

ECOLOGY OF HAWAIIAN SERGESTID SHRIMPS (PENAEIDEA: SERGESTIDAE)

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ABSTRACT

This paper describes the vertical distribution and migration, population size, seasonal size-frequency distribution, and diet of 20 species of sergestid shrimps collected between 1970 and 1973 in the vicinity of Oahu, Hawaii.

During the daytime, half-red sergestids live between 450 and 725 m, while all-red sergestids range from 650 to at least 1,200 m. At night all but two species migrate into the 0- to 300-m region, half-red and all-red groups mixing together. One nighttime group lives above 100 m, another lives between 125 and 300 m. Moonlight depresses the shallow group below 150 m; it has little effect on the deep group. In addition, some species stop migrating around full moon, remaining at their daytime depths.

All species examined eat zooplanktonic crustacea in the 1- to 3-mm size range. Some species can also utilize smaller zooplankton around 0.4-0.6 mm. This ability is unrelated to the enlarged maxillipeds found in some species.

Most species appear to spawn mostly during the spring, although ovigerous females can be found at any time of the year. Life span appears to be 1 yr for all species except *Sergia bisulcata*, which lives 2 yr. One species does not reproduce in Hawaiian waters.

Hawaiian sergestids are specialized by size, morphology, and vertical distribution. The most closely related species pairs are always separated by size. The Hawaiian sergestid assemblage is very similar to assemblages reported from two areas of the tropical Atlantic.

Shrimps of the family Sergestidae (Decapoda, Penaeidea) are one of the most characteristic groups of micronekton over much of the open ocean. They dominate the crustacean micronekton over large areas of the North Pacific, where they form sound-scattering layers (Barham 1957) and feed baleen whales (Omori et al. 1972). Two speciose sergestid assemblages have been described from the subtropical Atlantic by Foxton (1970) and Donaldson (1973, 1975). This paper examines the sergestid assemblage from the central Pacific near the Hawaiian Islands, reporting vertical distribution and migration, abundance, growth and reproduction, and diet.

MATERIALS AND METHODS

Sampling Area

All the sergestids examined in this study were collected off the leeward (west) coast of Oahu, Hawaii at about lat. 21°30'N, long. 158°20'W. Most trawling was done 10-25 km offshore in water 1,500-4,000 m deep. Physical and chemical data for

this area, as well as the nearby Gollum Station (lat. 22°10'N, long. 158°00'W), have been reported by Gundersen et al. (1972) and Gordon (1970). The mixed layer is 50-80 m thick with a temperature of 23°-26°C. The annual variation in temperature of the mixed layer is only about 3°C (Gordon 1970). A broad thermocline extends to approximately 500 m, where the temperature is 5°-7°C. Salinity varies from 34.0 ‰ at 400-500 m to 35.2 ‰ at 100 m; oxygen varies from 7 mg/liter at 100 m to 1 mg/liter at 700-900 m. The water is very clear. In situ measurements of irradiance to 500 m at lat. 28°29'N, long. 155°14'W in August 1972 gave an extinction coefficient of 0.029 m⁻¹ at a wavelength of 471 nm for depths below 200 m; surface irradiance at 471 nm was 7 × 10² μW/cm² per nm, decreasing to 1 × 10⁻⁴ μW/cm² per nm at 500 m (E. M. Kampa, pers. commun.). Annual net primary productivity has been estimated at 50 g C/m² (S. A. Cattell in T. A. Clarke 1973:431). Nakamura (1967) found an annual mean standing crop of zooplankton of 2.6 g/m² in the upper 200 m.

The sampling area was chosen as the deep water nearest to Honolulu. It has the further advantage of being in the lee of Oahu under normal tradewind conditions, an important practical consideration when working from RV *Teritu*. In

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spite of its proximity to land, the area appears to be representative of the open waters of the central North Pacific. Meroplankton is sometimes abundant, particularly larval stomatopods, but never dominates the zooplankton. The light regime at night may be affected by light from the urbanized areas of Oahu, although direct light from Honolulu is shielded by mountains. Doty and Oguri (1956) found enhanced values of primary productivity near the Hawaiian Islands (the "island mass effect"), but Gilmartin and Revelante (1974) found this effect only within about 1 km of land. The advantages of nearness to port and convenience of study greatly outweigh the potential disadvantages of being affected by nearshore processes.

Vertical Distribution: Teuthis Sampling Program

Most of the material studied was collected during the "Teuthis" program, a series of 23 cruises during 1971-73 by the University of Hawaii's RV *Teritu*. The primary objective of the program was to determine the vertical distributions of the various species of micronekton during the daytime and at night. For this purpose an extensive series of horizontal tows was made using a modified Tucker trawl (MT) with a mouth 3 m wide. The trawl can be opened and closed at the desired sampling depth, avoiding contamination of the sample by organisms from shallower depths during setting and retrieval. It is lined with knotless nylon mesh, with apertures about 7 mm in diameter. The cod end is a 1-m plankton net of 303- μ m Nitex.² Mounted on the trawl is a time-depth recorder (Benthos 1170) which provides a record of the depths sampled by the trawl.

This basic configuration was extensively modified during the course of the sampling program to obtain more reliable operation and better data. The original acoustic-controlled opening-closing system (Inter-Ocean) was replaced by a more reliable messenger-operated double-trip mechanism (modified General Oceanics No. 4020). A digital flowmeter (General Oceanics No. 2030) was added at the beginning of 1972, giving a more accurate estimate of the volume of water sampled by the trawl. An acoustic telemeter (AMF No. 1024) allowed real-time monitoring of trawl depth beginning in November 1972; earlier tows wan-

dered vertically over 10-20% of their maximum depth.

The limitations of time and unreliability of sampling gear forced abandonment of plans for a uniform series of standard tows. Each cruise attempted instead to sample depths not yet sampled or to answer questions raised by previous sampling. Informal as this protocol was, the actual depths sampled often differed greatly from the plan. Before a telemeter was available, the sampling depth was set by the amount of wire paid out; two tows with the same amount of wire out often showed a twofold variation in modal depth. Over the course of the program the upper 1,200 m was sampled rather thoroughly, with a few deeper tows down to 2,300 m.

A typical cruise lasted 4 days. On each day two tows were made during the daytime and two at night, avoiding the twilight periods when many mid-water animals are migrating. Tows sampled for 3 h at a towing speed of about 4 knots. The catch was immediately placed in chilled seawater, and live specimens were removed to an aquarium for observation. The rest of the catch was sorted and preserved in buffered 5% Formalin seawater. The inside of the net was picked clean of animals after each tow to prevent contamination of subsequent tows. Physical conditions recorded included ship's position at the beginning and end of sampling, weather conditions and sea state, time of sunrise and sunset, and lunar phase. Bathythermograph casts were made during the early cruises, later replaced with expendable bathythermograph casts; at least one was taken per cruise (Maynard et al. 1975). The 1973 cruises also recorded biological sound scattering at 25 kHz and surface light irradiance (Walters in prep.). In the laboratory, the sergestids were sorted to species, sexed, and counted, and the carapace length (CL) from the base of the rostrum to the posterior margin of the carapace at the dorsal midline was measured to the nearest 0.1 mm with an eyepiece micrometer in a dissecting microscope.

Between February 1971 and June 1973, 16 cruises produced 160 horizontal tows (Table 1). Daytime (DAY) tows were lumped together, but nighttime tows were divided into tows during the dark of the moon or with the moon obscured by clouds (NIGHT) and tows made under substantial amounts of moonlight (MOON). Total trawling time for each 25-m interval of the water column to 1,500 m for the entire series was calculated from time-depth records (Table 2).

²Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 1.—Summary of sampling, 1970-73.

Cruise	Dates	Samples	Remarks
70-12	8-10, 13-17 Dec. 1970	31	3-m IKMT ¹ horizontal open tows
Teuthis IV	19-21 Feb. 1971	8	3-m MT ² horizontal opening-closing tows
Teuthis V	15-19 Mar. 1971	14	
Teuthis VI	22-26 Apr. 1971	12	
Teuthis VII	24-26 May 1971	7	
Teuthis VIII	21-25 June 1971	12	
Teuthis IX	30 July-1 Aug. 1971	8	
Teuthis X	22-24 Sept. 1971	1	
Teuthis XI	28 Jan.-1 Feb. 1972	8	
Teuthis XII	25-29 Feb. 1972	6	
Teuthis XIII	25-29 Mar. 1972	11	
Teuthis XV	23-27 May 1972	11	
Teuthis XVI	29 June-2 July 1972	12	
Teuthis XVII	1-5 Aug. 1972	10	
Teuthis XIX	3-7 Nov. 1972	12	
Teuthis XXI	4-7 May 1973	13	
Teuthis XXIII	13-17 June 1973	15	
Teuthis XVIII	30 Sept.-4 Oct. 1972	25	3-m IKMT shallow and deep oblique open tows
Teuthis XXII	23-27 May 1972	15	
DSB III	2-3 Feb. 1973	14	3-m MT horizontal and oblique open tows
Echo IV	5-11 Dec. 1973	25	3-m IKMT stratified oblique open tows

¹IKMT = Isaacs-Kidd midwater trawl.

²MT = modified Tucker trawl.

Oblique Series: Teuthis XVIII and XXII

Teuthis XVIII, 30 September to 4 October 1972, represented a departure from our normal sampling program. It consisted of a series of oblique tows with a 3-m Isaacs-Kidd midwater trawl (IKMT) designed to assess the relative importance in numbers and biomass of the various groups of micronekton, and also to determine the proportion of the mid-water community undergoing diurnal vertical migration (Table 1). Two series of oblique tows were taken: "deep" tows from the surface to 1,200 m, and "shallow" tows from the surface to 400 m. The catches were preserved unsorted in 5% Formalin seawater and returned to the laboratory, where they were sorted into the major taxa, blotted dry, counted, and weighed. Further details of sampling methods and results can be found in Maynard et al. (1975). The sergestids were divided into half-red and all-red types, counted, and weighed. They were later separated by species, counted, and sexed, and the carapace length measured.

Teuthis XXII, 23-27 May 1973, followed the same sampling protocol as Teuthis XVIII, with series of shallow and deep oblique tows. Sergestids from this cruise were separated by species, counted, and sexed, and the carapace length measured.

Effects of Moon: 70-12 and Echo IV

The Teuthis cruises were unevenly spaced in

time, making it difficult to use the data for studying growth rates and other aspects of population dynamics. In particular there were no cruises at all between early November and late January. To fill this gap in the seasonal coverage, I examined the sergestids from the December 1970 cruise of T. A. Clarke (70-12). This cruise used a 3-m IKMT for an extensive series of 2- and 3-h horizontal open tows in the upper 1,250 m of the water column (Table 1). Further details of sampling can be found in T. A. Clarke (1973). While the material from this cruise helped balance the seasonal data, it raised new questions about the vertical distribution of sergestids. Many of the species in the 70-12 samples showed abnormal vertical distributions. Since the cruise took place near full moon, it appeared that the abnormalities, in particular the absence of normal vertical migration patterns in some species until the final two nights of the cruise, were related to lunar phase. Unfortunately, shallow and deep tows were not taken on the same night, so it was unclear whether entire populations were affected and on which night normal behavior resumed.

The sampling program of Echo IV attempted to clarify these problems. We planned to make shallow and deep oblique tows with a 3-m IKMT from first quarter to full moon in an attempt to find when vertical migration ceased. Mechanical difficulties postponed the cruise until three nights before full moon; migration had already ceased by this time. The sampling protocol called for a shallow tow, either 0-200 m or 200-400 m; an

TABLE 2.—Number of tows and total towing time for each depth interval, 0-1,500 m, Teuthis sampling program.

Depth (m)	DAY			NIGHT			MOON		
	No. of tows	No. of tows >10 min	Total min	No. of tows	No. of tows >10 min	Total min	No. of tows	No. of tows >10 min	Total min
	3	0	6	7	3	433	13	0	38
	3	0	6	7	4	425	14	4	514
	3	0	8	7	5	313	13	5	350
100 --	3	0	9	8	5	385	12	5	604
	3	1	124	6	6	381	8	2	124
	4	2	95	6	3	336	8	2	51
	3	1	91	6	6	486	8	5	530
200 --	3	1	106	5	5	306	6	4	324
	4	2	121	1	0	2	5	4	204
	4	2	83	2	1	131	3	2	335
	3	2	105	4	4	337	2	1	180
300 --	2	2	116	5	3	149	3	3	208
	3	3	122	3	2	118	4	3	199
	4	4	115	3	3	61	2	2	162
	4	4	150	3	3	48	1	0	9
400 --	4	3	302	4	4	123	0	0	—
	6	4	160	5	5	266	2	1	42
	8	6	291	4	2	135	2	2	211
	13	9	609	3	3	241	2	2	95
500 --	14	11	406	5	2	94	2	2	49
	10	7	508	3	2	86	2	2	236
	9	8	260	4	2	140	1	1	14
	12	9	370	4	1	23	1	0	5
600 --	14	11	492	4	1	75	2	0	11
	15	14	559	6	4	216	3	2	71
	10	7	225	6	4	147	4	4	293
	8	5	274	7	3	82	6	5	205
700 --	12	7	371	5	3	172	5	4	210
	13	8	388	4	3	249	5	5	115
	14	10	459	3	1	40	3	3	143
	12	9	341	3	2	88	2	1	35
800 --	13	11	449	2	1	51	2	2	114
	11	7	379	4	2	91	3	2	74
	9	7	206	4	2	119	3	2	62
	7	6	190	4	1	29	3	2	69
900 --	9	6	165	3	2	62	2	1	13
	10	6	185	3	1	57	2	1	24
	10	7	179	2	1	44	1	0	2
	9	4	197	2	2	29	1	0	4
1,000 --	8	4	148	1	1	17	1	0	5
	5	3	166	1	0	6	1	0	4
	5	2	209	1	0	7	1	0	4
	5	2	62	1	0	7	1	0	8
1,100 --	4	1	26	1	1	15	1	1	12
	3	2	47	1	1	85	1	0	8
	3	2	126	1	0	2	1	1	48
	2	1	14	0	0	—	1	1	12
1,200 --	2	2	42	0	0	—	0	0	—
	2	2	89	0	0	—	0	0	—
	3	2	39	0	0	—	0	0	—
	3	1	62	0	0	—	0	0	—
1,300 --	3	2	71	0	0	—	0	0	—
	3	3	53	1	1	10	0	0	—
	3	3	104	1	1	20	0	0	—
	3	2	59	1	1	45	0	0	—
1,400 --	2	1	18	1	1	23	0	0	—
	2	1	18	1	0	7	0	0	—
	2	2	27	2	2	80	0	0	—
	1	0	6	2	0	10	0	0	—
1,500 --	1	1	16	2	0	8	0	0	—

intermediate tow of 400-600 m; and a deep tow of 400-1,200 m, each night of the cruise. Daytime trawling investigated possible moon-related changes in the daytime distribution of sergestids and included a 400- to 800-m tow and a 600- to 1,000-m tow each day. The actual depths sampled by the trawl deviated somewhat from the protocol, as we used no telemetry on the trawl. The last daytime tow was an all-day affair sampling from 1,100 to 1,900 m. The sergestids from this cruise were identified to species and counted, but not sexed or measured.

Feeding Study: DSB III

An important problem in any study of feeding in mid-water animals is the effect of the sampling gear on feeding behavior. A mid-water trawl concentrates animals in the cod end to unnaturally high densities. Often the trawl lumps together animals from different depth zones. A predator feeding on the contents of the cod end is likely to eat prey it would not normally take in the natural state, either because predator and prey do not occur at the same depth or because the prey can normally escape the predator. Examination of sergestid stomach contents from the Teuthis series suggested that many shrimp had been feeding in the trawl. A modification of the trawl became necessary to get reliable feeding data.

The DSB III cruise of 2-3 February 1973 was designed to investigate the feeding behavior of mid-water animals. The MT was modified by tying off the cod end ahead of the plankton net, allowing zooplankton to escape through the meshes. The trawl mouth was tied open. Daytime and nighttime oblique and horizontal tows were taken, the main objective being to obtain as large and varied a collection of mid-water animals as possible without much concern for their depth of capture (Table 1). The samples were preserved in 5% Formalin seawater and returned to the laboratory, where the sergestids were sorted out and their stomach contents identified.

Using the MT in this fashion produced one unexpected bonus. In addition to flushing out prey-sized zooplankton, the water current forced the catch and the inner lining of the net through the coarse outer net in pockets. Within each pocket the animals were firmly held by the force of the water, preventing movement and feeding. Future feeding studies might profit from deliberately designing this effect into the sampling gear.

Analysis of Vertical Distribution Data: The Contamination Problem

Most previous studies of vertical distribution (e.g., Foxton 1970, T. A. Clarke 1973, Donaldson 1975) have assumed that all the animals captured in a horizontal tow were taken at a single depth. While such an assumption simplifies the presentation and interpretation of the data, it can produce a misleading picture of the vertical structure of the mid-water community if the tows actually fish over a substantial depth range. Open trawls like the IKMT are the most susceptible to contamination of the catch by animals from other depths, since they fish during setting and retrieval. In this case, contamination usually takes the form of shallow-living animals appearing to have been captured below their normal depth. Rapid setting and retrieval can minimize but not eliminate the problem (T.A. Clarke 1973). Foxton (1970) and Donaldson (1975) have shown that animals from other depths can contaminate IKMT samples even when the trawl is fitted with opening-closing cod end buckets. Some animals become temporarily entangled in the net early in the tow. When they break free later on, the trawl may be fishing at a different depth, resulting in a sample that mixes shallow and deep animals in an unknown proportion.

Even an opening-closing trawl like the MT can give misleading results if it is allowed to wander vertically while open. In such a case, assigning the entire catch to the modal depth broadens out the apparent vertical range in both directions. Our experience has shown that towing the MT deeper than 200 m results in substantial vertical wandering unless its depth is constantly monitored and adjusted. Since a working telemeter was available only during the latter part of our program, most of our "horizontal" tows actually have a vertical range of 50-100 m. The problem increases with depth; tows below 800 m commonly wander 200 m or more. Assigning the catch to a modal depth would produce a misleading vertical distribution pattern.

The vertical distribution diagrams presented in this paper allow for vertical wandering of the trawl and for unequal sampling time with depth. Only horizontal tows are considered. The water column is divided into 25-m zones, and the amount of time each tow spent in each zone is determined from the various depth zones in proportion to the time towed in each zone. Let c_i be the number of

shrimp captured by the i th tow and $t_{i,j}$ be the amount of time tow i spent in the j th depth zone. Then the proportional catch $c_{i,j}$ from the i th tow in the j th depth zone is

$$c_{i,j} = \frac{c_i}{t_{i,j}} \quad (1)$$

For each depth zone j , summing proportional catches from all tows and dividing by total trawling time in the zone gives the catch rate r_j :

$$r_j = \frac{\sum_i c_{i,j}}{\sum_i t_{i,j}} \quad (2)$$

Ideally, the catch rate is proportional to the population density, so that dividing the catch rate by trawl filtering rate gives an estimated population density; i.e.,

$$D_j = \frac{r_j}{M_e \cdot f \cdot v} \quad (3)$$

where D_j is the estimated population density in the j th zone, M_e is the effective mouth area of the trawl (because of the design of the trawl, this quantity decreases with increasing towing speed), f is the filtering efficiency of the trawl, and v is the towing speed.

Proportional allotment of the catch by this method assumes that a particular shrimp is equally likely to have been captured at any instant during the tow. This assumption is clearly false for tows that spend only part of their time in the shrimp's actual depth range. However, spurious catch rates outside the actual depth range are minimized by additional tows in these zones that do not enter the actual depth range and do not catch shrimp; these tows increase the denominator of Equation (2) without increasing the numerator. It follows that this method of estimating vertical distributions works best when each depth zone is sampled many times.

Table 2 shows that during the daytime all depth zones between 400 and 1,075 m were sampled at least five times and that at least five tows spent more than 10 min in all zones between 425 and 950 m. Nighttime sampling was less thorough because tows were split into two groups on the basis of moonlight. In both groups all zones in the upper 200 m were sampled at least five times, as was the 600- to 700-m range (NIGHT) and 650- to 725-m

range (MOON). NIGHT tows in the 200- to 225-m zone sampled only 2 min; estimated population densities for this zone, while generally plausible-looking, should be regarded cautiously. The 0- to 25-m zone for MOON tows were sampled many times for brief periods by open tows that spent nearly all their time at depths of 50-150 m, but was never sampled extensively by any tow. Many species show spuriously high estimated population densities in this zone. There were no NIGHT tows between 1,150 and 1,300 m, and no MOON tows between 375 and 400 m or below 1,175 m. Night-time sampling was generally sparse below 800 m, and the estimated population densities for this region are very crude.

A second major assumption of this method of presenting vertical distribution data is that the vertical distribution remains constant throughout the sampling period, allowing data from many different cruises to be summed together. The resulting estimated population densities represent an average over the entire sampling period. The actual vertical structure on any given cruise may vary considerably from this average. The separation of nighttime tows into NIGHT and MOON tows is the only systematic attempt to show variations in vertical distribution; other variations are discussed in the species accounts.

Presentation of Results

A brief explanation will aid in interpreting the vertical distribution figures that follow (e.g., Figure 1). Catch rates were converted to estimated population densities in numbers per 10^5 m^3 by assuming an average trawling speed of 2 m/s, effective trawl mouth area of 5.1 m^2 (at 2 m/s), and filtering efficiency of 90%. DAY, NIGHT, and MOON (see above) distributions are shown for the entire population as histograms on the right side of the figure. The number to the right of each histogram is the sample size. In addition, the catches were divided into size classes, and population densities were estimated by the same method for each size class. Species with a maximum carapace length less than 17.0 mm were divided into 0.5-mm classes, while larger species were divided into 1.0-mm classes. The result was an array of estimated population densities as a function of size and depth. Interpolation produced a series of contours of equal population density. The lowest contour level represents 0.2 shrimp per 10^5 m^3 per mm CL; each successive contour level

represents a tenfold increase over the previous one.

The oblique tows of September 1972 (Teuthis XVIII) and May 1973 (Teuthis XXII) provided data that yield two estimates of the population densities of the various species, using the method of Maynard et al. (1975). Summing over the entire water column the depth-specific population densities obtained from the horizontal tows provides a third estimate of population densities. The results of these estimates are reported as numbers per 100 m² of ocean surface in Table 3. Sample sizes and standard deviations are given for the mean values of the oblique series. Because of the nature of the calculations for the horizontal tows, no standard deviations can be figured, but the variation is probably of the same order as those of the oblique series, since horizontal tows sampled each depth interval about the same number of times and for roughly the same total amount of time as the oblique tows.

The Teuthis data are poorly suited for investigating growth and reproduction of sergestids. The sampling program was designed primarily to investigate the vertical distribution of mid-water animals. Depth coverage varied widely from cruise to cruise, and the cruises were spaced irregularly throughout the year. In order to smooth the irregularities as much as possible, the data are lumped into 3-mo periods. The cruises involved are:

Jan. - Mar.	T4, T5, T11, T12, T13
Apr. - June	T6, T7, T8, T15, T16, T21, T23
July - Sept.	T9, T10, T17, T18
Oct. - Dec.	T19, 70-12.

Histograms show the size-frequency distribution of males and females for each species. For *Sergestes pectinatus* only, data from the oblique series of May 1973 (Teuthis XXII) are added into the second quarter histogram.

Because of the problem of feeding in the trawl (discussed above), only the stomach content data from DSB III (February 1973) are presented. Table 4 shows the average condition of the stomach contents for each tow. The two indices reported represent the quantity of food present and its state of digestion. Both are based on an arbitrary scale of 1 to 5:

<i>Contents</i>	<i>Digestion</i>
1. Packed full, distended.	Whole animal, with little evidence of digestion.

2. More than half full.	Body still mostly intact, appendages separated, some digestion of soft parts.
3. 25-50% full.	All soft parts digested, cuticle remaining, usually disarticulated.
4. Less than 25% full.	Cuticle broken into small fragments.
5. Empty.	Empty.

Stomach contents with a digestion state of 1 were seldom found in the DSB III samples but were rather common in the Teuthis material, probably because of feeding in the trawl.

Table 5 shows the kind and number of food items found in the stomachs of each species. Often the stomach contents were too well digested for identification. Food items were not identified beyond the general categories presented except for the calanoid copepod genus *Pleuromamma*, which has a prominent shiny knob on the side of the metasome that is highly resistant to digestion.

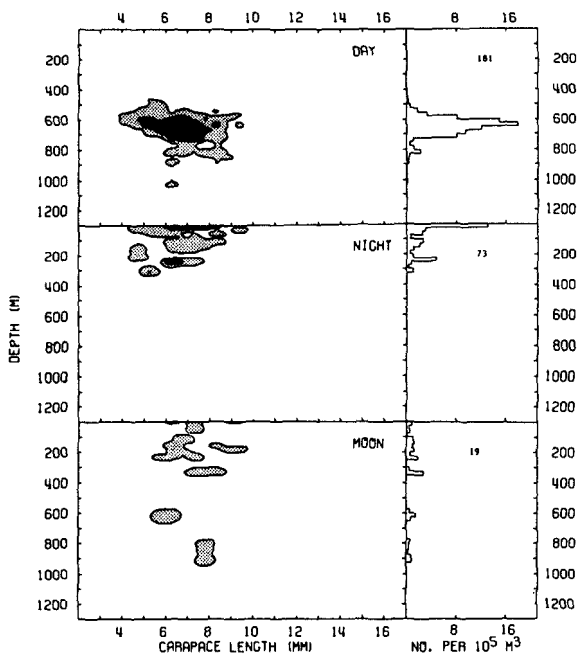
RESULTS

Sergestid species occurring in Hawaiian waters are listed in Table 6, along with the total number caught. *Sergestes* and *Sergia* until recently were considered to be subgenera of genus *Sergestes* s.l.; however, Omori (1974) has rightly elevated the subgenera to full genera. This paper follows his usage but gives feminine endings to species of *Sergia*. A paper presenting systematic descriptions of Hawaiian species is in preparation.

Sergestes atlanticus Milne Edwards 1830

Vertical Distribution (Figure 1)

The normal daytime range of *S. atlanticus* was 550 to 725 m. Small individuals had a more restricted range than the larger ones; shrimp less than 5.5 mm CL stayed between 550 and 650 m. *Sergestes atlanticus* was occasionally taken at 800 m or below. The small concentrations between 800 and 1,050 m in Figure 1 all resulted from the June 1973 cruise. In addition, the December 1970 cruise took seven shrimp in an 800-m tow. At night *S. atlanticus* occurred over a wide range from the surface to about 300 m. The large concentration in the upper 25 m resulted from a single large capture in May 1973. This depth interval was extensively sampled by only three tows, so it is unclear

FIGURE 1.—Vertical distribution of *Sergestes atlanticus*.

whether the bulk of the population normally occurs so shallow. A number of night tows in the 75- to 150-m range took small numbers of *S. atlanticus*, and one tow at about 250 m captured five individuals. There appeared to be no significant variation of depth with size. Tows on moonlit nights took small numbers of *S. atlanticus* from the surface to about 350 m, with a possible concentration around 150-175 m. Several captures were made between 600 and 925 m, suggesting that at least part of the population did not always migrate. The December 1970 cruise took substantial numbers (up to seven) near full moon between 250 and 300 m, and also between 550 and 800 m, indicating that only part of the population was migrating. Later in the cruise when the moon was waning, tows between 30 and 100 m took *S. atlanticus* in moderate numbers (four to six).

Population Size, Growth, and Reproduction (Figure 2)

Sergestes atlanticus was moderately abundant, turning up regularly in tows at the appropriate

TABLE 3.—Estimated population sizes of Hawaiian sergestids from all horizontal tows and two series of oblique tows (no. per 100 m²).

Species	Teuthis XVIII				Teuthis XXII				Horizontal		
	(¹)	\bar{x}	s	n	(¹)	\bar{x}	s	n	(¹)	\bar{x}	n
<i>Sergestes atlanticus</i>	DD	4.36	3.66	28	DD	1.17	1.67	9	D	2.10	180
	DN	2.66	1.31	19	DN	1.10	1.47	6	N	0.84	68
	SN	4.28	3.09	47	SN	0.28	0.56	2	M	0.46	19
		3.79	2.75	94		0.88	1.33	17		1.31	267
<i>Sergestes erectus</i>	DD	7.22	3.06	45	DD	1.79	1.25	13	D	5.55	542
	DN	5.30	3.83	39	DN	1.91	1.00	10	N	2.02	156
	SN	5.46	2.61	59	SN	2.28	0.80	16	M	2.83	151
		5.85	3.03	143		1.97	1.01	39		3.81	849
<i>Sergestes armatus</i>	DD	12.37	14.47	73	DD	1.18	1.85	8	D	2.48	251
	DN	12.16	7.69	84	DN	1.46	1.70	8	N	2.63	141
	SN	7.61	3.61	83	SN	0.87	0.80	6	M	1.83	41
		10.22	8.28	250		1.15	1.45	22		2.35	433
<i>Sergestes vigilax</i>	DD	3.33	2.52	20	DD	0.76	0.96	6	D	0.52	57
	DN	2.30	1.55	17	DN	0.72	0.81	4	N	0.28	30
	SN	4.63	1.42	50	SN	0.99	0.83	2	M	0.15	13
		3.58	1.95	87		0.61	0.75	12		0.35	100
<i>Sergestes orientalis</i>	DD	5.54	4.12	34	DD	0.65	0.92	5	D	1.61	160
	DN	5.11	2.00	38	DN	0.18	0.31	1	N	1.39	130
	SN	12.45	5.03	130	SN	0.99	0.83	7	M	0.75	42
		8.43	5.29	202		0.64	0.80	13		1.32	332
<i>Sergestes consobrinus</i>	DD	6.72	3.70	42	DD	2.48	1.42	18	D	0.72	81
	DN	3.30	1.28	24	DN	2.10	1.96	11	N	1.99	231
	SN	5.82	4.13	63	SN	1.45	1.03	10	M	0.57	13
		5.26	3.46	129		2.08	1.40	39		1.05	325
<i>Sergestes sargassi</i>	DD	10.37	7.85	68	DD	1.55	1.41	11	D	0.64	71
	DN	3.53	1.40	25	DN	1.68	0.95	9	N	1.07	77
	SN	4.91	2.16	52	SN	2.06	1.60	15	M	0.40	26
		5.84	4.73	145		1.74	1.29	35		0.70	174
<i>Sergestes pectinatus</i>	DD	23.24	17.36	141	DD	6.95	4.04	51	D	2.01	245
	DN	24.14	14.13	178	DN	2.58	1.34	14	N	1.54	136
	SN	30.44	20.86	330	SN	2.89	2.04	21	M	1.40	86
		26.67	17.30	649		4.70	3.59	86		1.71	467

TABLE 3.—Continued.

Species	Teuthis XVIII				Teuthis XXII				Horizontal		
	(¹)	\bar{x}	<i>s</i>	<i>n</i>	(¹)	\bar{x}	<i>s</i>	<i>n</i>	(¹)	\bar{x}	<i>n</i>
<i>Sergia fulgens</i>	DD	0.35	0.69	2	DD	24.15	19.01	186	D	1.55	185
	DN	0.29	0.40	2	DN	8.63	4.17	46	N	2.21	237
	SN	0.63	0.60	12	SN	9.15	5.08	64	M	3.57	134
		0.45	0.55	16		15.95	14.91	296		2.26	556
<i>Sergia scintillans</i>	DD	9.86	8.55	40	DD	5.12	4.41	39	D	3.69	355
	DN	6.80	5.17	51	DN	0.72	0.81	4	N	3.59	329
	SN	12.14	6.95	130	SN	3.80	2.17	27	M	2.35	151
		9.90	6.83	221		1.90	2.25	70		3.31	835
<i>Sergia gardineri</i>	DD	8.80	2.13	55	DD	5.12	4.41	17	D	11.22	964
	DN	11.74	9.23	88	DN	0.72	0.81	15	N	9.95	793
	SN	9.44	3.88	100	SN	0.56	0.45	4	M	2.67	51
		10.00	5.58	243		1.90	2.25	36		8.65	1,808
<i>Sergia bigemnea</i>	DD	2.50	2.04	16	DD	0.29	0.45	2	D	0.37	27
	DN	3.19	2.57	23	DN	0.76	0.84	4	N	1.48	116
	SN	1.67	0.95	18	SN	0.00	0.00	0	M	0.19	2
		2.35	1.85	57		0.31	0.53	6		0.64	145
<i>Sergia inequalis</i>	DD	2.01	1.76	12	DD	0.38	0.63	3	D	0.63	16
	DN	0.61	1.37	5	DN	0.57	0.56	3	N	0.76	50
	SN	0.57	0.60	6	SN	0.00	0.00	0	M	0.19	10
		0.94	1.29	23		0.31	0.52	6		0.55	76
<i>Sergia bisulcata</i>	DD	1.15	1.09	7	DD	1.03	1.19	8	D	1.04	91
	DN	1.31	1.76	9	DN	0.37	0.64	2	N	1.32	68
	SN	1.12	0.48	12	SN	0.82	0.90	6	M	1.96	38
		1.19	1.08	28		0.82	0.96	16		1.35	197
<i>Sergia tenuiremis</i>	DD	0.43	0.52	3	DD	0.77	0.97	6	D	0.93	39
	DN	0.86	1.17	6	DN	0.55	0.96	3	N	0.99	25
		0.67	0.91	9		0.70	0.91	9	M	0.73	14
										0.89	78
<i>Petalidium suspilosum</i>	DD	1.09	0.73	7	DD	1.50	2.29	10	D	1.94	53
	DN	1.30	1.09	9	DN	0.93	0.58	5	N	0.82	13
		1.21	0.90	16		1.31	1.85	15	M	2.84	22
									1.84	88	

¹DD—Deep Day tows (0-1,200 m): T18 four tows, T22 six tows.
 DN—Deep Night tows (0-1,200 m): T18 five tows, T22 three tows.
 SN—Shallow Night tows (0-400 m): T18 seven tows, T22 five tows.
 D—DAY Horizontal tows.
 N—NIGHT Horizontal tows.
 M—MOON Horizontal tows.

TABLE 4.—Feeding chronology of sergestids from DSB III.

Species	DAY (Tow no. 1-3, 12)				NIGHT (Tow no. 5-10)			
	Number examined	Empty (%)	Content ¹	Digestion ¹	Number examined	Empty (%)	Content ¹	Digestion ¹
<i>Sergestes atlanticus</i>	0	—	—	—	2	0	1.5	3.5
<i>Sergestes erectus</i>	12	17	3.7	3.9	38	26	3.3	3.8
<i>Sergestes armatus</i>	11	82	4.8	4.7	20	65	3.7	4.3
<i>Sergestes vigilax</i>	0	—	—	—	1	100	5.0	5.0
<i>Sergestes orientalis</i>	1	100	5.0	5.0	1	0	3.0	4.0
<i>Sergestes sargassi</i>	0	—	—	—	10	30	3.5	4.0
<i>Sergestes pectinatus</i>	0	—	—	—	9	22	2.7	3.6
<i>Sergia fulgens</i>	2	50	4.0	4.5	6	67	4.1	4.2
<i>Sergia scintillans</i>	0	—	—	—	28	18	2.8	3.8
<i>Sergia gardineri</i>	3	67	3.7	4.1	8	37	3.2	4.2
<i>Sergia bigemnea</i>	2	0	3.0	4.0	76	11	3.0	3.6
<i>Sergia inequalis</i>	0	—	—	—	1	0	4.0	3.5
<i>Sergia bisulcata</i>	2	0	3.2	4.0	5	20	3.0	3.6
<i>Sergia tenuiremis</i>	1	100	5.0	5.0	0	—	—	—
Total sample	34	62	4.1	4.2	205	22	3.1	3.7

¹See text.

depths, but seldom in numbers greater than five or six for a 3-h tow. The average population density estimated from all horizontal tows was 1.31 per 100

m². Daytime tows caught larger numbers than nighttime tows, the population density from daytime horizontal tows being 2.10 per 100 m². The

TABLE 5.—Diet of sergestids from DSB III.

Number of shrimp containing	<i>Sergestes atlanticus</i>	<i>Sergestes erectus</i>	<i>Sergestes armatus</i>	<i>Sergestes vigilax</i>	<i>Sergestes orientalis</i>	<i>Sergestes sargassi</i>	<i>Sergestes pectinatus</i>	<i>Sergia tulgens</i>	<i>Sergia scintillans</i>	<i>Sergia gardineri</i>	<i>Sergia bigemnea</i>	<i>Sergia inequalis</i>	<i>Sergia bisulcata</i>	<i>Sergia tenuiremis</i>
Calanoid copepods	1	27	6			3	7	1	7	2	23	1		
<i>Pleuromamma</i> ¹	1	8	1			1	5		2		3			
Cyclopoid copepods									3		6			
Amphipods	1	3	3					1	3		6		1	
Ostracods					1			1	1	1	15		2	
Euphausiids		1	1			1							1	
Decapod larvae			1						1	1	1		1	
Bivalve larvae	1							1	18	1	16		1	
Foraminifera								3	10	2	4		1	
Chaetognath spines											3			
Unidentified crustacea		19	1			3	3	1	17	3	33		3	
Fibrous matter									5		2		1	
Other ²	1	1						1	5	1	4			
Empty		17	29	1	1	3	2	2	5	13	11		1	3
Total number examined	3	62	41	1	2	10	12	9	35	19	88	1	8	3

¹Included with calanoid copepods.

²Including gastropod larvae, radiolarians, pteropods, fish eggs, and fish scales.

TABLE 6.—Numbers of Hawaiian sergestids captured, 1970-73.

Half-red species	
<i>Sergestes atlanticus</i> Milne-Edwards	546
<i>Sergestes cornutus</i> Krøyer	17
<i>Sergestes erectus</i> Burkenroad	1,371
<i>Sergestes armatus</i> Krøyer	1,113
<i>Sergestes vigilax</i> Stimpson	271
<i>Sergestes orientalis</i> Hansen	1,030
<i>Sergestes tantillus</i> Burkenroad	21
<i>Sergestes consobrinus</i> Milne	647
<i>Sergestes sargassi</i> Ormann	497
<i>Sergestes pectinatus</i> Sund	1,541
<i>Sergia tulgens</i> (Hansen)	1,118
<i>Sergia scintillans</i> (Burkenroad)	1,610
All-red species	
<i>Sergia gardineri</i> (Kemp)	3,096
<i>Sergia bigemnea</i> (Burkenroad)	398
<i>Sergia inequalis</i> (Burkenroad)	149
<i>Sergia bisulcata</i> (Wood-Mason)	350
<i>Sergia maxima</i> (Burkenroad)	2
<i>Sergia tenuiremis</i> (Krøyer)	147
<i>Petalidium suspiciosum</i> Burkenroad	170

September 1972 oblique series gave a figure of 3.79 per 100 m², and the May 1973 oblique series yielded 0.88 per 100 m²; these figures are probably close to the maximum and minimum population density.

Recruitment was highest during the third quarter (July-September), the only time of year when immature shrimp less than 4 mm CL were taken. The largest shrimp were most abundant during the second quarter (April-June).

Diet (Table 5)

Only three individuals examined had recognizable stomach contents: a calanoid copepod (*Pleu-*

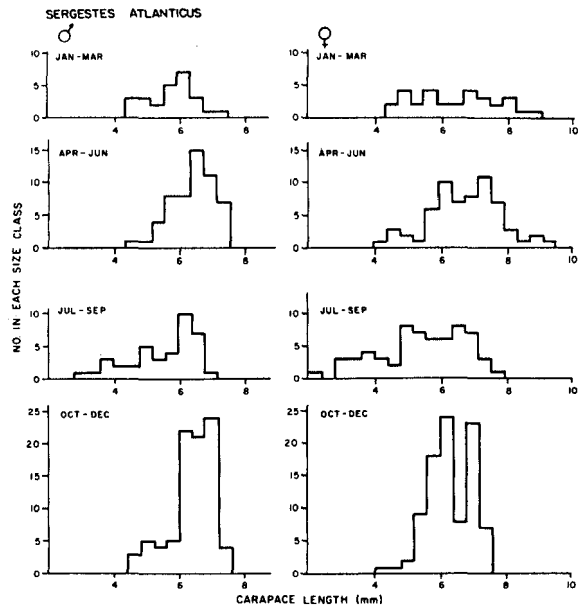


FIGURE 2.—Quarterly size-frequency distribution of *Sergestes atlanticus*.

romamma), an amphipod, and fragments of larval bivalve shells.

Sergestes cornutus Krøyer 1855

Vertical Distribution

Only four individuals were captured in horizon-

tal closing tows; these were all daytime tows between 450 and 550 m. Several were captured in 0- to 400-m oblique night tows, indicating that *S. cornutus* is a vertical migrator. Donaldson (1975) found *S. cornutus* mostly in the upper 50 m at night.

Population structure and diet were not studied because of the small sample size.

Sergestes erectus Burkenroad 1940

Vertical Distribution (Figure 3)

Sergestes erectus was abundant in our collection, but nearly half of the shrimp came from daytime tows of the November 1972 cruise. The daytime vertical range was about 550 to 800 m, with maximum catches between 625 and 750 m. Immature shrimp did not occur below 750 m. The nighttime range varied with size. Small immature shrimp less than 12 mm CL occurred between the surface and 200 m, mostly below 125 m. Intermediate-sized shrimp between 12 and 16 mm CL, including immature and newly mature shrimp, ranged between 150 and 250 m. Adult shrimp larger than 16 mm CL were found between 250 and 325 m. Moonlight depressed the vertical range of adults very little, although there were some cap-

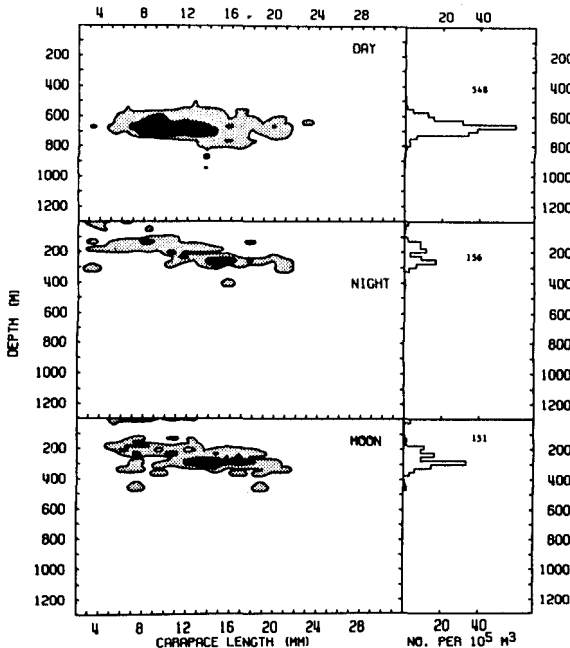


FIGURE 3.—Vertical distribution of *Sergestes erectus*.

tures in the 350- to 475-m range; immatures were found between 175 and 250 m. The peak in the upper 25 m is a sampling artifact. There was no positive evidence of full moon nonmigration in the horizontal samples, but the December 1970 cruise took a dozen shrimp in the 575- to 700-m range, suggesting that about 20-30% of the population was not migrating.

Population Size, Growth, and Reproduction (Figure 4)

Sergestes erectus was the second most abundant species in the horizontal series, the average population density estimated from all horizontal tows amounting to 3.81 per 100 m². Like *S. atlanticus*, it was taken in larger numbers during the daytime than at night, the population density estimated from daytime horizontal tows amounting to 5.55 per 100 m². These numbers reflect its extreme abundance during the November 1972 cruise, when as many as 157 were taken in a single 3-h tow. The oblique series of September 1972 and

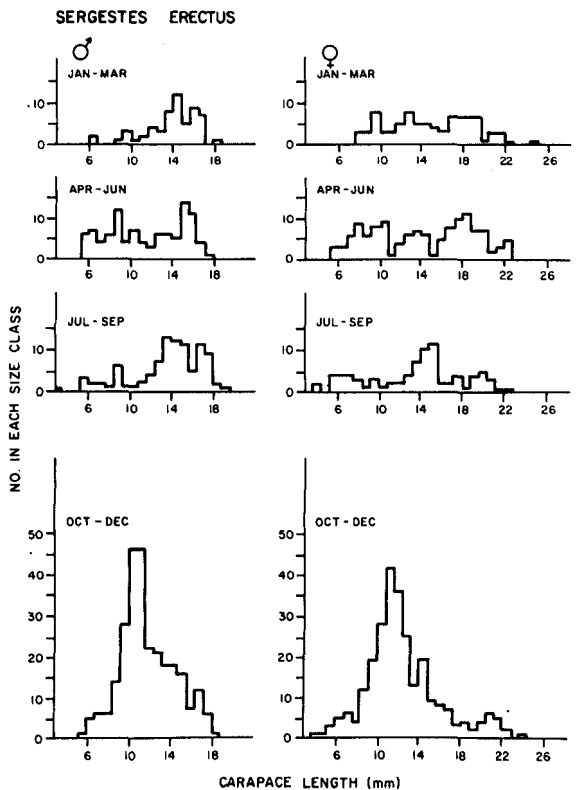


FIGURE 4.—Quarterly size-frequency distribution of *Sergestes erectus*.

May 1973 yielded figures of 5.85 and 1.97 per 100 m², respectively.

Recruitment was not noticeably high during any particular quarter. However, medium-sized shrimp in the 10- to 14-mm CL range were significantly more abundant during the fourth quarter (October-December) than at other times of the year (Kolmogorov-Smirnov test, $P < 0.05$).

Diet (Table 5)

Calanoid copepods made up the bulk of the stomach contents of the *S. erectus* from DSB III. A few amphipods and a single euphausiid were also found. One individual had some material very tentatively identified as a small fish, the only one found in the DSB III collection. No food items in the 0.4- to 0.6-mm size range were found.

Sergestes armatus Kröyer 1855

Vertical Distribution (Figure 5)

The daytime vertical distribution of *S. armatus* varied somewhat with size. Immature shrimp ranged between 450 and 600 m; adults were generally between 550 and 650 m, but sometimes as shallow as 450 m. One tow in November 1972 took 13 shrimp at about 675 m. The December 1970

cruise took nine shrimp in open tows below 800 m; most of these were probably contaminants. The nighttime range also varied with size; shrimp smaller than 8 mm CL usually occurred between 100 and 200 m, while adults were found mostly between 150 and 300 m, with occasional captures as deep as 450 m. Moonlight did not depress the vertical distribution of *S. armatus*. The peak in the upper 25 m is a sampling artifact. The open tows of the December 1970 and December 1973 cruises took small to moderate numbers of *S. armatus* at the daytime depth. If these shrimp were not contaminants, they suggest that about 5-20% of the December 1973 population was not migrating.

Population Size, Growth, and Reproduction (Figure 6)

Sergestes armatus was abundant in the horizontal series, the average population density of 2.35 per 100 m² estimated from all horizontal tows making it the fourth most abundant sergestid. The catch was even greater during the September 1972 oblique series, which yielded a figure of 10.22 per 100 m², second only to *S. pectinatus*. The May 1973 oblique series took much smaller numbers, amounting to only 1.51 per 100 m².

Recruitment was much higher during the second quarter (April-June) than during the rest of the year. Large individuals were most abundant during the fourth quarter (October-December).

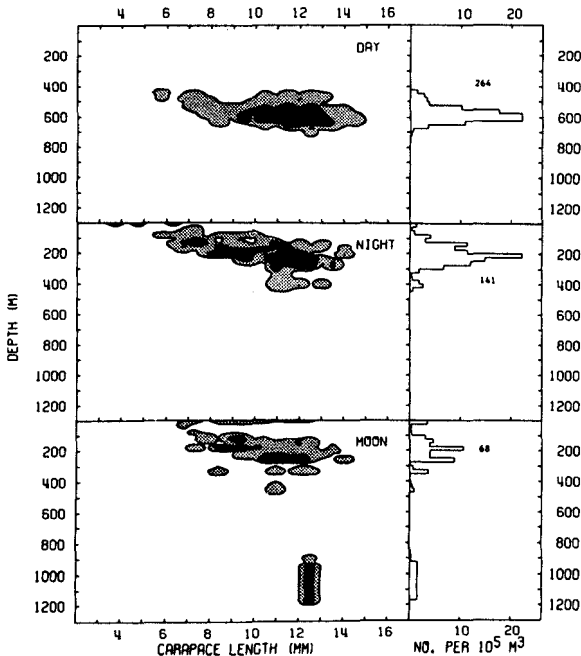


FIGURE 5.—Vertical distribution of *Sergestes armatus*.

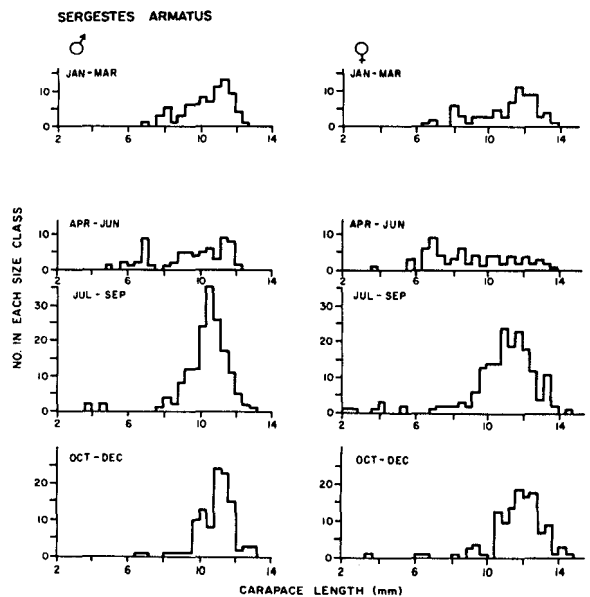


FIGURE 6.—Quarterly size-frequency distribution of *Sergestes armatus*.

Diet (Table 5)

DSB III took over 40 *S. armatus*, but two-thirds had empty stomachs. Food items included calanoid copepods, amphipods, an euphausiid, and an unidentified decapod larva. Prey in the 0.4- to 0.6-mm size range, such as foraminifera or bivalve larvae, were not found.

Sergestes vigilax Stimpson 1860

Vertical Distribution (Figure 7)

The daytime vertical range of *S. vigilax* was about 550 to 725 m, with a concentration at about 675 m. Nighttime captures were all in the 0- to 200-m depth range, peaking at about 50-75 m. Moonlight depressed the peak to 150-200 m, but some individuals remained shallower. There was no evidence of full moon nonmigration.

Population Size, Growth, and Reproduction (Figure 8)

Sergestes vigilax was not abundant in Hawaiian waters. The average population density estimated from all horizontal tows was only 0.35 per 100 m². Daytime catches were larger than night catches, the population estimate from the day tows being

0.52 per 100 m². The oblique series of September 1972 and May 1973 took larger numbers, yielding estimates of 3.57 and 0.61 per 100 m², respectively. These larger population sizes may indicate that the finer mesh of the IKMT sampled *S. vigilax*, a relatively small species, more efficiently than did the MT used for the horizontal tows.

The seasonal size-frequency histograms are not significantly different from one another. Shrimp less than 5 mm CL were most abundant in the third quarter (July-September).

Diet (Table 5)

Only a single individual was examined; it had an empty stomach.

Sergestes orientalis Hansen 1919

Vertical Distribution (Figure 9)

The daytime vertical distribution of *S. orientalis* varied with size; small shrimp less than 6.5 mm CL were taken from 450 to 575 m, while larger ones were found between 500 and 625 m, mostly between 550 and 600 m. The nighttime range was from the surface to 125 m, with largest numbers in the 25- to 50-m and 75- to 100-m zones. Small shrimp less than 6 mm CL stayed above 75 m. Moonlight depressed most of the nighttime

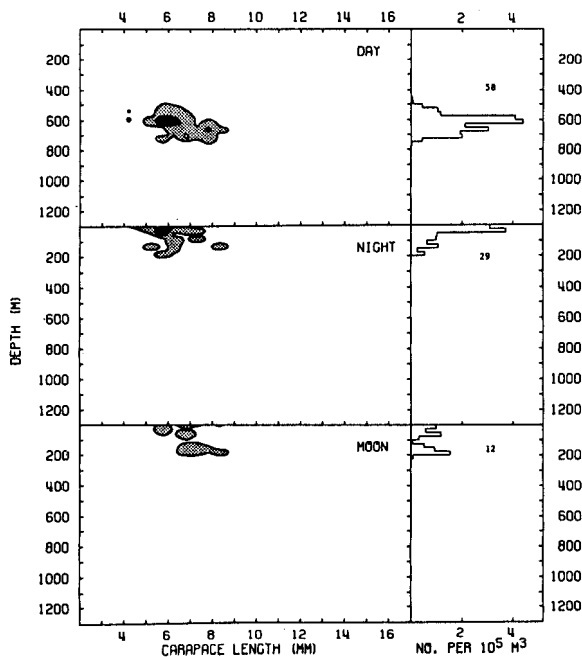


FIGURE 7.—Vertical distribution of *Sergestes vigilax*.

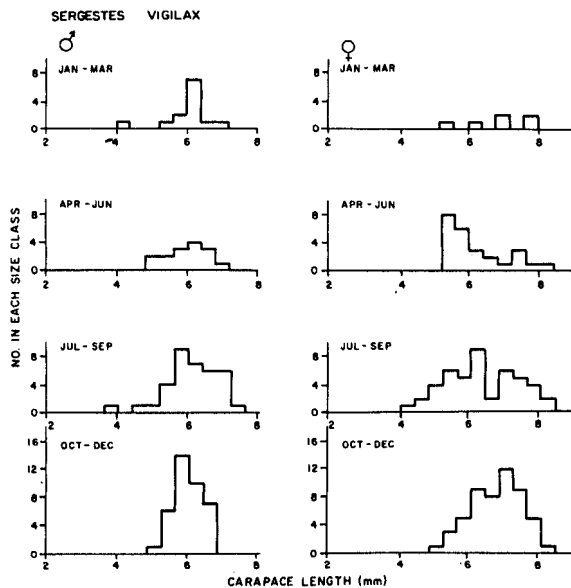


FIGURE 8.—Quarterly size-frequency distribution of *Sergestes vigilax*.

population into the 100- to 200-m range, although some remained shallower. A few nighttime captures were made in the daytime depth range. The December 1970 cruise took large numbers near full moon at 550-600 m (up to 40), and also at 150-200 m (up to 21). Apparently at least 50% of the population was not migrating. Later in the cruise, when the moon was waning, large numbers of *S. orientalis* were taken in tows between 30 and 120 m (up to 70). There was no evidence of full moon nonmigration during the December 1973 cruise.

Population Size, Growth, and Reproduction (Figure 10)

Sergestes orientalis was moderately abundant in Hawaiian waters. The average population density estimated by all the horizontal tows was 1.32 per 100 m², daytime and night tows giving similar figures. The oblique series of September 1972 yielded a higher figure of 8.43 per 100 m², *S. orientalis* being the second most abundant species in the shallow night tows. On the other hand, it was much scarcer during the oblique series of May 1973, which gave a population density of only 0.64 per 100 m². *Sergestes orientalis* was particularly abundant during the December 1970 cruise, when as many as 70 were taken in a single 3-h IKMT tow.

The seasonal size-frequency histograms are all very similar to one another. Shrimp smaller than 6 mm CL were proportionally most abundant during the first quarter (January-March), but the difference was not statistically significant (Kolmogorov-Smirnov test, $P > 0.05$).

Diet (Table 5)

Only two individuals from DSB III were examined. One had an empty stomach; the other had eaten an ostracod.

Sergestes tantillus Burkenroad 1940

Vertical Distribution

Because of the rarity of *S. tantillus*, little can be inferred about its vertical distribution. Single shrimp were taken in daytime tows between 410 and 915 m. The largest night catch was at 50 m (four shrimp), with individual captures to about 200 m. A tow between 635 and 715 m on a moonlit night took six shrimp.

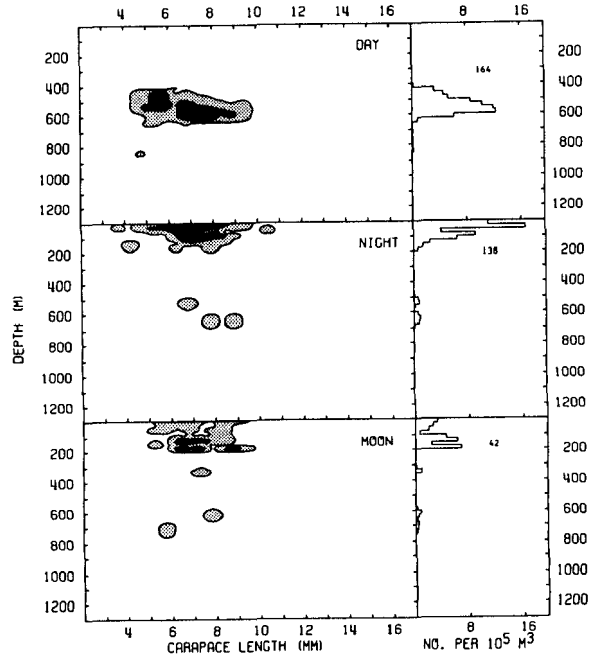


FIGURE 9.—Vertical distribution of *Sergestes orientalis*.

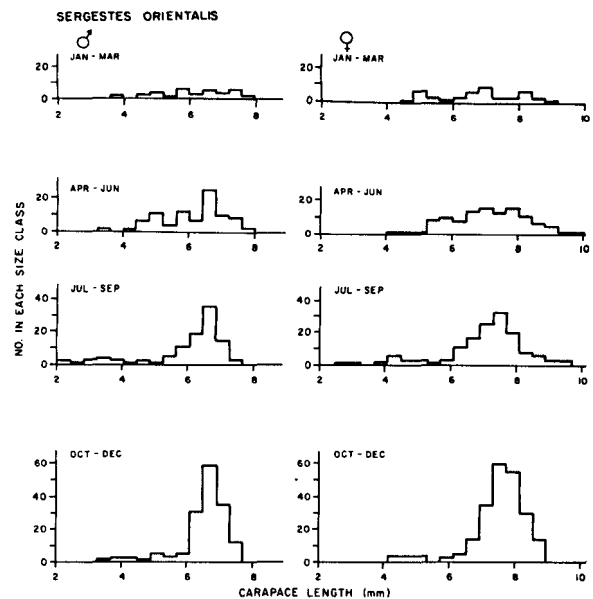


FIGURE 10.—Quarterly size-frequency distribution of *Sergestes orientalis*.

Growth, reproduction, and diet were not studied because of the small sample size.

Sergestes consobrinus Milne 1968

Vertical Distribution (Figure 11)

Nearly two-thirds of the captures during the Teuthis series were from shallow night tows during the May 1973 cruise (Teuthis XXI); it was also fairly abundant in the oblique series of September 1972 and May 1973 (Teuthis XXII).

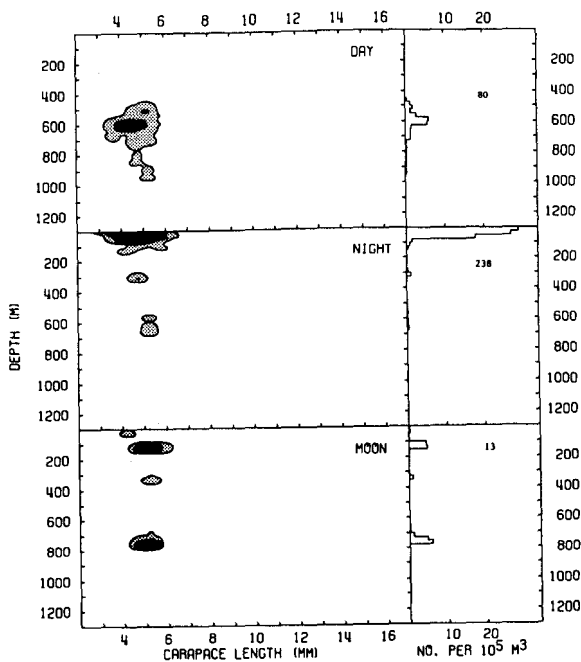


FIGURE 11.—Vertical distribution of *Sergestes consobrinus*.

Sergestes consobrinus was broadly distributed during the daytime, from 450 to 725 m. The population maximum appeared to be around 600 m, but most daytime catches were small. A few captures were made between 800 and 950 m; these may have been contaminants. The nighttime distribution showed a broad peak from the surface to 75 m, with lesser numbers to 125 m. These numbers were strongly influenced by the May 1973 captures. Moonlight depressed most of the population to 100-150 m, with a substantial number remaining at the daytime depth. The December 1970 cruise took *S. consobrinus* near full moon in tows between 140 and 180 m, and also in a 700- to 800-m tow. Later catches when the moon was waning were in the upper 120 m, with a large catch at 30 m.

Population Size, Growth, and
Reproduction (Figure 12)

Like *S. vigilax*, *S. consobrinus* appears to have been undersampled by the MT. The average population size estimated by all horizontal tows was 1.05 per 100 m². The figure for only the night tows was 1.99 per 100 m², reflecting the large night catches of the May 1973 cruise (Teuthis XXI)—up to 76 in a single 3-h tow. The oblique IKMT series of September 1972 and May 1973 (Teuthis XXII) yielded higher figures of 5.42 and 2.08 per 100 m², respectively, presumably because the finer mesh of the IKMT retained more of the small shrimp.

The seasonal size-frequency histograms show a maximum proportion of small individuals in the third quarter (July-September). The largest shrimp were taken in the first and second quarters, although first quarter catches were small.

Diet was not examined, since none were taken during DSB III.

Sergestes sargassi Ortmann 1893

Vertical Distribution (Figure 13)

With the possible exception of *S. cornutus*,

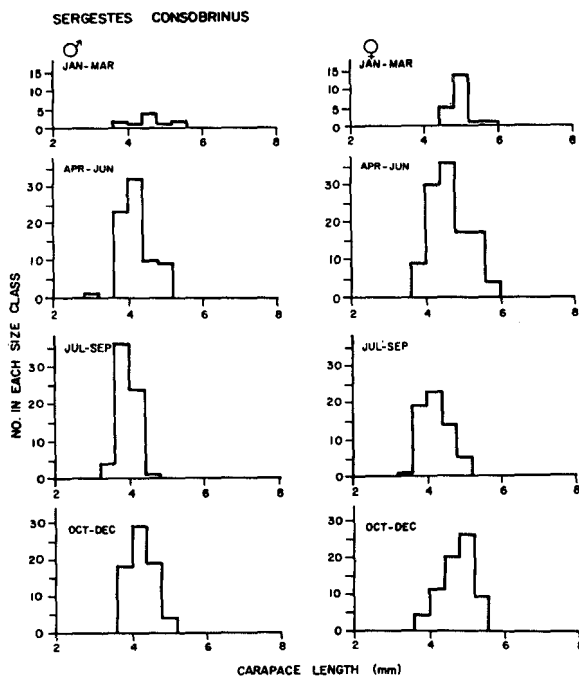


FIGURE 12.—Quarterly size-frequency distribution of *Sergestes consobrinus*.

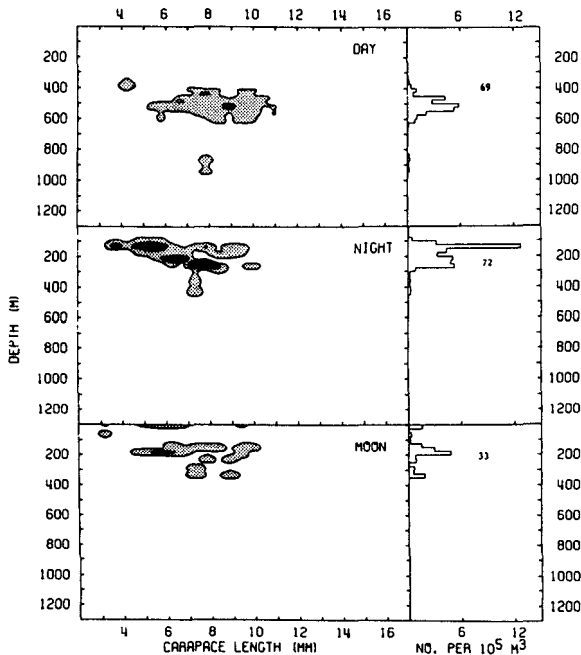


FIGURE 13.—Vertical distribution of *Sergestes sargassi*.

which is very rare in Hawaiian waters, *S. sargassi* had the shallowest daytime range of the local species: 450-575 m, with a maximum around 475 m. No significant variation of depth with size was noted, perhaps because of the small number caught. One immature shrimp was captured between 340 and 425 m, and oblique tows from the surface to about 350 m took a few immature specimens in September 1972. There was a pronounced variation of size with depth at night. Immature individuals less than 6 mm CL occurred between 100 and 200 m, mostly in the 125- to 150-m range. Larger shrimp were found from 125 to 300 m, mostly from 225 to 275 m. Most of the adults captured at night were males; the few females were mostly taken between 125 and 175 m. This apparent segregation by sex was probably a sampling artifact, since the December 1970 cruise took both males and females in tows from 250 to 300 m. Moonlight had little effect on the depth range of adults; immature individuals were depressed to about 150-200 m. The peak in the upper 25 m is a sampling artifact. There was no evidence of full moon nonmigration.

Population Size, Growth, and Reproduction (Figure 14)

Sergestes sargassi was not very abundant in the

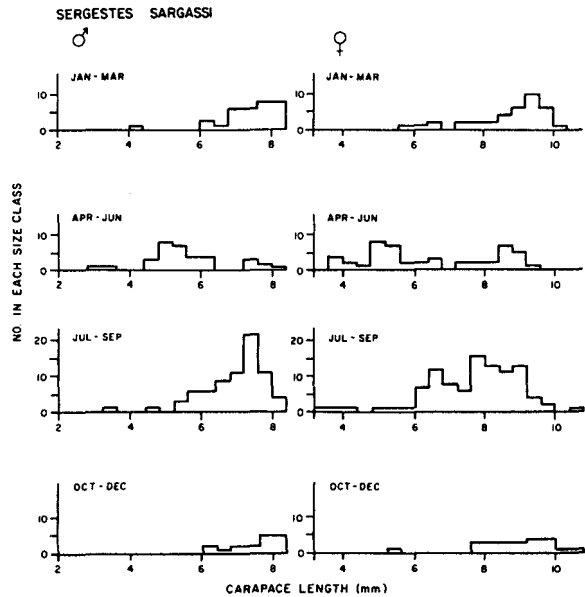


FIGURE 14.—Quarterly size-frequency distribution of *Sergestes sargassi*.

horizontal collections, the estimated average population density being only 0.70 per 100 m². The night tows gave a higher total than the daytime tows, 1.07 and 0.64 per 100 m², respectively. The two IKMT oblique series of September 1972 and May 1973 produced higher estimates, 5.84 and 1.74 per 100 m², respectively; the daytime figure of 10.37 per 100 m² in September was the third highest such total for that cruise. These higher figures for the IKMT tows were not the result of more efficient filtering, as appears to be the case for the smaller species, since *S. sargassi* is a moderately large species, about the same size as *Sergia scintillans* and *Sergia gardineri*, neither of which showed any signs of significant undersampling by the MT.

Recruitment was highest during the second quarter (April-June), when nearly 70% of the population was immature. Growth during the summer was about 1.0-1.3 mm CL per month, slowing during the third and fourth quarters to 0.2-0.5 mm CL per month. Maximum sizes were attained in December and the first quarter (January-March).

Diet (Table 5)

DSB III took 10 *S. sargassi*. Three had empty stomachs. The rest had eaten zooplanktonic

crustacea, including calanoid copepods and a euphausiid.

Sergestes pectinatus Sund 1920

Vertical Distribution (Figure 15)

The daytime range of *S. pectinatus* was broad, extending from 425 to 725 m. The peak at 425-450 m came from a single tow in the June 1971 cruise, and the peak at 650-675 m was also from a single tow in the November 1972 cruise. Most large catches centered around 575 to 625 m. There was a poorly defined size-depth trend. Small shrimp less than 4 mm CL seldom occurred below 600 m, while the very large females seldom occurred above 550 m. At night the size-depth trend was pronounced. Males less than 3.5 mm CL were found in the upper 100 m, mostly between 25 and 75 m. From 4 to 5 mm CL, maximum catches were in the 75- to 250-m range, peaking around 150 m. The largest males were taken in the 200- to 275-m range. Females showed a similar trend; maximum catches of shrimp less than 4.5 mm CL occurred around 50 m, increasing to 150 m for shrimp between 4.5 and 6 mm CL, and 200 m for shrimp larger than 6 mm CL. A few shrimp were taken below 300 m; these may have been contaminants. The moon depressed

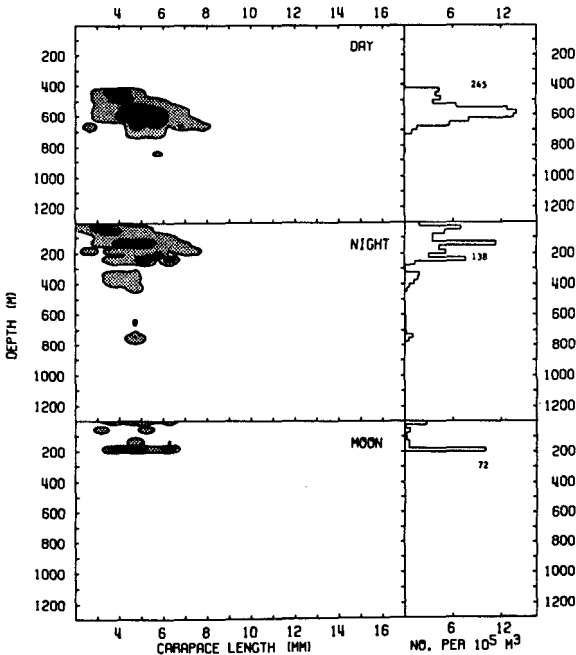


FIGURE 15.—Vertical distribution of *Sergestes pectinatus*.

most of the population to about 150-250 m. The peak in the upper 25 m is a sampling artifact. None of the Teuthis samples showed any indications of full moon nonmigration. The December 1970 cruise took 14 specimens in three open tows between 400 and 600 m, probably representing less than 10% of the population.

Population Size, Growth and Reproduction (Figure 16)

Sergestes pectinatus appeared to be significantly undersampled by the MT. The average population density estimated by all horizontal tows was 1.71 per 100 m². The IKMT with its finer mesh captured many more shrimp than the MT. *Sergestes pectinatus* was the most abundant sergestid in the September 1972 oblique series, which yielded a population density estimate of 26.67 per 100 m². The shrimp from this cruise composed nearly 40% of the entire catch of *S. pectinatus*. The May 1973 series gave a figure of 4.70 per 100 m², second only to *S. fulgens*. In both cases, the average size of an individual was considerably smaller than in a typical MT tow. Interpretation of the size-frequency histograms is complicated by the undersampling problem. For *S. pectinatus* only, data from the May 1973 oblique series were added to the second quarter horizontal data. This means

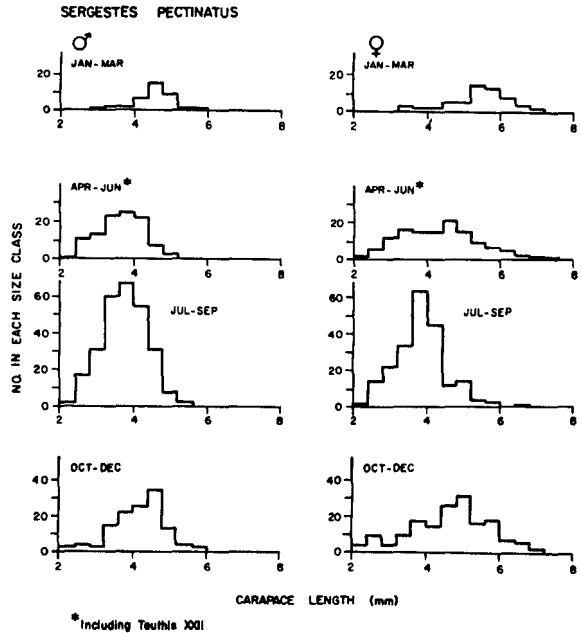


FIGURE 16.—Quarterly size-frequency distribution of *Sergestes pectinatus*. April-June quarter includes data from Teuthis XXII.

that IKMT data were included in three of the four quarters, only the first quarter (January-March) lacking IKMT data. Small shrimp were proportionately most abundant during the third quarter (July-September), and large shrimp were most abundant during the first quarter, although lack of IKMT data probably affected the shape of the first quarter histogram.

Diet (Table 5)

Seven of the twelve shrimp from DSB III had eaten calanoid copepods, mostly *Pleuromamma* spp.

Sergia fulgens (Hansen 1919)

Vertical Distribution (Figure 17)

Because of the peculiar fluctuations in abundance during the course of the sampling program, the vertical distribution patterns of *S. fulgens* derived from the data should be regarded strictly as estimates. All the daytime captures lay between 550 and 625 m; there was no variation in depth with increasing size. The open tows of the December 1970 cruise took nine specimens between 525 and 630 m. Most nighttime captures lay between 75 and 125 m for immature shrimp less than 8 mm CL, with some as shallow as 25-50 m. Nearly all the adults came from a single tow at 150-200 m; a few captures came as shallow as 75 m. Almost all of the captures near full moon came during the June 1973 cruise, which took immature shrimp between 250 and 475 m; there were three captures of adults between 150 and 325 m. The peak in the upper 25 m is a sampling artifact. The December 1970 cruise took nine adults in open tows between 160 and 300 m and one adult at 400 m. There was no evidence of full moon non-migration.

Population Size, Growth, and Reproduction (Figure 18)

Sergia fulgens fluctuated drastically in abundance during the sampling program. The first 13 cruises of the Teuthis series (Teuthis IV-XVII, February 1971-August 1972) caught a total of 13 specimens. After the September 1972 cruise it turned up in many tows, often in very large numbers. Nearly all the specimens were immature shrimp less than 10 mm CL. However, one hor-

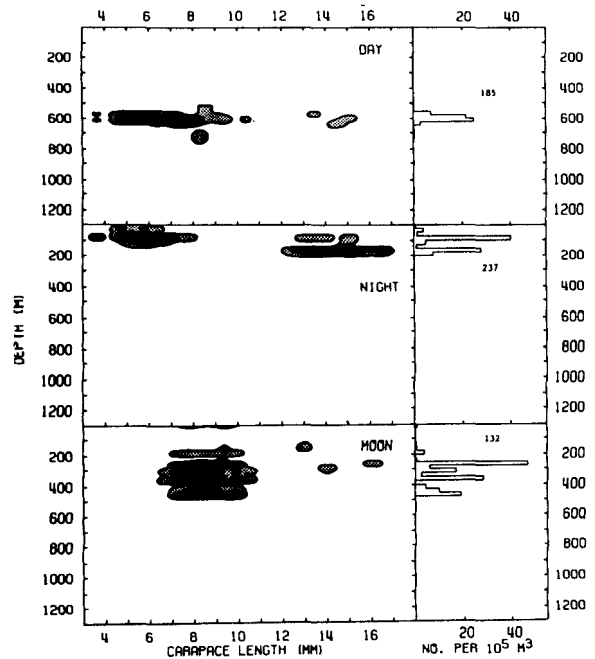


FIGURE 17.—Vertical distribution of *Sergia fulgens*.

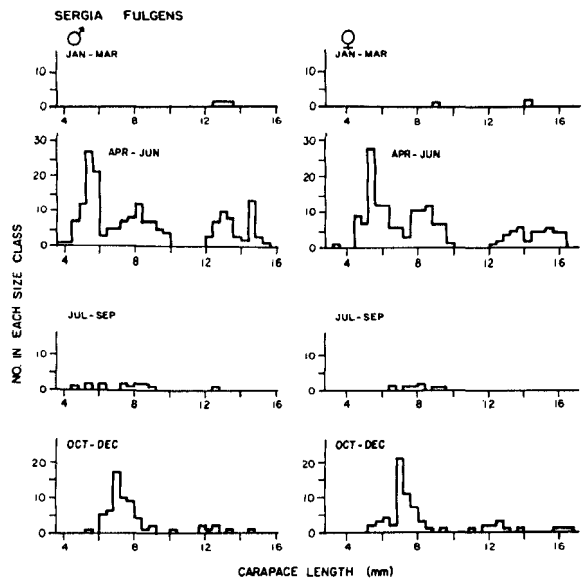


FIGURE 18.—Quarterly size-frequency distribution of *Sergia fulgens*.

izontal night tow in May 1973 took 89 adults. In addition, the December 1970 cruise caught a total of 21 *S. fulgens*; 19 of these were adults. Combining the very low numbers from the first 13 horizontal series with the very high numbers from the last 3 horizontal series gives an average population

density of 2.26 per 100 m², an estimate of doubtful meaning. The two oblique series produced very different estimates. The September 1972 cruise gave a figure of only 0.43 per 100 m², making *S. fulgens* the least abundant of the 16 regularly occurring species. On the other hand, the May 1973 cruise gave a figure of 15.95 per 100 m², more than 3 times greater than any other species, and 37 times the September figure.

The seasonal size-frequency histograms reflect the fact that nearly all *S. fulgens* were caught in the second and third quarters. The second quarter (April-June) histogram is trimodal. The peaks at 5.5 and 8 mm CL represent the same cohort as sampled in May and June (the *Teuthis* XXII oblique series of late May took 6.5-mm shrimp), giving a growth rate of 2.1-2.2 mm CL per month for immature shrimp in this size range. The assumption that the peak at 13-15 mm in May is the same cohort as the peak at 7.5 mm from the preceding November yields a growth rate of 1.0-1.2 mm CL per month, reflecting a slowing of the growth rate as the shrimp approach maturity. The presence of large numbers of immature shrimp in the second and fourth quarters implies that *S. fulgens* either has a very broad spawning period or has two widely separated spawning peaks.

Diet (Table 5)

DSB III took nine *S. fulgens*. Seven of these had food in their stomachs, including a calanoid copepod, an amphipod, and an ostracod, plus smaller prey including larval bivalve and foraminifera.

Sergia scintillans (Burkenroad 1940)

Vertical Distribution (Figure 19)

The vertical distribution of *S. scintillans* showed a slight tendency for smaller shrimp to live deeper than larger ones, both day and night. Daytime ranges were about 575 to 700 m for individuals less than 7 mm CL and 525 to 650 m for those larger than 7 mm CL, with maximum catches between 575 and 625 m. The small peak at 325-350 m resulted from two shrimp taken in a tow that dipped as deep as 480 m; they were probably captured at the deep end of the tow. At night the adults were mostly between 25 and 125 m, but immature shrimp less than 6 mm CL ranged

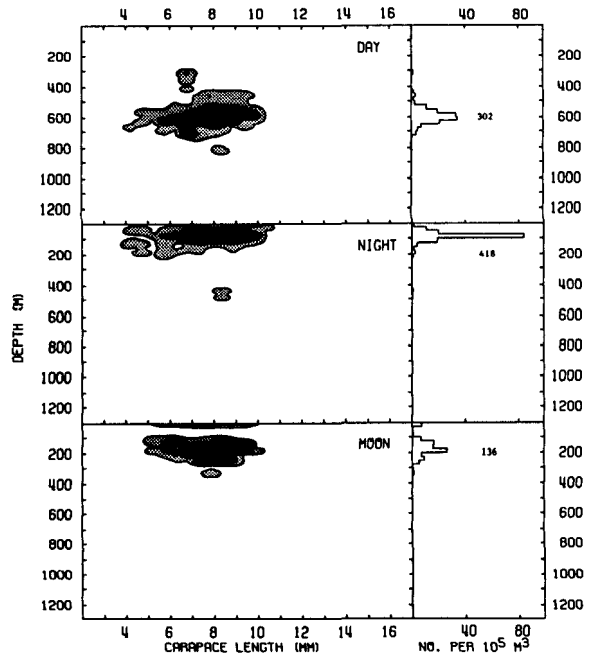


FIGURE 19.—Vertical distribution of *Sergia scintillans*.

between 50 and 225 m. Although the population was centered at 100-125 m for both sexes, few males occurred shallower than 50 m. Three shallow tows from the May 1973 cruise that caught 40 females and 12 males are primarily responsible for this difference. Moonlight depressed the depth of most of the population to 100-275 m, peaking around 200 m. The peak in the upper 25 m is a sampling artifact. There was no evidence of full moon nonmigration.

Population Size, Growth, and Reproduction (Figure 20)

Sergia scintillans was one of the most abundant sergestids in Hawaiian waters. The average population density estimated by all horizontal tows was 3.31 per 100 m², the daytime and nighttime figures being similar. It was particularly abundant in the shallow night tows of the May 1973 cruise (*Teuthis* XXI), one 3-h tow taking 179 shrimp. The oblique series of September 1972 and May 1973 (*Teuthis* XXII) produced figures of 9.90 and 3.70 per 100 m², respectively.

Small shrimp were proportionally most abundant in the third quarter (July-September). First and second quarter populations were similar in size-frequency, although the larger females occurred in the second quarter (April-June).

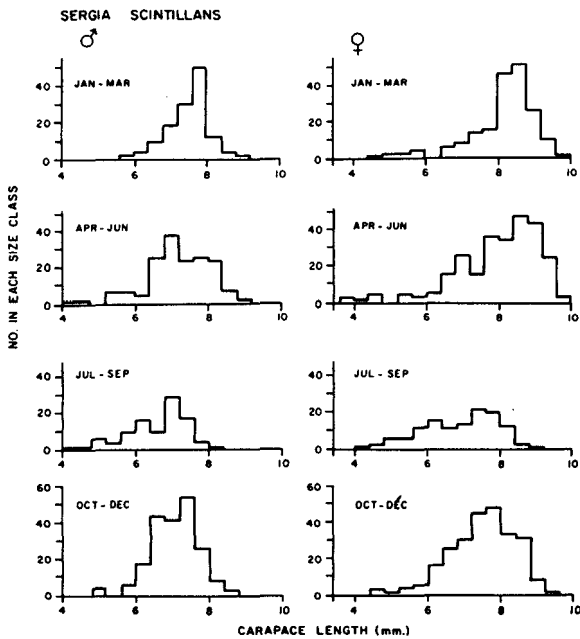


FIGURE 20.—Quarterly size-frequency distribution of *Sergia scintillans*.

Diet (Table 5)

The DSB III material showed that *S. scintillans* ate the usual variety of zooplanktonic crustacea, including calanoid copepods, amphipods, and an ostracod. The 0.4- to 0.6-mm size fraction was also taken; bivalve larvae, foraminifera, and cyclopoid copepods were found in many individuals. Other food items included the large cyclopoid copepod *Sapphirina*, a larval decapod, and masses of an unidentified greenish, fibrous material.

Sergia gardineri (Kemp 1913)

Vertical Distribution (Figure 21)

Sergia gardineri was usually found between 650 and 775 m during the daytime, although shrimp smaller than 5 mm CL seldom occurred below 700 m. The extremely high values in this range were largely due to the catches of the November 1972 cruise. On certain occasions the population seemed to extend downward to at least 1,200 m. The June 1973 cruise took 59 specimens in three tows between 850 and 1,050 m, and only 8 specimens in four tows between 650 and 850 m. The December 1970 cruise caught only nine specimens in an open tow at 650-680 m, but tows below 800 m caught

large numbers, including 77 in a tow from 1,150 to 1,250 m. On the other hand, all four daytime tows on the May 1972 cruise between 650 and 950 m took only one shrimp.

The nighttime distribution was strongly influenced by large catches from the May 1973 cruise. It showed a concentration in the upper 150 m, with shrimp less than 6 mm CL restricted to 25-100 m. All large shrimp in the upper 25 m were females, the result of a single tow in May 1973 that fished between 15 and 45 m, taking 36 adult females and 1 very small male. A tow at 20 m on the same cruise took no *S. gardineri*, indicating that this species probably does not reach the surface. There were a few captures below the normal range on moonless nights, notably a 250-m tow in September 1971 that took four, and a 480- to 550-m tow in November 1972 that took five.

Most captures of *S. gardineri* on nights with much moonlight were at the daytime depth, except for the March 1971 cruise, which took 16 shrimp at 320-340 m and 20 shrimp at 100-150 m, although a tow at 170-200 m did not take any. Three open tows near full moon on the December 1970 cruise took 207 *S. gardineri* between 700 and 1,000 m, while a 550- to 600-m tow took 9. Later in the cruise when the moon was waning, they were captured at 80 and 30 m (but not at 100-110 or 50 m!). The

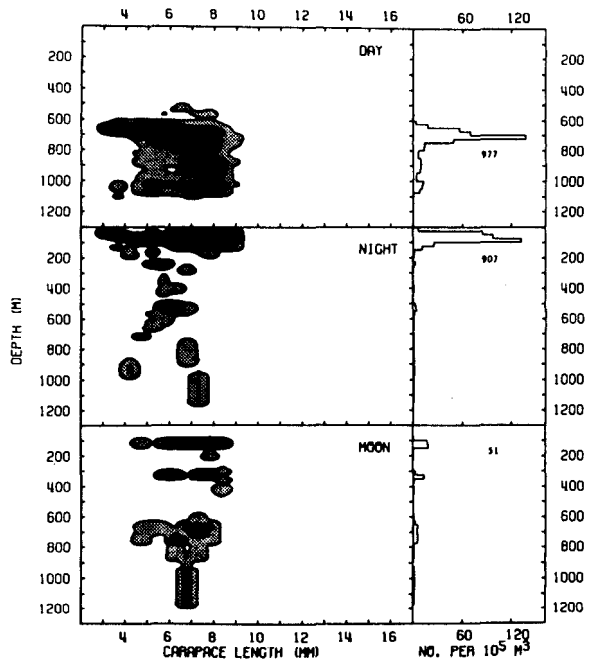


FIGURE 21.—Vertical distribution of *Sergia gardineri*.

December 1973 cruise took only two immature specimens at night in 10 oblique tows less than 650-m maximum depth. Six oblique tows from 400 to 1,200 m took a total of 62 shrimp, although high seas resulted in some catch spillage in two cases. *Sergia gardineri* clearly does not migrate near full moon.

Population Size, Growth, and Reproduction (Figure 22)

Sergia gardineri was by far the most numerous sergestid in the Teuthis collections, the average population density of 8.65 per 100 m² estimated from all horizontal tows being more than twice as high as the next most abundant species. Horizontal tows taking more than 100 shrimp occurred in February 1971 (night), June 1971 (day and night), November 1972 (day), and May 1973 (night). In addition, the open tows of the December 1970 cruise took large numbers, including 129 in a night tow. *Sergia gardineri* appeared to have been much less abundant during the first half of 1972, although most of these cruises occurred near full moon, when the normal vertical distribution patterns seem to be disrupted. The estimate from night tows affected by moonlight, 2.66 per 100 m², was much lower than the daytime or moonless night estimates. The oblique series of September

1972 and May 1973 gave figures of 10.00 and 1.90 per 100 m², respectively.

Recruitment was highest during the third quarter (July-September), although small shrimp began to enter the population in June. The median carapace length increased from 4.9 mm to 6.4 mm between the September 1972 and November 1972 cruises, giving a growth rate of about 1.2 mm CL per month. From November to May the growth rate was much lower, about 0.25 mm CL per month. The average size of females was largest in May, although a few very large females were still present in June. *Sergia gardineri* has a total life span of about 1 yr.

Diet (Table 5)

Thirteen of the nineteen specimens of *S. gardineri* taken during DSB III had empty stomachs. The others contained calanoid copepods, an ostracod, a larval decapod, bivalve larvae, foraminifera, and greenish fibrous matter.

Sergia bigemnea (Burkenroad 1940)

Vertical Distribution (Figure 23)

Most of the few daytime captures of *S. bigemnea* during the Teuthis series were of immature shrimp less than 8 mm CL. A tow between 610 and 690 m took 15 in July 1971; 5 were caught in November 1972 in a tow probably around 750 m. The peak around 1,100 m resulted from two tows that fished as shallow as 820 m. Two of the three daytime captures of adults during the Teuthis series were between 1,000 and 1,100 m; the other was around 750-850 m. The December 1970 cruise took 20 adults in open tows between 800 and 1,200 m. The nighttime distribution varied with size; shrimp smaller than 10 mm CL generally occurred between 50 and 225 m, while the adults ranged between 125 and 250 m. The February 1973 cruise (DSB III) took several large hauls of *S. bigemnea*, including 49 specimens in a 1-h tow at 150-175 m. Only a few were caught under moonlit conditions; most of these were between 250 and 350 m. The December 1970 cruise took 5 *S. bigemnea* at 250 m and 11 at 750 m, indicating that much of the population was not migrating.

The vertical distribution patterns of *S. bigemnea* appeared to be affected by avoidance. While the females of most sergestid species grow considerably larger than the males, in *S. bigemnea*

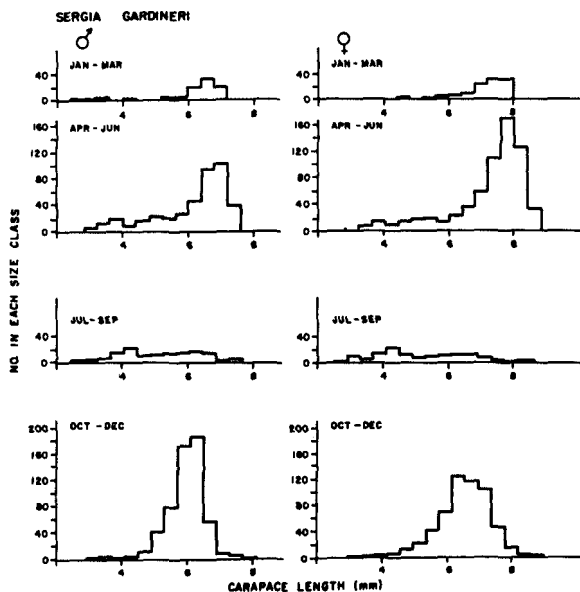
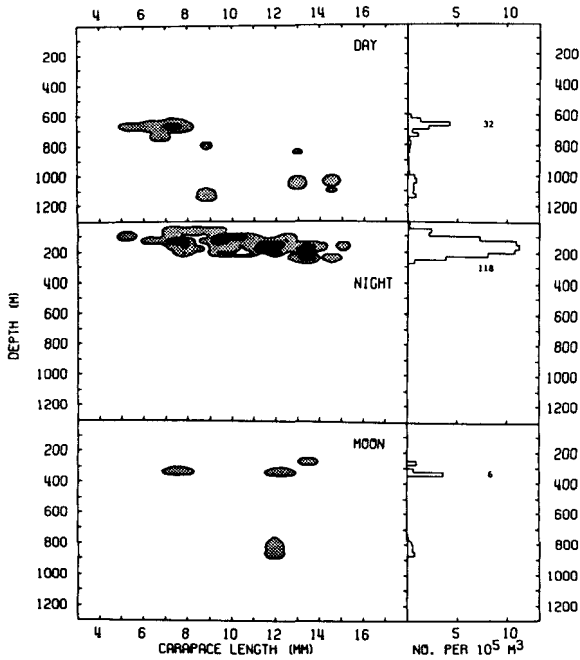


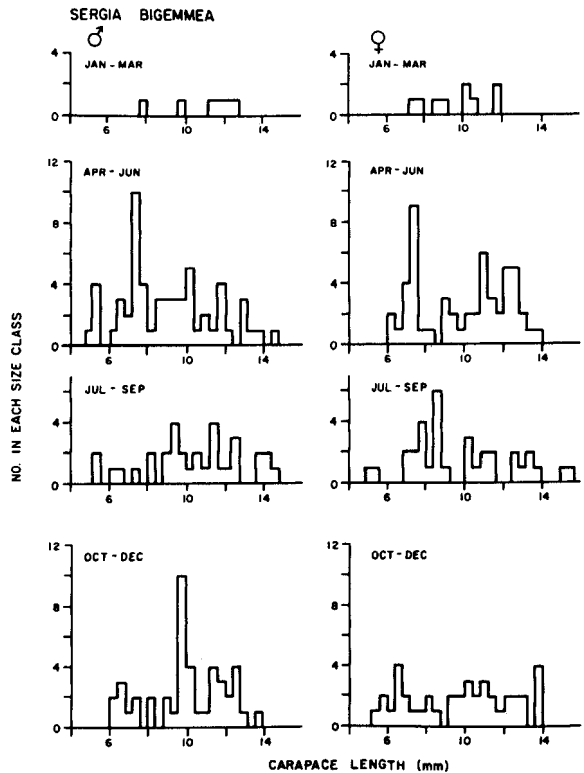
FIGURE 22.—Quarterly size-frequency distribution of *Sergia gardineri*.

FIGURE 23.—Vertical distribution of *Sergia bigemnea*.

the maximum size was the same in both sexes, suggesting that the largest shrimp were escaping capture. Daytime catches were much smaller than nighttime catches, indicating that avoidance was more effective during the day. However, the maximum size captured was the same during the daytime as at night. It is curious that neither *Sergestes erectus* nor *Sergia fulgens* showed any signs of avoidance, though those caught are larger than *S. bigemnea*; perhaps *S. bigemnea* is particularly fast for its size or better at sensing the approach of the trawl.

Population Size, Growth, and Reproduction (Figure 24)

Sergia bigemnea was one of the less common sergestids in our collection; the average population density estimated from all horizontal tows was only 0.64 per 100 m². Most catches occurred at night, the figure for nighttime tows being 1.48 per 100 m². Very few *S. bigemnea* were captured during the first half of 1972, when most sampling was done near full moon. The oblique series of September 1972 took moderate numbers, producing a population density figure of 2.35 per 100 m², higher than any other all-red sergestid except *S. gardineri*. It was also moderately abundant dur-

FIGURE 24.—Quarterly size-frequency distribution of *Sergia bigemnea*.

ing the December 1970 cruise, which had the only large daytime catch: 23 in an 800- to 900-m open IKMT tow. The largest catches of *S. bigemnea* occurred during the February 1973 cruise (DSB III) when it was the most abundant species taken, with 49 in a 1-h open tow. The May 1973 oblique series took only a handful, giving a population density estimate of 0.31 per 100 m².

None of the seasonal size-frequency histograms are significantly different from the others (Kolmogorov-Smirnov test: $P > 0.05$). Females larger than 12 mm CL were proportionately most abundant in the third quarter (July-September).

Diet (Table 5)

The surprisingly large catch of *S. bigemnea* during DSB III produced a more detailed picture of its diet than for the other species. Only 11 of the 88 shrimp had empty stomachs. *Sergia bigemnea* ate crustacean zooplankton, including calanoid copepods, amphipods, and ostracods; ostracods appeared to be a more important prey item than in the other species. Smaller prey were also

eaten—larval bivalves, small cyclopoid copepods, and foraminifera commonly occurring in the diet. *Sergia bigemina* was the only species in which chaetognath spines were found. Other food items included the large cyclopoid copepod *Sapphirina*, a single larval decapod, and unidentified fibrous matter.

Sergia inequalis (Burkenroad 1940)

Vertical Distribution (Figure 25)

As with *S. bigemina*, *S. inequalis* may have avoided the trawl. The few daytime captures were nearly all below 750 m; the peak near 550 m resulted from a tow in June 1971 that dipped to 760 m. Maximum daytime depth appeared to be 1,100-1,200 m. The December 1970 cruise took *S. inequalis* in open tows between 800 and 1,250 m—seven in a 950- to 1,000-m tow and four in a 1,150- to 1,250-m tow. The nighttime distribution varied with size. Small shrimp less than 12 mm CL were found in the upper 100 m; larger shrimp occurred between 100 and 250 m. Moonlight did not significantly affect the adults; there were no captures of small shrimp under these conditions. The Teuthis series showed no evidence of full moon nonmigration, but the December 1970 cruise

took five specimens at night between 550 and 800 m.

Population Size, Growth, and Reproduction (Figure 26)

Sergia inequalis was not abundant in Hawaiian waters; the average population density estimated from all horizontal tows was only 0.55 per 100 m², less than any other regularly occurring all-red sergestid. The largest catch of adults was only seven, from an open tow in December 1970. The oblique series of September 1972 and May 1973 gave estimates of 0.94 and 0.31 per 100 m², respectively.

In spite of its relative rarity, *S. inequalis* showed a clear seasonal cycle of growth, although because of the small sample size, the differences among histograms are only marginally significant statistically (Kolmogorov-Smirnov test, II different from III, 0.10 > P > 0.05). Recruitment was greatest in the second quarter (April-June), and

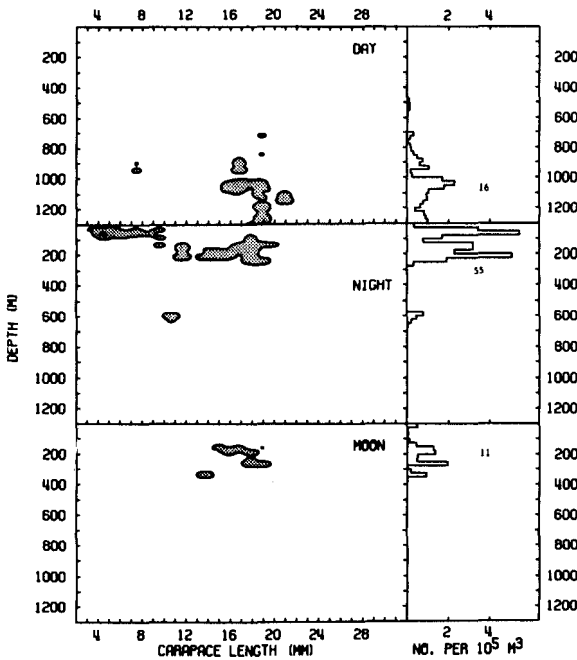


FIGURE 25.—Vertical distribution of *Sergia inequalis*.

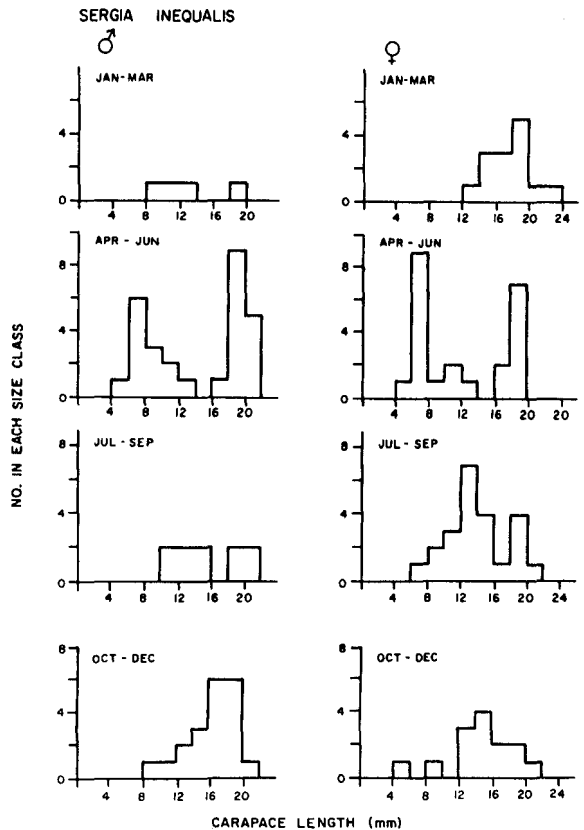


FIGURE 26.—Quarterly size-frequency distribution of *Sergia inequalis*.

the population increased in average size of individuals in succeeding quarters, the largest females being proportionately most abundant in the first quarter (January-March).

Diet (Table 5)

The single *S. inequalis* taken by DSB III had a calanoid copepod in its stomach.

Sergia bisulcata (Wood-Mason 1891)

Vertical Distribution (Figure 27)

As with *S. bigemma*, equality in size of the sexes and small daytime catches indicate that *S. bisulcata* was avoiding the trawl. Immature shrimp were mostly taken between 675 and 750 m during the daytime, adults mostly from 700 to 900 m, with a few catches as deep as 1,100 m. The December 1970 cruise took 19 individuals, including both immatures and adults, in an open tow from 650 to 680 m, with much smaller catches down to 1,200 m. At night, immature shrimp occurred between 175 and 300 m, adults mostly from 225 to 350 m, with occasional captures as deep as 450 m. Moonlight depressed the population below 300 m; two tows at 450 m during the June 1973 cruise took

10 and 8 individuals, respectively. There was no evidence of full moon nonmigration.

Population Size, Growth, and Reproduction (Figure 28)

Sergia bisulcata was the second most abundant all-red sergestid in the Teuthis collection, though far below *S. gardineri* in numbers. The average population density figure from all horizontal tows was 1.35 per 100 m². The figure for tows on moonlit nights was higher, 1.96 per 100 m², probably a sampling artifact. The two oblique series produced similar numbers; September 1972 gave 1.19 and May 1973 gave 0.82 per 100 m².

While quarterly variations in the size-frequency distributions of most Hawaiian sergestids suggest that they live about 1 yr, only in *S. bisulcata* is there evidence for a longer life span. Small immature shrimp around 7-9 mm CL were recruited in the second quarter (April-June) and grew to sexual maturity at about 14-18 mm CL in 1 yr. They continued to grow at a rate of approximately

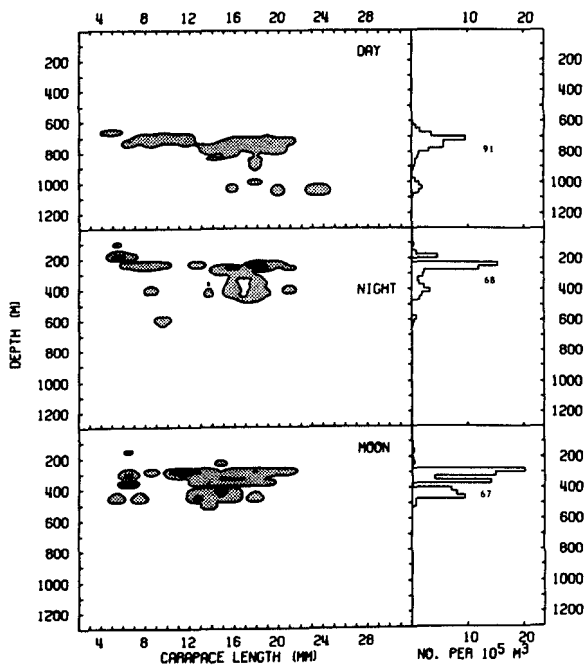


FIGURE 27.—Vertical distribution of *Sergia bisulcata*.

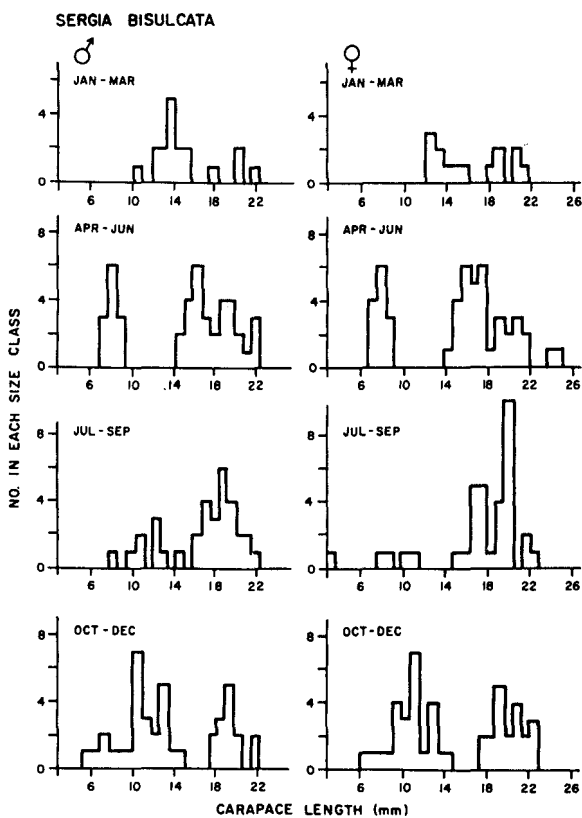


FIGURE 28.—Quarterly size-frequency distribution of *Sergia bisulcata*.

0.6 mm CL per month for up to one additional year. Few males appeared to live beyond 18 mo, but a few large females greater than 22 mm CL were probably a full 2 yr old. The pattern of growth appears clear cut, but the small sample size means that the data should be treated cautiously. The Kolmogorov-Smirnov test showed that only the third and fourth quarter size-frequency curves for the females were significantly different from each other ($0.05 > P > 0.01$).

Diet (Table 5)

Seven of the eight *S. bisulcata* taken by DSB III had food in their stomachs. Food items included ostracods, an amphipod, foraminifera, bivalve larva, and crustacean remains probably including a euphausiid and a larval decapod. No copepods were found, probably because of the small sample size.

Sergia maxima (Burkenroad 1940)

Only two individuals of this species were captured, one on the March 1972 cruise in a 480- to 615-m daytime tow and the other on the December 1973 cruise in an open tow between 400 and 550 m. Both individuals were immature males.

Sergia tenuiremis (Krøyer 1855)

Vertical Distribution (Figure 29)

During the daytime most of the population was below 800 m, although shrimp were sometimes taken as shallow as 700-750 m. A single immature individual was taken in June 1971 between 610 and 690 m. The deepest capture was in a tow between 1,220 and 1,500 m in August 1972. Tows below 1,500 m did not capture *S. tenuiremis*, but total trawling time in this region was rather small. Immature shrimp less than 15 mm CL were vertical migrators, moving up to 300-500 m at night. The adult population did not migrate as a whole, but part spread upward at night as shallow as 550-600 m. Moonlight had no effect on the nighttime vertical distribution of *S. tenuiremis*.

Population Size, Growth, and Reproduction (Figure 30)

Sergia tenuiremis is not abundant in Hawaiian waters. The average population density estimated

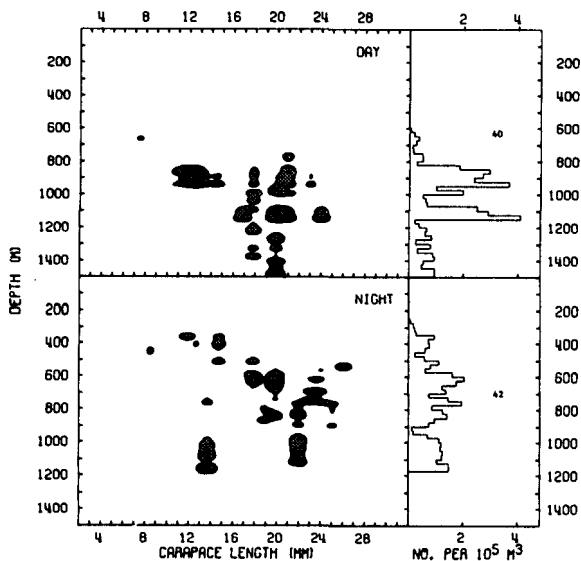


FIGURE 29.—Vertical distribution of *Sergia tenuiremis*. NIGHT and MOON data combined.

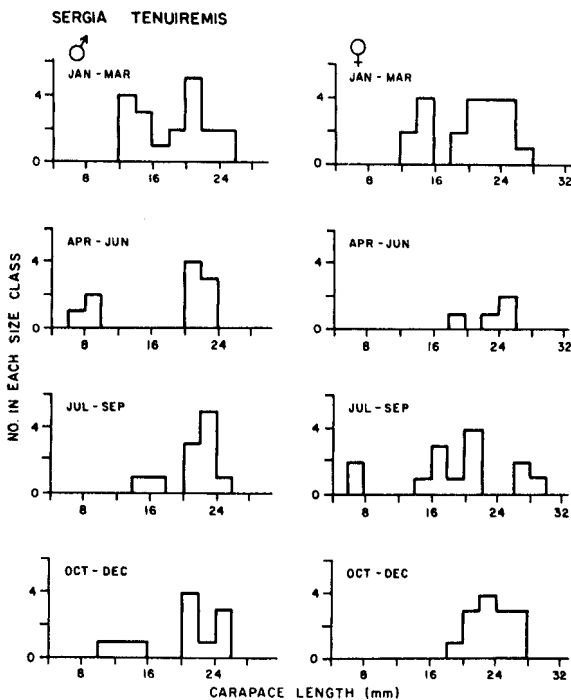


FIGURE 30.—Quarterly size-frequency distribution of *Sergia tenuiremis*.

by all horizontal tows was 0.89 per 100 m², day and night values being similar. The two oblique series produced slightly smaller values, 0.67 per 100 m² in September 1972 and 0.70 in May 1973. Since these

series sampled only to 1,200 m, they may have missed the deeper portion of the population.

The seasonal size-frequency histograms are not significantly different from one another.

Diet (Table 5)

DSB III took only three specimens, all with empty stomachs.

Sergia laminata (Burkenroad 1940)

Vertical Distribution

Only four individuals were captured in closing tows, all in daytime tows during the November 1972 cruise. A tow at 650-725 m took three shrimp, and a tow at about 750-800 m took one shrimp. At night oblique tows in the upper 400 m took single shrimp during the September 1972 and May 1973 cruises, suggesting that *S. laminata* may be a vertical migrator. On the other hand, the December 1970 cruise captured one shrimp in an open horizontal tow at 550-600 m at night, suggesting that *S. laminata* may not migrate near full moon.

The small sample size did not allow studies of growth, reproduction, or diet.

Petalidium suspiriosum Burkenroad 1937

Vertical Distribution (Figure 31)

A deep-living nonmigrator, *P. suspiriosum* generally stayed below 800 m day and night. The shallowest captures came during the June 1972 cruise, which took six in a 750- to 800-m day tow and five in two night tows between 630 and 720 m. Maximum depth appeared to be at least 1,500 m; as with *S. tenuiremis*, limited trawling below 1,500 m did not catch any *P. suspiriosum*.

Population Size, Growth, and Reproduction (Figure 32)

Petalidium suspiriosum is more abundant than its small numbers in our collection would seem to indicate, since the depths below 800 m where it lives were not as thoroughly sampled as the shallower waters. The average population density estimated from all horizontal tows was 1.84 per 100 m², making it the second most abundant all-red sergestid. Like *S. tenuiremis*, the oblique series

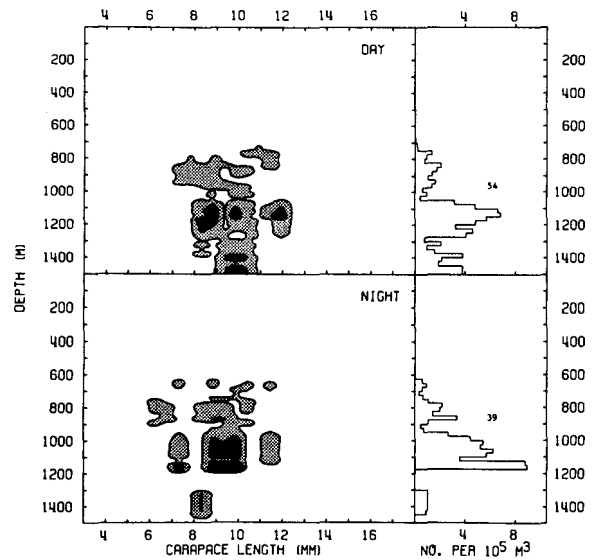


FIGURE 31.—Vertical distribution of *Petalidium suspiriosum*. NIGHT and MOON data combined.

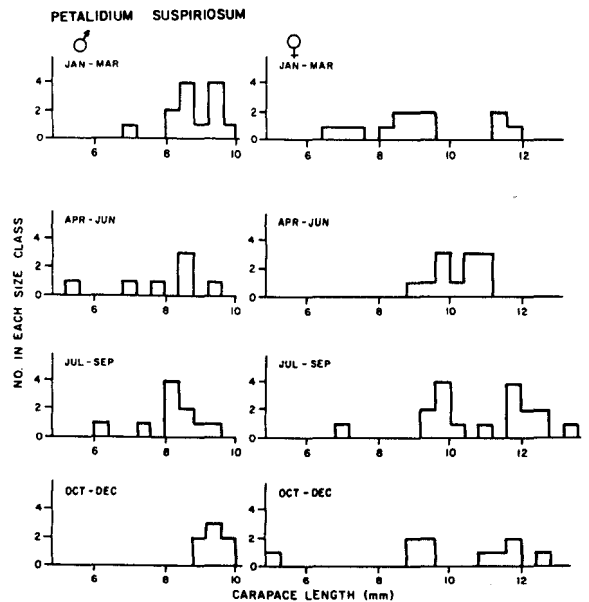


FIGURE 32.—Quarterly size-frequency distribution of *Petalidium suspiriosum*.

gave lower numbers, 1.21 per 100 m² in September 1972 and 1.31 in May 1973, probably because some of the population was below the 1,200 m maximum of the oblique tows.

Because of its susceptibility to damage, it was possible to make accurate measurements of carapace length on only about two-thirds of the specimens in the collection. There was no

significant seasonal trend in the size-frequency distributions of *P. suspiciosum*.

DSB III did not take *P. suspiciosum*, so its diet was not examined.

DISCUSSION

Color Pattern and Daytime Vertical Distribution: Role of Countershading

Sergestids display two basic color patterns. One group, including *Sergestes* and species of *Sergia* in Yaldwyn's (1957) "*S. challengerii*" species group, is "half-red," that is, its members are semitransparent except for the eyes and viscera, with red, stellate, subcuticular chromatophores scattered over the body and appendages, most concentrated on the cephalothorax. All half-red sergestids have well-developed photophores; *Sergestes* species have internal photophores, the organs of Pesta, and the half-red *Sergia* species have external cuticular lensed photophores. The other group, including the remaining species of *Sergia* and *Petalidium*, is "all-red," that is, its members are covered with a relatively uniform red cuticular pigment. All-red sergestids have simple lensless cuticular photophores or else lack photophores altogether.

Foxton (1970) showed that most mid-water decapods in the Fuerteventura area (Canary Islands) are either half-red or all-red. He found that half-red shrimps generally live shallower than 700 m during the daytime, while all-red shrimps generally live below 700 m. He concluded that the half-red color pattern and complex photophores are adaptations for concealment by countershading to match the light intensity of the surrounding waters when viewed from any angle, the photophores producing a ventrally directed beam of light to fill in the shadow of the animal. He suggested that the half-red pattern gives way to the all-red pattern at the depth where bioluminescent light becomes more important than penetrating surface light. Although many all-red decapods have simple photophores, he concluded that their function does not involve daytime countershading. Donaldson (1975) did not discuss this phenomenon, but an examination of his vertical distribution data for the Bermuda area shows the same daytime pattern of shallower half-red sergestids and deeper all-red sergestids, the dividing line again being approximately 700 m.

Other mid-water animals show similar depth-related changes in color patterns during the daytime. Badcock (1970) noted that mesopelagic fishes in the Fuerteventura area tend to be silvery above 650-700 m and dark below that depth. Amesbury (1975) found the same pattern in Hawaiian mesopelagic fishes, several independent analyses of community structure locating a major faunal boundary at 675-700 m between mostly silvery shallow mesopelagic fishes and mostly dark deep mesopelagic fishes.

Figure 33 shows how half-red and all-red sergestids differ in depth during the daytime in Hawaiian waters. The half-red species range from 425 to 725 m, with maximum abundance in the 600- to 625-m interval. The all-red species range from 625 to 1,500 m, with maximum abundance at 700-725 m.

Rather surprisingly, the depths of maximum abundance for the two types are only 100 m apart, and there is a large amount of overlap in their ranges, particularly in the zone between 650 and 725 m. Nearly half of the half-red sergestids below 650 m are *Sergestes erectus*, a species often taken in large numbers in tows that also take large

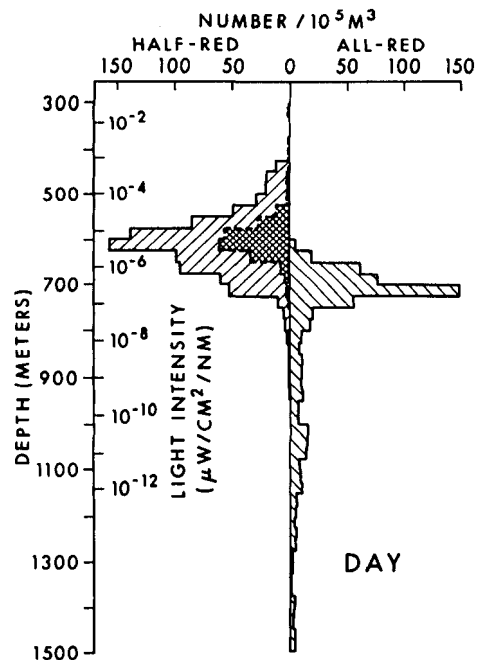


FIGURE 33.—Daytime vertical distribution of half-red and all-red Hawaiian sergestids. Half-red species are on the left (half-red *Sergia* spp. crosshatched), all-red species on the right. Scale of light intensity is from unpublished data of E. M. Kampa, at lat. 28°N.

numbers of *Sergia gardineri*, the most abundant all-red sergestid. To see if this overlap is real and not an artifact produced by vertical excursions of the trawl or seasonal variations in the position of a sharper transition depth, Teuthis XIX extensively sampled the 600- to 800-m zone in November 1972, using depth telemetry to try and maintain the trawl within a 25- to 50-m depth range. One tow between 630 and 680 m took 139 *Sergestes erectus* and 31 *Sergia gardineri*, another from 650 to 730 m took 157 *Sergestes erectus* and 289 *Sergia gardineri*, and a third from 700 to 740 m took 19 *Sergestes erectus* and 312 *Sergia gardineri*. On this occasion, at least, substantial numbers of both color patterns were living between 650 and 725 m.

Other investigators have found similar transition zones. In Hawaii, Riggs (pers. commun.) has found that the all-red species *Gennadas propinquus* (Penaeidae, Benthosicymae) lives as shallow as 600 m, with maximum numbers at 650-675 m. Ziemann (1975) obtained similar results for another all-red shrimp, *Systellaspis debilis* (Caridea, Oplophoridae), 75% of the adult population being found above 650 m on one occasion. In the Atlantic, Foxton's (1970) data show the half-red *Sergestes corniculum* (closely related to *S. erectus*) extending to at least 800 m, overlapping the ranges of the all-red species *Sergia robusta* and *Systellaspis debilis* (although most of the catch of the latter species were lightly pigmented juveniles). Donaldson's (1975) data show a transition zone from 650 to 800 m occupied by the half-red *Sergestes atlanticus* and *S. corniculum* and the all-red *Sergia grandis*. In view of this extensive overlap in the distribution of half-red and all-red decapods, it is necessary to review the conditions under which countershading is an effective concealment strategy and, in particular, Foxton's conclusion that only half-red decapods countershade.

The angular distribution of light in the mesopelagic environment is independent of solar elevation and depth (Denton and Nicol 1965). At any given point, the background light intensity is highest directly overhead, falling off rapidly to the sides, with a very low light intensity of back-scattered light from below. The intensity of the background light 90° from the vertical is only 3-4% of the zenith value, decreasing to 0.3-0.5% at 180° from the zenith (Tyler and Preisendorfer 1962). Changes in surface irradiance or depth change the intensity but not its angular distribution. Countershading mechanisms match the animal to this

background pattern; thus mid-water fishes use a dark dorsal surface, silvery sides, and ventral photophores for countershading (W. D. Clarke 1963; Nicol 1967; Badcock 1970). Foxton (1970) concluded that the half-red coloration of shallow mesopelagic decapods is a countershading mechanism using transparency rather than reflectors for lateral countershading. I propose that some deep mesopelagic all-red decapods also countershade ventrally and that ventral countershading can be effective below the transition zone from half-red to all-red decapods.

As depth increases and the intensity of the penetrating light dwindles, bioluminescence becomes relatively more and more important as a source of light in the mesopelagic environment. Bioluminescent light has a much different temporal and spatial distribution from the penetrating surface light. The bioluminescent light field is the sum of glows and flashes from many point sources whose angular distribution is more or less random. Countershading is an ineffective concealment strategy against bioluminescence; the silvery sides which camouflage a mid-water fish against the penetrating sunlight may in deeper water reflect a bioluminescent flash and reveal the fish against a black background. The best strategy of concealment in an environment lit only by random flashes is to be as nonreflective as possible. The dark brown or black fishes and all-red crustacea of the deep mesopelagic zone reflect blue light poorly (Nicol 1958), presumably indicating their use of this strategy.

Another effect of increasing depth is that the penetrating light eventually becomes too dim to be seen. The absolute visual threshold for deepsea fishes has been estimated as about $3 \times 10^{-20} \mu\text{W} / \text{cm}^2$ by Clarke and Denton (1962), a figure that undoubtedly varies in other groups of animals correlated with the degree of development of the eye. A slightly higher intensity is required before countershading becomes necessary. The maximum depth of effective countershading depends on the angular distribution of the penetrating light; thus in Hawaiian waters the threshold of lateral countershading is reached 110-120 m higher in the water column than the threshold for ventral countershading. Between these two depths lateral countershading is not needed but ventral countershading can still be effective.

The all-red sergestids with photophores appear to combine an antibioluminescent color pattern

with a ventral array of simple photophores for low-intensity ventral countershading. This interpretation implies that the transition from half-red to all-red sergestids at 650-725 m marks the upper limit of bioluminescence as an important source of ambient light. The lower limit of all-red sergestids with photophores should then mark the threshold of ventral countershading. Unfortunately, this study produced good daytime vertical distribution data for only one such species, *Sergia gardineri*. If its lower limit under normal conditions is typical of the other species, then the threshold of ventral countershading should lie at approximately 775 m. This depth is also the approximate upper limit of the two sergestids, *Sergia tenuiremis* and *Petalidium suspiciosum*, that lack photophores (Figures 29, 31). If 775 m is the threshold of ventral countershading, then the threshold for lateral countershading should be 110-120 m higher or about 660 m, approximately the depth of the transition from half-red to all-red sergestids.

It thus appears that the transition from half-red to all-red sergestids does not mark the absolute lower limit of countershading, but is related to the depth at which lateral countershading becomes ineffective and bioluminescent light forces a change in concealment strategy. Although the all-red color pattern hides the shrimp from bioluminescent flashes, enough of the penetrating light remains directly overhead that ventral countershading continues to be effective more than 100 m below the transition zone. The simple lensless photophores of the all-red sergestids presumably produce low levels of light in this dimly lit region. Other mid-water animals that lack lateral countershading mechanisms but have ventral arrays of photophores, such as many of the black stomiatoid fishes, may have evolved the same kind of camouflage.

Nighttime Vertical Distribution and Migration

The structure of the sergestid assemblage changes drastically as day gives way to night. All Hawaiian sergestid species except *Sergia tenuiremis* and *Petalidium suspiciosum* migrate into the upper 300 m of the water column. As figure 34 shows, the division into a shallow half-red and a deep all-red mesopelagic sergestid assemblage disappears on moonless nights. The species fall with little overlap into a shallow and a deep migratory group, adults of the shallow group

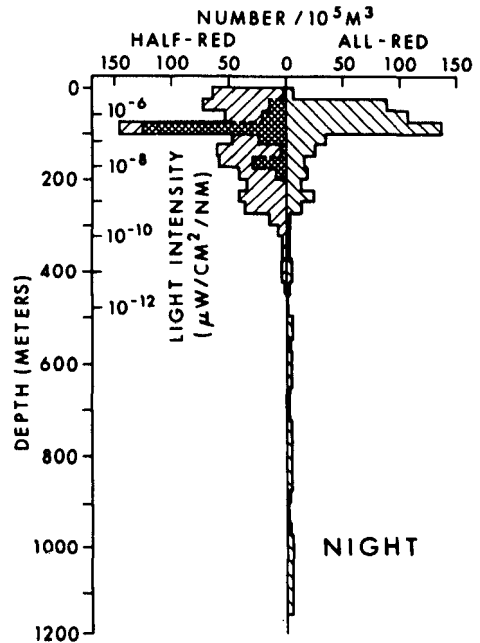


FIGURE 34.—Nighttime vertical distribution of half-red and all-red Hawaiian sergestids (moonless conditions). Hachure, etc., as in Figure 33. Light intensity estimated from unpublished daytime data of E. M. Kampa at lat. 28°N, using G. L. Clarke's (1968) values for relative intensity of day vs. night.

living in the upper 100 m, adults of the deep group living from 125 to 300 m. The shallow group includes *Sergestes vigilax*, *S. consobrinus*, *Sergia scintillans*, and *S. gardineri*. The deep group includes *Sergestes erectus*, *S. armatus*, *S. sargassi*, *Sergia bigemnea*, *S. inequalis*, and *S. bisulcata*. The single large nighttime capture of adult *Sergia fulgens* is at about 175 m, probably placing this species also in the deep group. In addition, *Sergestes pectinatus* is broadly distributed from 25 to 250 m, and *S. atlanticus* may likewise be broadly distributed if the single large catch in the upper 25 m is not representative of its normal distribution. T. A. Clarke (1973) found a similar pattern in the nighttime distribution of Hawaiian myctophid fishes, with a shallow group down to 125 m, a deep group at 150-250 m, and a few species broadly distributed in the upper 250 m. Closely related pairs of myctophid species separate into a shallow species and a deep species. Most sergestid species pairs are found at the same nighttime depths, except for *Sergestes armatus* and *S. vigilax*, and probably *Sergia scintillans* and *S. fulgens*.

The division of the nighttime sergestid assemblage at 100-125 m may possibly be related to

the penetrating surface light. The scale at the left of Figure 34 is an estimate, derived by assuming the value of light intensity at the surface on a moonless night to be 10^7 times fainter than during the day, a figure used by G. L. Clarke (1968), and applying this correction to the daytime light curve of E. M. Kampa (unpubl. data) used in Figure 33. The lower limit of daytime ventral countershading, estimated above as approximately 775 m, is equivalent to a nighttime depth of approximately 125-150 m, suggesting that the shallow group, but not the deep group may countershade at night. The lower limit of daytime lateral countershading, estimated as about 660 m, is equivalent to about 50 m at night, the approximate upper limit of *S. gardineri*, the shallowest all-red sergestid at night. Although these figures admittedly pile estimate on estimate, they suggest that light may influence the vertical distribution of sergestids at night as well as during the daytime.

W. D. Clarke (in Barham 1970:118) and Foxton (1970) have suggested that countershading may occur primarily at night in some mid-water animals. While nighttime ventral countershading appears feasible for some species of Hawaiian sergestids, these species all may need to countershade during the daytime also (Table 7). A number of species maintain approximately constant illumination day and night. Some species live in much brighter waters during the daytime than at night. No species, however, lives in brighter waters at night than during the daytime, as would be expected if countershading were occurring only at night.

Only two species of Hawaiian sergestids definitely do not migrate. *Sergia tenuiremisa* appears to migrate to 300-400 m when less than 15

mm CL. The adult population spreads upward from an upper limit of 750-800 m during the day to about 600 m at night, although many shrimp remain in the daytime depth range. *Petalidium suspiciosum* remains below 750-800 m both day and night. Few Hawaiian sergestids occupy the depths between 300 and 600 m at night, in contrast to the Atlantic, where Donaldson (1973) found *Sergestes corniculum* and *Sergia grandis* and Foxton (1970) found *Sergestes corniculum* and *Sergia robusta* in this depth range. The reasons for this difference are unknown.

Although considerable evidence links diurnal vertical migration to the diurnal light cycle (e.g., Marshall 1954), the exact relation of light to vertical migration is complex and poorly understood. The simplest scheme, merely maintaining a constant light intensity around the clock, is not used by all Hawaiian sergestids, as Table 7 shows. The daytime sergestid assemblage cannot shift en masse to equivalent light levels at night, because the light intensity at the surface on a moonless night is approximately equivalent to that at 600 m during the daytime. Instead, we find species with similar daytime ranges but different nighttime ranges, such as *Sergestes armatus* and *S. consobrinus*; species with similar nighttime ranges but different daytime ranges, such as *Sergia scintillans* and *S. gardineri*; and species that exchange relative positions, such as *Sergestes sargassi* and *Sergia gardineri*. Vertical migration is a more complicated behavior than merely maintaining a constant light level.

A further complication of the vertical migration mechanism involves the response of sergestids to moonlight. When the moon increases the nighttime surface irradiance, the two groups of migrators react in different ways. The deep group remains relatively unaffected by moonlight, the young often moving downward to the depth of the adults. Moonlight drastically affects the shallow group, depressing most of the species below 150 m. The two assemblages, which separate by depth on dark nights, mix together on moonlit nights.

In addition to the normal response of sergestids to moonlight, there appears to be a period of about a week around full moon when some species stop migrating entirely, remaining at their daytime depths. This behavior is poorly shown by the results of the Teuthis cruises, showing up better in the supplementary data from 70-12 and Echo IV. Not all species react the same way to the full moon period. *Sergia gardineri* and probably *Sergestes*

TABLE 7.—Estimated light intensities for daytime and dark night habitats of Hawaiian sergestids. Numbers are negative logarithms of light intensity (smaller numbers mean brighter light).

Species	Daytime habitat	Night habitat	
<i>Sergestes atlanticus</i>	5.0- 6.7	5.5- 6.0	D ~ N
<i>Sergestes erectus</i>	5.5- 6.7	9.0-10.0	D >> N
<i>Sergestes armatus</i>	4.7- 6.0	8.2- 9.7	D >> N
<i>Sergestes vigilax</i>	5.0- 6.7	5.5- 7.7	D ~ N
<i>Sergestes orientalis</i>	4.0- 5.2	5.5- 7.2	D > N
<i>Sergestes consobrinus</i>	4.7- 5.2	5.5- 6.2	D > N
<i>Sergestes sargassi</i>	3.5- 5.0	7.7- 9.5	D >> N
<i>Sergestes pectinatus</i>	4.2- 6.2	7.5- 9.0	D > N
<i>Sergia fulgens</i>	4.7- 5.5 ?	7.7- 8.2 ?	D > N ?
<i>Sergia scintillans</i>	4.2- 6.5	5.7- 7.2	D ~ N
<i>Sergia gardineri</i>	4.7- 7.2	5.7- 7.2	D ~ N
<i>Sergia bigemnea</i>	(7.0-11.0)	7.7- 9.0	D ~ N
<i>Sergia inequalis</i>	(7.0-11.0)	7.7- 9.0	D ~ N
<i>Sergia bisulcata</i>	6.5- 8.7	8.7-10.2	D > N

atlanticus appear to stop migrating altogether. During cruise 70-12 part of the populations of *Sergestes orientalis* and *S. consobrinus* migrated, while the rest of the populations remained at their daytime ranges; during Echo IV both species appeared to migrate normally. Other species, such as *Sergestes vigilax* and *Sergia scintillans*, have shown no indications of nonmigratory behavior. Species showing the best evidence of nonmigration are all members of the shallow migratory group, but sampling was inadequate to determine definitely whether any species in the deep group are also nonmigrators. The data from cruise 70-12 and the June 1973 Teuthis cruise further suggest that when a species is not migrating its daytime depth can also be abnormal. *Sergia gardeneri*, normally found between 650 and 775 m during the daytime, was taken as deep as 1,200 m on these cruises, and *Sergestes atlanticus*, normally found between 600 and 725 m, was taken down to 800 m.

The nonmigration of some sergestids around full moon is a separate behavior from the moonlight depression below 150 m. Nonmigration is not a direct effect of increased light levels. During Echo IV the moon was often heavily obscured by cloud, yet the nonmigratory species remained deep. During Cruise 70-12, nonmigratory species remained deep until the next-to-last night, when normal migration resumed, although light intensity in the surface waters could not have been radically different than on the previous night. Nonmigratory behavior has been observed in December and June, suggesting that it occurs during most seasons of the year.

Studies of seasonal variation in vertical migration can be complicated by moon effects. For example, Donaldson (1973) found abnormally deep distributions day and night for *Sergia splendens* during a February 1972 cruise. He also cited data from the same cruise showing that sergestid numbers were strongly influenced by moonlight in the upper 100 m, both at the quarter and at full. Knowing only that the moon was in various phases during the February 1972 cruise, it is impossible to separate seasonal effects from moonlight effects for *S. splendens*. Other mid-water groups show nonmigratory behavior not tied to lunar phase. Riggs (pers. commun.) found that species of the penaeid shrimp *Gennadas* did not migrate during our November 1972 cruise, which sampled near new moon when sergestids appeared to be migrating normally, and concluded that a seasonal factor was involved. In summary, the depth struc-

ture of the mesopelagic community changes in a bewilderingly complex manner under the influence of ambient light, lunar phase, season, and probably other undiscovered effects.

Feeding Chronology and Diet

In studies of the diets of mesopelagic animals, the time of day when feeding takes place is as interesting a datum as the kinds of prey eaten. The most widely accepted theory of the function of vertical migration holds that mesopelagic animals move into the food-rich shallow water at night to feed in the dark and retreat into deeper water at sunrise to escape the efficient visual predators of the epipelagic zone (Marshall 1954). If this theory is correct, an examination of the feeding chronology of vertical migrators should reveal that the majority, at least, of feeding occurs at night.

Table 4 compares the stomach contents of day-caught with night-caught sergestids from the DSB III cruise of February 1973. The night samples as a whole had a lower percentage of empty stomachs, a greater amount of food in the stomachs, and a lesser degree of digestion than the day samples, indicating that most feeding occurred at night. Unfortunately, only two species were abundant both day and night. *Sergestes armatus* fed more at night than during the daytime, although most specimens had empty stomachs regardless of time of day. *Sergestes erectus* actually had a lower percentage of empty stomachs during the daytime than at night, but the night specimens on the average were fuller than the day specimens. Other studies of feeding chronology in sergestids, notably those of Omori (1969) on *Sergia lucens*, Judkins and Fleminger (1972) on *Sergestes similis*, and Foxton and Roe (1974) on a variety of Atlantic species, also indicated that most feeding occurs at night. However, the DSB III day samples contained a number of individuals with appreciable amounts of food in their stomachs, showing that a certain amount of feeding occurs during the daytime. Donaldson (1973) found that *Sergestes sargassi*, *S. pectinatus*, and *Sergia japonica* appeared to feed around the clock. The first two species also live in Hawaiian waters; unfortunately, they only occurred in the night samples of DSB III, so this study could not test his observations.

If Hawaiian sergestid species have specialized by dietary preference, they might be expected to exhibit specialized structures for catching prey.

One important systematic character, the third maxilliped, appears directly related to feeding. Many species of *Sergestes* have greatly enlarged third maxillipeds, armed with stout spines and varying in length and development among the different species. *Sergestes pectinatus* in particular has highly modified third maxillipeds, with a series of short, comblike setae between the longer spines. The division of Hawaiian sergestids into a long-maxilliped group and a short-maxilliped group would seem logically to indicate a difference in diet between the two groups.

The results of the DSB III study (Table 5) are rather unexpected. All the species captured fed largely on zooplankton-sized crustacea in the 1- to 3-mm size range, chiefly calanoid copepods, myodocopid ostracods, and hyperiid amphipods. Some species also ate smaller zooplankton in the 0.4- to 0.6-mm size range, chiefly larval bivalves, foraminifera, and cyclopoid copepods. Ability to utilize prey in the small size range appeared to depend not on the length of the third maxillipeds but on the degree of setation of the first three pairs of pereopods and (when not enlarged) the third maxillipeds. Species feeding on small zooplankton all have long setae spaced about 0.3-0.4 mm apart. All well-sampled species in the short-maxilliped group except *Sergestes erectus* fed on the small zooplankton. Within the long-maxilliped group, there is a gradation in degree of setation of the pereopods from *S. armatus*, which has very short, sparse setae, through the *S. orientalis* group, which have somewhat longer, more numerous, but still rather sparse setae, to *S. sargassi* and *S. pectinatus*, which have rather long setae spaced about 0.5-0.6 mm apart. Of this group only *S. armatus* was captured in quantity during DSB III; its diet definitely lacked small zooplankton. A few specimens of *S. sargassi* and *S. pectinatus* were captured; none contained small zooplankton, but with the small sample size their status remains in doubt.

The dietary specializations of Hawaiian sergestids thus appear more related to size than to type of prey. The variety of copepods, amphipods, and ostracods that compose the large zooplankton fraction all seem to be equally acceptable as prey. The various modifications of the third maxilliped may reflect specialized methods of capturing prey rather than a specialized diet. In particular, the diet of *S. pectinatus* lacks any distinctive characteristics which can be associated with its unusual maxillipeds. While large zooplankters are prob-

ably seized individually, the small zooplankton appear to be sieved from the water onto the long setae, spaced so as to retain zooplankton and pass water, a process akin to filter feeding.

The small zooplankton probably represent a supplementary rather than a primary resource for sergestids. Larval bivalves, as meroplankton, are unlikely to be abundant all year around (they were abundant in the zooplankton during the December 1973 cruise; I have not examined other zooplankton samples) and are unlikely to be abundant far from land. Many of the individuals containing small zooplankton also contain masses of an unidentified greenish, fibrous material. Judkins and Fleminger (1972) reported similar material in *Sergestes similis*, and Foxton and Roe (1974) reported similar material in a number of Atlantic species. If this material is detritus and not the digested remains of some unidentified organism, it would represent another resource available to sieving sergestids, potentially very important when small zooplankton is sparse. The inefficient-looking sieving mechanism of the Hawaiian sergestids are a reminder that none of these species feed solely, or even primarily, on the small zooplankton. Any modifications for increased sieving ability must not hamper the animal's ability to seize large zooplankton.

The results from DSB III are quite different from those reported by Donaldson (1975). He found a much larger proportion of large prey, such as euphausiids and fishes, and also many more chaetognaths. Part of the difference is due to his much larger sample, where infrequently eaten prey are more likely to turn up. Large sergestids captured in very small numbers during the DSB III cruise, particularly *Sergia bisulcata*, *S. inaequalis*, and perhaps *S. tenuiremis*, are likely to eat larger prey than is reported here. However, some of the difference between Donaldson's results and the DSB III results may be due to a higher degree of feeding in the trawl during Donaldson's study. The abnormal conditions in the cod end of a mid-water trawl are apt to lead to abnormal feeding. Judkins and Fleminger found a much lower proportion of euphausiids in the stomachs of sergestids caught by albacore than in trawl-caught shrimp. They also found fish scales only in trawl-caught shrimp, an unlikely food item under natural conditions. These results emphasize the need for future feeding studies to take whatever steps are necessary to minimize or eliminate feeding in the trawl.

Reproduction and Growth

It is difficult to determine when sergestids spawn. Copulation occurs long before spawning; female *Sergia gardineri* whose ovaries have not started to mature often bear spermatophores. Eggs are spawned directly into the water rather than being carried on the appendages as in the carideans. Some spawning probably occurs year around, as sexually mature females can be captured at any time of the year. In *Sergestes*, the anterior lobes of the ovary vary greatly in size, filling much of the carapace at maximum development. However, there is no correlation of ovary development with carapace length in adult females. One possible explanation is that a female may spawn several batches of eggs over a period of several months, the ovaries regressing in size between batches.

Recruitment to a catchable size can be determined from the quarterly size-frequency histograms. Omori (1969) found that *Sergia lucens* required about 2 mo from spawning to recruitment; assuming the time is similar for Hawaiian species, a maximum in recruitment implies a maximum in spawning about one quarter earlier. Most Hawaiian sergestids showed peak recruitment in either the second (April-June) or third (July-September) quarter. Species with maximum recruitment in the second quarter included *Sergestes armatus*, *S. sargassi*, *Sergia unequalis*, and *S. bisulcata*. Species with maximum recruitment in the third quarter included *Sergestes atlanticus*, *S. consobrinus*, *S. pectinatus*, *Sergia scintillans*, and *S. gardineri*. Some species showed no significant difference from one quarter to the next; these included *Sergestes orientalis*, *Sergia bigemina*, and probably *S. tenuiremis* and *Petalidium suspiriosum*. *Sergestes vigilax* had somewhat higher recruitment in quarters two and three than during the rest of the year. *Sergestes erectus* showed no particular recruitment maximum, but intermediate-sized shrimp were most abundant in the fourth quarter. *Sergia fulgens* is a peculiar case, to be discussed later.

Size-frequency data indicate that most Hawaiian sergestids appear to live about 1 yr, in agreement with most other studies (Pearcy and Forss 1969; Omori 1969; Donaldson 1973). The size-frequency histograms of *Sergia bisulcata* indicate that this species has a 2-yr life span, though the conclusion is based on a small sample. Donaldson concluded that *S. robusta* may also live

2 yr. Genthe (1969) arrived at a 2-yr life span for *Sergestes similis* off California, though Pearcy and Forss found a 1-yr life span for the same species off Oregon. Genthe asserted that juveniles less than 5 mm CL are 9 to 11 mo old, which seems too old. His data support a 1-yr life span if a 2- to 3-mo larval development time is assumed. Probably only a few large all-red species live more than a single year.

Sergia fulgens differed from all other Hawaiian species by showing an extremely modal size-frequency distribution and varying drastically in abundance from one month to the next (Figure 18). This behavior can best be explained by assuming that *S. fulgens* is an expatriate species occasionally moving into Hawaiian waters from elsewhere. Adult females from the December 1970 cruise and the May 1973 cruise (Teuthis XXI) had small ovaries with eggs about 150 μm in diameter. Mature females of the closely related but smaller species *S. scintillans* had proportionately larger ovaries with eggs about 260 μm in diameter. Omori (1969) reported an average diameter of 255 μm for another closely related species, *S. lucens*. It thus appears that the large female *S. fulgens* are not ripe. While it is possible that female *S. fulgens* continue to grow to 18 or 20 mm CL before spawning and that ripe females have never been captured, it seems more likely that *S. fulgens* do not reproduce in Hawaiian waters and that the local population is carried in by currents from its normal breeding range. Unfortunately, the geographic range of *S. fulgens* is almost totally unknown; in addition, it is very similar or identical to *S. talismani* in the Atlantic. Influxes of *S. fulgens* did not coincide with captures of *Sergestes tantillus*, an equatorial species occasionally found in Hawaiian waters, but little more can be inferred about the source of the local population of *S. fulgens*.

Interspecific Relationships

The 20 species of Hawaiian sergestids exhibit a variety of specializations in morphology and habit that appear to minimize interspecific competition and allow them to coexist as a stable assemblage. Most obvious is the division into half-red and all-red species, related to shallow and deep daytime depth ranges and the different concealment strategies required. The all-red sergestids are subdivided by size and nighttime vertical distribution, as are the half-red sergestids, which are also further subdivided by photophore type and

length of third maxillipeds. Finally, nearly all species cooccur with at least one other species that is much more closely related than any of the other Hawaiian sergestids. Interspecific competition should be strongest between members of a species pair; the ways in which two closely related sergestids divide up the mid-water environment should suggest the kinds of competition that occur in the mid-water environment and how competition is minimized.

Table 8 shows some observed parameters of Hawaiian sergestids. The dendrogramlike pattern at the left is a subjective representation of the affinities among the species, based on morphological features. Some differences will be noted in the vertical distribution patterns of the species pairs; for example, *Sergestes vigilax* is more broadly distributed than *S. armatus* and tends to live shallower at night. However, most species pairs are commonly found together over much of their vertical ranges. The most striking difference among closely related species is adult size. In every case the most closely related species show little or no overlap in the adult size range. For example, *Sergia scintillans* appears nearly identical to *S. fulgens*, differing chiefly in the number of photophores on the antennal scale and exopod of the uropod. However, adult *S. scintillans* vary from 5.5 to 10.5 mm CL, while adult *S. fulgens* vary from 11 to 16.5 mm CL. The only exception to this rule, the species triplet *Sergestes orientalis*-*S. tantillus*-*S. consobrinus*, is a revealing case. *Sergestes*

orientalis is well separated in size from *S. consobrinus*, the largest females of *S. consobrinus* overlapping only slightly with the smallest males of *S. orientalis*. However, *S. tantillus*, while somewhat smaller in average size than *S. orientalis*, still overlaps considerably in size with the larger species. In this case it turns out that *S. tantillus* is primarily an equatorial species (Judkins 1972), occurring only rarely in Hawaiian waters. MacArthur (1972) has shown on theoretical grounds that when three similar species differ in only one parameter, such as body size, the competition pressures are strongest on the middle species. One of the factors determining the northern limit of *S. tantillus* may be this competition from both a larger and a smaller species.

Specialization solely by adult size could still result in competition if adults of the small species cooccur with similar-sized juveniles of the large species. In this case, other specializations appear to become important. When the species have similar vertical ranges, the juveniles may live shallower than the adults. For example, adult *Sergia bigemmea* and adult *S. inequalis* both occur at about 150 to 225 m at night. Juvenile *S. inequalis* in the 10- to 13-mm CL range, the size of adult *S. bigemmea*, are mostly found between 50 and 150 m, so that similar-sized individuals of the two species seldom occur together.

Competition could occur if the large species lives somewhat deeper than the small species, so that juveniles of the large species live at about the

TABLE 8.—Characteristics of Hawaiian sergestid species. Dendrogram shows estimated phylogenetic affinities among species.

Species	Adult size (CL, mm)	Day depth (m)	Night depth (m)	Population size (no./100 m ²)
<i>Sergestes orientalis</i>	5.5-10	500- 625	0- 125	1.32
<i>Sergestes tantillus</i>	5.5- 8	450- 650?	0- 100?	<0.10
<i>Sergestes consobrinus</i>	3.8- 6	450- 725	0- 75	1.05
<i>Sergestes armatus</i>	9 -14.5	550- 650	150- 300	2.35
<i>Sergestes vigilax</i>	6 - 8.5	550- 725	0- 200	0.35
<i>Sergestes atlanticus</i>	5 - 9	550- 725	0- 300	1.31
<i>Sergestes cornutus</i>	3.5- 5	450- 550?	(0- 50)?	<0.10
<i>Sergestes erectus</i>	13 -24.5	550- 800	250- 325	3.81
<i>Sergestes sargassi</i>	7 -10.5	450- 575	125- 300	0.70
<i>Sergestes pectinatus</i>	3.2- 7.5	450- 725	75- 275	1.71
<i>Sergia fulgens</i>	11 -16.5	550- 625?	75- 200?	2.26
<i>Sergia scintillans</i>	5.5-10.5	525- 700	25- 125	3.31
<i>Sergia gardineri</i>	4.5- 9	650- 775	25- 150	8.65
<i>Sergia bigemmea</i>	9.5-14.5	750-1,100?	125- 250	0.84
<i>Sergia inequalis</i>	13.5-22	750-1,100?	100- 250	0.55
<i>Sergia bisulcata</i>	16.5-23	700- 900	225- 350	1.35
<i>Sergia maxima</i>	(41.5)	?	?	<0.10
<i>Sergia tenuiremis</i>	18.5-29	750-1,300+	550-1,200+	0.89
<i>Sergia laminata</i>	7 -10	700- 800?	?	<0.10
<i>Petalidium suspiciosum</i>	8.5-12	800-1,300+	800-1,200+	1.84

same depth as adults of the small species. The clearest example of this type in Hawaiian waters is *Sergestes vigilax* and *S. armatus*, where most juvenile *S. armatus* in the 6- to 8.5-mm CL range live around 100 to 150 m at night, overlapping somewhat with adult *S. vigilax* in the same size range (most *S. vigilax* live above 100 m, but adults often occur somewhat deeper). However, it appears that adult *S. vigilax* are most abundant from October to March, while juvenile *S. armatus* in the same size range are most abundant from April to June (Figures 6, 8). Thus the actual overlap at any one time is probably small.

The Hawaiian sergestid assemblage can thus be described by size, morphology, and vertical distribution. Consider the half-red species first. Those with short maxillipeds are divided into a pair of species with lensed cuticular photophores and three species with organs of Pesta. The pair with cuticular photophores includes a large species, *Sergia fulgens*, and a small species, *S. scintillans*; these species may also live at different depths at night. Of the three species with organs of Pesta, *Sergestes erectus* is very large, distantly related to the other two, and lives deeper at night; *S. atlanticus* is larger than *S. cornutus* and may live deeper during the daytime. Long third maxillipeds appear to have evolved at least twice, possibly three times, in *Sergestes* (Burkenroad 1937; Foxton 1972). The *S. sargassi*-*S. pectinatus* pair is distinct

from the others; again, *S. sargassi* is large and *S. pectinatus* is small, with specialized maxillipeds and broader vertical distributions day and night. The other two groups are more closely related, but the *S. armatus*-*S. vigilax* pair has longer maxillipeds than the *S. orientalis*-*S. tantillus*-*S. consobrinus* triad. *Sergestes armatus* is larger than *S. vigilax* and lives deeper at night; the other group has been discussed above.

Among the all-red Hawaiian sergestids, a similar organization prevails. The *Sergia inequalis*-*S. bigemnea*-*S. gardineri* group are respectively large, medium-sized, and small; in addition, *S. gardineri* lives shallower than the other two at night, and perhaps during the daytime. The *S. bisulcata*-*S. maxima* pair is related to the above triad, but *S. bisulcata* is somewhat larger than *S. inequalis* and lives deeper at night, while the rare *S. maxima* is extremely large. Two species without photophores are nonmigrators; *S. tenuiremis* is much larger than *Petalidium suspriosum*. The rare *S. laminata*, while related to *S. tenuiremis*, is smaller, has photophores (Walters 1975), and appears to migrate.

Studies of sergestid assemblages in the subtropical Atlantic by Foxton (1970) near Fuerteventura (Canary Islands) and Donaldson (1975) near Bermuda showed interesting parallels to the present study in the subtropical Pacific (Table 9). The two Atlantic areas were very similar to one

TABLE 9.—Atlantic and Hawaiian sergestid assemblages.

Hawaii	Bermuda ¹	Fuerteventura ²
<i>Sergestes consobrinus</i>	(<i>Sergestes edwardsii</i>)	n.e. ³
<i>Sergestes orientalis</i> }	n.e.	n.e.
(<i>Sergestes tantillus</i>) }		
<i>Sergestes armatus</i>	<i>Sergestes armatus</i>	<i>Sergestes armatus</i>
<i>Sergestes vigilax</i>	<i>Sergestes vigilax</i>	<i>Sergestes vigilax</i>
<i>Sergestes atlanticus</i>	<i>Sergestes atlanticus</i>	(<i>Sergestes atlanticus</i>)
(<i>Sergestes cornutus</i>)	<i>Sergestes cornutus</i>	n.e.
<i>Sergestes erectus</i>	" <i>Sergestes corniculum</i> " ⁴	" <i>Sergestes corniculum</i> " ⁴
<i>Sergestes sargassi</i>	<i>Sergestes sargassi</i>	<i>Sergestes sargassi</i>
<i>Sergestes pectinatus</i>	<i>Sergestes pectinatus</i>	<i>Sergestes pectinatus</i>
<i>Sergia fulgens</i>	(<i>Sergia talismani</i>)	n.e.
<i>Sergia scintillans</i>	n.e.	n.e.
<i>Sergia gardineri</i> }	<i>Sergia splendens</i>	<i>Sergia splendens</i>
<i>Sergia bigemnea</i> }	<i>Sergia robusta</i>	<i>Sergia robusta</i>
<i>Sergia inequalis</i>		
<i>Sergia bisulcata</i> }	<i>Sergia grandis</i>	n.e.
<i>Sergia maxima</i> }		
(<i>Sergia laminata</i>)	(<i>Sergia lillicta</i>)	n.e.
<i>Sergia tenuiremis</i>	<i>Sergia tenuiremis</i>	<i>Sergia tenuiremis</i>
n.e.	<i>Sergia japonica</i>	<i>Sergia japonica</i>
<i>Petalidium suspriosum</i>	—	—

¹From Donaldson (1975).²From Foxton (1970).³n.e. — no equivalent.⁴See text.

another except for the abundance of *Sergestes atlanticus* and *Sergia grandis* (Sund 1920) in Bermuda relative to Fuerteventura (the Fuerteventura material all came from a single cruise and may have lacked some of the less-abundant species). More surprising, the Atlantic sergestids were very similar to the Hawaiian species, particularly the half-red types. "*Sergestes corniculum* Krøyer 1855"³ replaced its close relative, *S. erectus* in the Atlantic, and two rare Bermuda species, *S. edwardsii* Krøyer 1855 and *Sergia talismani* (Barnard 1947), had close relatives, *Sergestes consobrinus* and *Sergia fulgens*, in Hawaiian waters; otherwise, all the half-red species in the two Atlantic studies also occurred in the present study. There were some differences in abundance and vertical distribution, partly real and partly due to differences in sampling. *Sergestes vigilax* was more abundant than *S. armatus* in the Atlantic studies, and *S. sargassi* was more abundant than *S. pectinatus*; the opposite was true in Hawaiian waters. *S. atlanticus* was more abundant near Bermuda and less abundant near Fuerteventura than near Hawaii. *Sergestes corniculum* was more broadly distributed at night than its Hawaiian counterpart, *S. erectus*. The biggest differences were the rarity or absence in the Atlantic collections of the *S. orientalis* types and the half-red *Sergia* species, both of which were abundant in Hawaiian waters. Still, the similarities between the subtropical Atlantic and Pacific were considerable: one or more large species with short third maxillipeds and with fairly deep nighttime distributions, one or two smaller species with short maxillipeds and living shallower at night (in Bermuda), and a variety of species with long maxillipeds occurring in closely related groups of large and small species.

The all-red sergestids also showed similarities between the subtropical Atlantic and Pacific, although the parallelism was not as striking as in the half-red types. *Sergia tenuiremis* was found in all three areas. The role of *S. gardineri* was filled in the Atlantic by the closely related *S. splendens* (Sund 1920). It was somewhat larger than *S. gardineri*, exceeding 11 mm CL, but had no po-

tential competition in the 10- to 15-mm CL size range like the Hawaiian *S. bigemina*. The nearest Atlantic equivalents of *S. inequalis* and *S. bisulcata*, respectively *S. robusta* (Smith 1882) and *S. grandis*, lived much deeper at night, in the 400- to 600-m zone, which was nearly devoid of sergestids around Hawaii. *Sergia flicta* (Burkenroad 1940) may be the Atlantic counterpart of *S. laminata*, but very little is known about either species. *Sergia japonica* (Bate 1881) had no Hawaiian equivalent, and *S. maxima* had no Atlantic equivalent. Neither Atlantic study mentioned *Petalidium*, so it is unclear whether there is an Atlantic counterpart to the Hawaiian *Petalidium suspiriosum* (*P. foliaceum* Bate 1881 occurs in the South Atlantic (Kensley 1971)). Both oceans thus contain an all-red assemblage consisting of one or more nonmigrators, a small, abundant species with a shallow nighttime range, and several larger species living deeper at night. In general, the Hawaiian area appears to have more half-red and fewer all-red sergestid species than the subtropical Atlantic.

While the parameters of Table 8 indicate that Hawaiian sergestids have partitioned the mid-water environment, this study has left unclear the ecological significance of most of the parameters. Differences in size, length of third maxilliped, and nighttime vertical range are presumably related to diet, but the data on feeding show little dietary specialization other than the ability of some species to eat submillimeter-sized zooplankton. A more elaborate study may reveal more subtle variations in diet, perhaps related to vertical distribution of prey or differences in hunting strategies. Daytime vertical distribution and color pattern seem most likely related to predation. Virtually nothing is known about predation on Hawaiian sergestids. The division of half-red sergestids into species with organs of Pesta and species with lensed cuticular photophores has an unknown ecological significance. Cuticular photophores are fixed in position, but I have observed sergestids with organs of Pesta rotating them through nearly 180°, maintaining a vertical orientation of the photophores regardless of the attitude of the animal (see also Omori 1974). Studies of live sergestids may reveal differences in behavior between the two groups related to the need for ventral countershading. Hawaiian sergestids appear to occupy distinct niches, but the niches cannot be defined yet in an ecologically meaningful way.

³Crosnier and Forest (1973) have reviewed the systematics of Atlantic species of Yaldwin's "*Sergestes corniculum*" species group. They replaced *S. corniculum* Krøyer with *S. henseni* (Ortmann 1893) and three new species—*S. paraseminudus*, *S. pediformis*, and *S. curvatus*. Donaldson's figure of *S. corniculum* corresponded to *S. curvatus*. Foxton gave no drawings of *S. corniculum*, but a later study in the same area, Foxton and Roe (1974) found *S. henseni* and *S. curvatus*.

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