulative catch represented 50% of the total catch.   PZ, protozoeal stages; Z, zoeal stages; PL, postlarval stages.

say whether this 1976 cohort represents the large-sized group or not. In the 10-ft IKMT samplings the most conspicuous female cohort of 10.5-13.0 mm CL in April reached 13.5-15.5 mm CL in October (Figure 8B). The males grew from an average 10.8 to 11.7 mm CL between April and August. In many cases, the size structure of the population showed the presence of only one or two obvious size groups, but in three cases (April 21, June 21, and July 29) the histograms of females indicated three size groups. Development of the smallest cohort of 0 age-group was traceable until August in both females and males, but in October and November, two cohorts of 0 age were apparent.

Some estimates of growth were attempted using changes in the average or modal lengths in various months. In order to show the growth trend more definitely, the results of all previous length measurements of *S. similis* from various waters were reanalyzed and the average or modal lengths for each size group were plotted together with the present data (Figure 9). Except for the points derived from the offshore population in the subarctic North Pacific, where the environment is quite different from that of southern California, the majority of cohorts had average or modal lengths which

fell within the growth curves of three year classes fitted by eye.

These data indicate the following: 1) as expected from spawning season data, in most cases the modal progressions are evident starting in winter or early spring, 2) growth trends of *S. similis* off southern California appear similar to the population off Oregon (Pearcy and Forss 1969), and 3) growth rates do not vary greatly among many different populations, although there is evidence that a few modal groups grew about twice as rapidly as the ordinary one.

The ratio of females to males in all collections was 1.3:1 (553:422). Sex ratio in a cohort was not skewed greatly towards females until the modal length of the female population reached about 13 mm CL. At that point, the males of the cohort rapidly disappeared from the collection, accounting for the observed imbalance in sex ratio (69:2).

DISCUSSION

Ontogenetic Migration

Omori (1979) found experimentally that: 1) ovigerous females of *S. similis* shed their eggs at night, 2) the eggs took 105 h to hatch into nauplii

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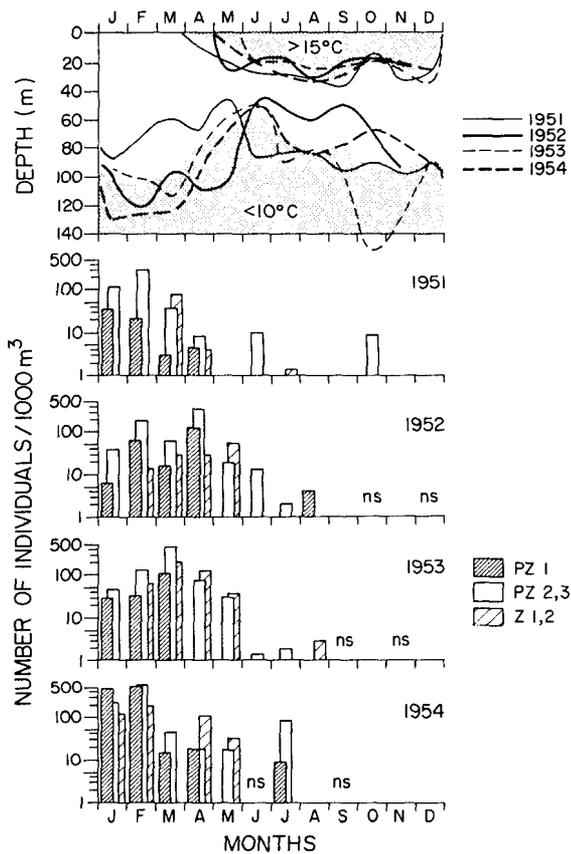
FIGURE 7.—Isotherms of 10° and 15°C and occurrence of larvae of *Sergestes similis* at CalCOFI Stn. 90.37, 1951-54, off southern California at 0-140 m. Shadow indicates zones where temperatures exceed the average 10°-15°C range of 1950-55. No sampling indicated by ns. PZ, protozoeal stages; Z, zoeal stages.

at 10°C, and 3) mortality increased greatly in temperatures beyond 10°-15°C. We do not know the depth where spawning and hatching of *S. similis* take place in the natural habitat. However, the laboratory observations, coupled with biological information on the other species of sergestids and euphausiids (Omori et al.[7]), indicate that the eggs of *S. similis* are shed in shallow water at night when ovigerous females rise upwards. Adult *S. similis* seldom occur above the 50-m level at night where the temperature is usually >13°C off southern California. Assuming that

FIGURE 8.—Length-frequency histograms of *Sergestes similis* collected with a 6-ft IKMT (A) and a 10-ft IKMT (B) off southern California. The samples were arranged in monthly order regardless of the year of sampling. Lines trace development of significant cohorts.

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[7]Omori, M., M. Mutoh, and M. Kaetsu. 1974. Prediction of *Sergia lucens* fishery in 1974/75 season. [In Jpn.] Unpubl. manuscr., 5 p., distributed at the annual meeting of the "Sakura-ebi" Fishing Unions, Shizuoka Prefecture, Japan.
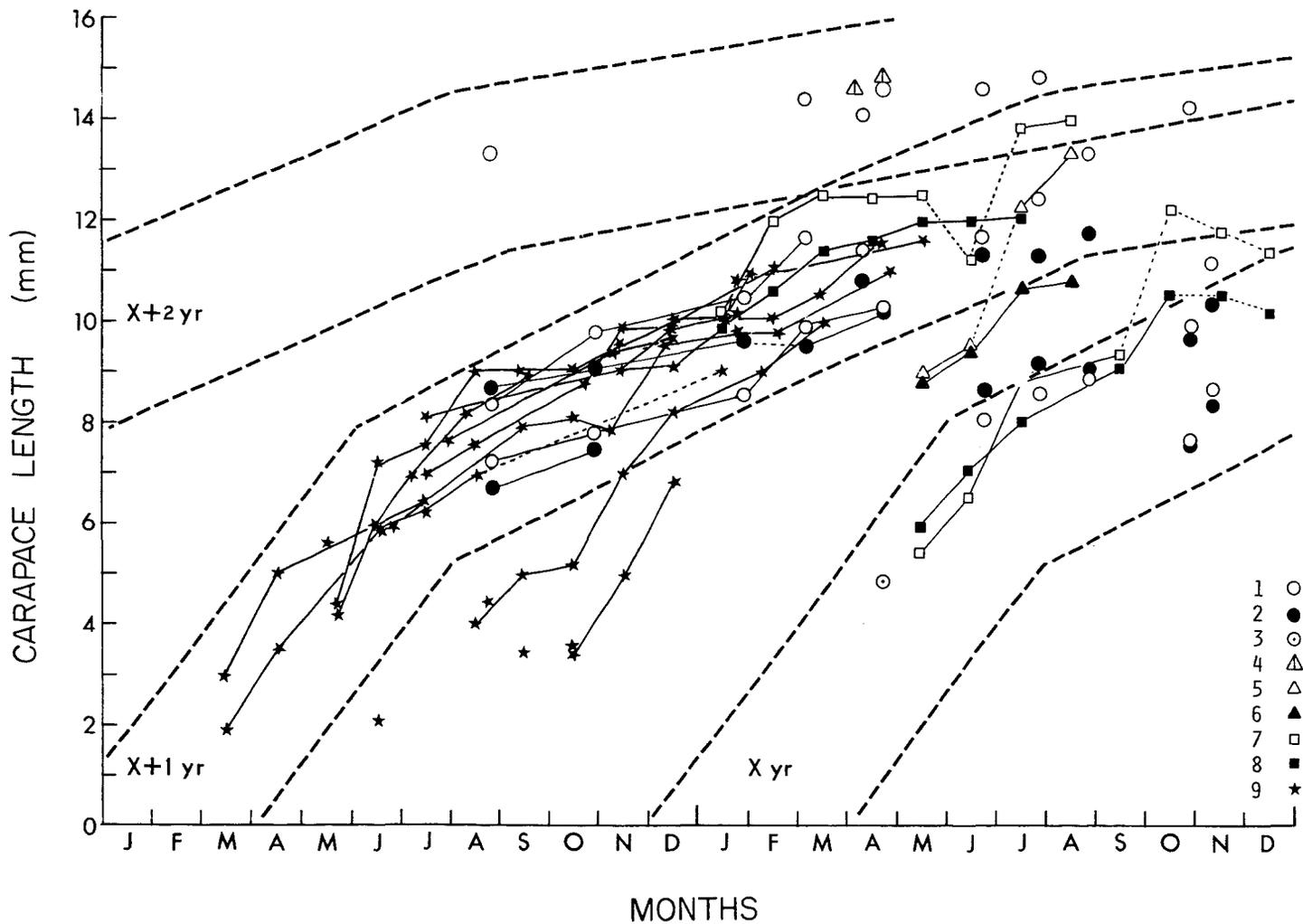
FIGURE 9.—Growth trends in different waters of *Sergestes similis*, derived from average modal length of different cohorts. Solid and dashed lines trace development of cohorts. Solid lines trace sequences considered clear, dashed trace those less clear. Data sources: 1, present study, female; 2, the same, male; 3, the same, unsexed juvenile; 4, off Japan, female (Mutoh and Omori 1978); 5, subarctic North Pacific, female (Omori et al. 1972); 6, the same, male; 7, off southern California, female (Genthe 1969); 8, the same, male; 9, off Oregon, sexes combined (Pearcy and Forss 1969).

spawning takes place around 50 m and using data on both the sinking velocity of the eggs and the development time of eggs at 10°C, we can estimate that the eggs sink to about 220-m depth before hatching. The ambient temperatures which eggs may encounter during their descent are 7°-13°C. It is probable that some eggs are laid deeper than 50 m. However, like the population off the Oregon coast (Pearcy and Forss 1969), *S. similis* is seldom distributed over the continental shelf off southern California. Therefore the majority of eggs would not sink to the bottom but remain within the water column.

A comparison of vertical distribution patterns at all stations confirms the following hypotheses: 1) the occurrence of larvae is restricted to water <140 m where the temperature range is 9°-16°C, 2) the larvae often appear in the 0-20 m level at night but rarely in the daytime, and 3) the larval distribution is more restricted inshore than offshore to a limited vertical range. The descent of eggs and ascent of naupliar larvae are well documented in the oceanic euphausiid *Euphausia superba* and *Meganyctiphanes norvegica* (Mauchline and Fisher 1969). Presumably the nauplii of *S. similis* rise from 200 m or deeper to layers where the temperature is usually >10°C. In this manner, the nauplius, which is probably highly vulnerable to predation, develops in the less hazardous layers which are deeper than the following larval stages. Protozoeal and zoeal larvae stay mostly in the shallower environment which is relatively rich in food (phytoplankton and microzooplankton). They perform daily vertical migration starting PZ1, and their downward migration at daytime becomes more marked with each stage. This hypothesis is further supported by the positive phototaxis in N3 to PZ1 larvae and negative phototaxis after PZ2 observed in the laboratory (Omori 1979).

According to Omori (1974), the larvae of pelagic shrimps can be classified into several types on the basis of their ontogenetic migration. The first group is composed of the species living in the epipelagic and upper mesopelagic zones. Their larvae perform migration within the euphotic zone. *Sergestes similis* belongs to this group, having a similar pattern to that described for *Sergia lucens* (Omori 1974), but the negatively buoyant eggs of *Sergestes similis* differ from *Sergia lucens* eggs which have density similar to seawater.

Adult *Sergestes similis* were abundant inshore off Oregon during the winter, but they tended to shift to an offshore distribution during the summer (Pearcy and Forss 1969). This inverse relationship between nearshore and offshore stations indicates a horizontal ontogenetic migration of this species by active swimming with the help of subsurface currents. The movement by a species to nearshore regions for spawning is a characteristic behavior among several sergestid shrimps (Omori 1974).

Relationship Between Spawning Season and Environment

Larvae of *S. similis,* in particular PZ1, were more abundant inshore than offshore, which indicates that the spawning of *S. similis* is taking place mainly close to shore above the continental slope off southern California (but not as far inshore as the continental shelf). The assumption by Pearcy and Forss (1969) that *S. similis* in the Oregon population spawns during most of the year with a seasonal minimum occurring during the summer was partially true in the southern California population as there were small pulses of spawning in summer and autumn. However, the southern California adult population appears to be recruited largely from the local population spawned from late December to early April.

One may argue that the decrease of larvae in the study area in summer and autumn was caused merely by the seasonal change off the southern California gyre. It would be interesting to compare our data with samples from stations outside of the northward flowing path of the gyre. However, we do not think that such an extreme absence of larvae in summer and autumn is taking place with the year-round spawning of *S. similis*. At least some larvae should have successfully remained in the study area to yield noticeable recruitment during those months. Incidentally, females having fully developed ovaries (Omori 1979) were seldom found in the IMKT collection from summer and autumn. Genthe (1969) assumed that maximum reproductive activity of *S. similis* from the Santa Barbara Channel was in summer and autumn, but his assertion that juveniles collected in August of 5.0-6.5 mm CL are 11 or 12 mo old is misleading. Shrimp of this size are more likely to be of the 6-7 mo class.

Omori et al. (see footnote 7) studied the relationship between environments and reproductive behavior of another sergestid, *Sergia lucens*, in Suruga Bay, Japan, and found that the com-

mencement of spawning and the survivorship of larvae are closely related to the ambient temperature rather than the quantity of food available. This study showed that: 1) *S. lucens* started spawning in June, immediately after the temperature exceeded 18°C at 20-50 m, and the number of larvae increased with increasing vertical thickness of the optimum temperature zone for the growth of larvae (18°-25°C), 2) the population size of *S. lucens* was determined by the abundance of larvae during the first half of the breeding season, June-August, and 3) the abundance of larvae was often related to the fluctuation in vertical width of the optimum temperature zone. During midsummer the warming of surface waters above to 25°C and the shoaling of cold water <18°C restricted the optimum temperature zone, and consequently the mortality of protozoeal larvae increased.

As with *S. lucens*, a rise in temperature may trigger the commencement of spawning of the *Sergestes similis* population in the northern subarctic waters where surface temperature is <10°C during most of the year. However, this seems not to be the case for the southern California population where favorable temperatures were available year-round in some stations between 50 and 100 m. Yet, the spawning began abruptly when the temperature around 100-m depth began to rise. Abundance of larvae was greatest during the period when the vertical thickness of the optimum temperature zone was the greatest, and spawning activity almost ceased both when the ambient temperature was lowered by coastal upwelling and when warm surface water subsequently appeared. Thus, the spawning season of *S. similis* is not always positively correlated with the upwelling which causes environmental enrichment and subsequent increase of plankton biomass in the southern California eddy. The correlation of spawning to coastal upwelling in *Euphausia pacifica*, another very abundant species of the California Current zooplankton assemblage, is the most striking difference affecting the spawning seasons of that organism and *S. similis*. Similar to *S. similis*, the southern California population of *E. pacifica* seems to be adapted for larval development between 12° and 16°C, but its spawning is highest when coastal upwelling is strongest in May-June (Brinton 1976). Although true mechanisms remain unexplained, we theorize that the distinctive spawning season of *S. similis* in southern California is based mainly on the adaptation of this species to the vertical thickness of optimum temperature. The vertical thickness of the optimum temperature zone was also correlated with the abundance and survival of larvae of *S. similis*. The cumulative depths of the optimum temperature ranges for *S. similis* from January to March were 220, 318, 311, and 380 m from 1951 to 1954 whereas the average numbers of protozeal larvae occurring from January to April were 129, 218, 224, and 543 individuals/1,000 m³, respectively. In 1951, zoeal larvae were found in the lowest numbers when the cumulative depth was the smallest.

One possible interpretation of the irregular small pulse of spawning of *S. similis* in seasons other than winter and early spring is that shrimp which reproduce during these periods are carried from northern offshore waters, i.e.,subarctic North Pacific, to the study area. If temperatures of 9°-10°C in the habitat of *S. similis* really trigger the commencement of spawning, those living in subarctic waters would start spawning later than July in most areas. The yearly mean velocity of the eastward component of the North Pacific Drift is about 3 cm/s at the surface in the areas lat. 45°N west of long. 150°W. On the other hand, a strong south-flowing current, which flows at the velocity of 5-10 cm/s but occasionally >20-30 cm/s is observed throughout the year both at the surface and at 200-m depth off the west coast of the United States (Wyllie 1966; Stidd[8]). If part of the population of *S. similis* near lat. 47°N, long. 140°W, e.g., where tremendous numbers are eaten by baleen whales (Omori et al. 1972), is carried southeastward by the currents, the shrimp can easily reach the southern California coast within 2 yr at a mean speed of 5 cm/s of flow. The spawning occurs in the summer off California due to continuous recruitment of such northern populations. An electrophoretic study of *S. similis* population may help to answer this question, although, due to diverse trophic regimes, genetic variability of the southern California population may be too large to distinguish it from the subarctic population (see Valentine and Ayala 1976).

Another possible interpretation is that the phenomenon is caused by the adaptation of the local population to mid latitude irregularities in oceanographic and trophic conditions. It has been observed for several penaeids, sergestids, and euphausiids in temperate and tropical regions

[8]Stidd, C. K. 1974. Ship drift components: means and standard deviations. SIO Ref. 74-33, 57 p.

that the ovary may contain ova at different developmental stages and that not all ova are necessarily released at once (King 1948; Mauchline 1968; Roger 1973; Omori 1974). We observed that S. similis off southern California always retained considerable numbers of immature ova after spawning. Because the volume of a pair of mature ovaries from this shrimp represents about 10% of the body volume, we can estimate from the volume of each egg that one female has at least 1,500 but probably closer to 2,000-2,500 eggs. Nevertheless, the number of eggs released by a female in the laboratory was always <1,140 (Omori 1979). Thus, as has been pointed out for Euphausia pacifica off southern California (Brinton 1976), it appears possible that under optimal environmental conditions small ova of S. similis may develop later and produce a second spawning. If a female, which produced the first clutch in late December, released the second clutch 3-4 mo later, two modal size-groups might be seen sometimes in the same age-group. It is probable that unfavorable environmental conditions would prevent the spent ovary from maturing again until the following year. Further evidence of this phenomenon is provided by the increase in the number of spent females and the decrease in the number of fully grown ova in ovaries of S. similis off southern California and Oregon during the summer (Genthe 1969; Pearcy and Forss 1969). The length-frequency histograms in October 1972, November 1975, and from August 1976 to March 1977 (Figure 8) indicate either the occurrence of multiple spawnings for S. similis or individuals from farther north being mixed into the southern California population.

Growth, Sexual Maturity, and Longevity

If S. similis population is composed of 0 age-group shrimp only and all attain sexual maturity after about 1 yr, the size structure of the population sampled shows the presence of only one or two size groups. However, the obvious occurrence of three size groups of females during certain periods of the year in this study indicates that the females of S. similis live 2 yr or more. Large females, 13-16 mm CL, carrying developed ovaries are sometimes collected, indicating that S. similis can reproduce at least twice during its lifetime. The absence of male individuals >14 mm CL resulted in a strong imbalance of sex ratio, indicating that the males die out at an age of <20 mo. Genthe (1969) showed

evidence of sex reversal (protandrous hermaphroditism) from male to female in S. similis. Similar phenomena have been observed in other sergestids of the genus Acetes (Omori 1975). A detailed study is needed to determine the meaning of these findings, although at the present time we believe that the variance may be explained by abnormalities, since the frequency of occurrence is small. The bias in sex ratio favoring females above a certain size indicates the possibility of multiple fertilizations by males. Thus some females of the 2 age-group may mate with males of the 1 age-group.

We obtained an average growth trend of S. similis throughout its life by shifting the average or modal lengths of populations off the California and Oregon coasts horizontally in accordance with the month of their sampling. The growth of S. similis >6 mm CL was best fitted by the von Bertalanffy equation (Figure 10):

$$l_t = 14.7(1 - e^{-0.00378t}) \text{ for females, and}$$
$$l_t = 12.0(1 - e^{-0.00481t}) \text{ for males,}$$

where l_t is the carapace length in millimeters at t days. Because of the large mesh sizes of the IKMT nets, however, any average or modal length calculated from these samples over considerable size ranges on either side of 7 mm CL is probably greater than the length of the natural population. Therefore, the initial modal length of the 3-mo old population was fit by eye and connected with those growth curves of larval and early postlarval stages at 10° and 14°C which were obtained under laboratory conditions. It took 52 days for S. similis to reach the first postlarval stage at 14°C (Omori 1979). Under these conditions the logistic equation (Figure 10B) seemed to give the better fit to the growth curves:

$$l_t = \frac{14.7}{1 - e^{-0.00920(t-234.5)}} \quad \text{for females,}$$

$$l_t = \frac{12.0}{1 - e^{-0.01254(t-188.4)}} \quad \text{for males.}$$

Growth is very rapid during the postlarval stages. The juveniles at 4-8 mo old grow, at 0.91 mm CL/mo, during the period from April to August (logistic equation). The biomass of total zooplankton, as well as young Calanus and Euphausia, which are considered to be the most important food for juvenile and adult S. similis,
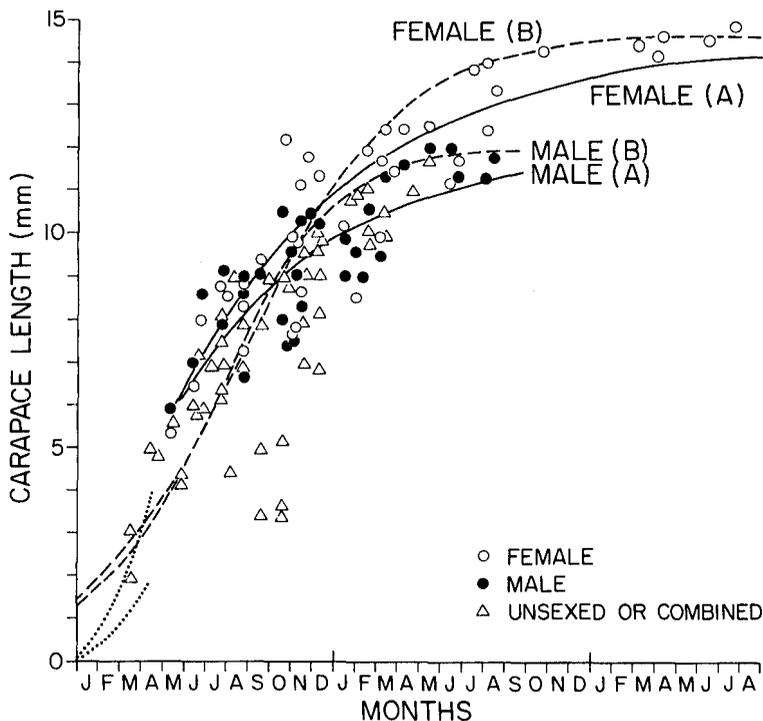
FIGURE 10.—Average growth of *Sergestes similis* off the California and Oregon coasts. Solid lines (A) are growth curves fit by the von Bertalanffy equation and (B) are those fit by the logistic equation. Dashed lines are growth curve of early developmental stages of 10° and 14°C determined in the laboratory (Omori 1979).

usually peaks in the April-July period in southern California waters (Mullin and Brooks 1970; Brinton 1976). Shrimp which encounter the best feeding conditions probably grow rapidly with low mortality rates and form distinctive modal groups such as those traced in Figure 9. The growth rate gradually decreases after 10-mo old, and the females add only 5 mm CL in 20 more months before dying. The difference in growth rates between the sexes becomes apparent after the shrimp attain a length of about 8 mm CL. The males grow slower than the females, but attain sexual maturity ½-1 mo earlier than females because the females become mature at 10.5-11.0 mm CL, whereas the males mature at 9.5-10.0 mm CL (see Genthe 1969; Omori 1979). Since five data points for females on the upper right-hand side of Figure 10 are on the asymptote, it is highly speculative whether these shrimps represent that age-group, or possibly an age-group spawned 5-6 mo later; in which case they would be placed on a different curve. It is apparent, however, that the longevity of the females of *S. similis* is more than 2 yr and that they spawn in two successive spawning seasons during their lives. These observations agree well with those of Matthews and Pinnoi (1973) on *Sergestes arcticus* Kröyer, which is the most closely related species to *S. similis* (Judkins 1972), in Kursfjordan, western Norway.

ACKNOWLEDGMENTS

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