QUANTITATIVE NATURAL HISTORY OF
PLEUROBRACHIA BACHEI IN LA JOLLA BIGHT

JED HIROTA[1]

ABSTRACT

An assessment of the quantitative natural history of *Pleurobrachia bachei* A. Agassiz was made by estimating growth rates, metabolic rates, distribution, abundance, occurrence of prey, predators and parasites, population parameters, and net production. These were then integrated to give an indication of the ecological significance of this animal in the plankton.

Rates of somatic growth and digestion of prey were observed in laboratory experiments and applied to field data. A comparison of growth curves of *P. bachei* at 20° and 15°C showed development rates from hatching to the same diameter which were 10–15 days faster at 20°C. In addition, a much higher mortality of the ctenophores was observed at 20°C. Maximum growth rate coefficients on a daily basis were 0.21–0.47 and were for 2.5- to 6.5-mm ctenophores (0.1–2 mg bodily organic weight). Studies on the rates of digestion of six frequently ingested prey species by various sizes of *P. bachei* showed marked differences between species. Although *Labidocera* was the largest prey offered, it was digested the fastest per unit weight.

The horizontal, offshore distribution of *P. bachei* postlarvae often showed maxima within 5 km from the shore and decreased about tenfold by 10 km. Patterns of water movement in La Jolla Bight were described as a prerequisite to the distributional studies. The near–surface current velocities showed counterclockwise rotational motion over the submarine canyon complex of La Jolla Bay; otherwise the water generally moved onshore and towards the north at speeds of about 5 km/day. The high abundances of the animal nearshore are believed to be caused in part by these water movements. The ctenophores occurred in the upper 50–60 m, living mostly in the upper 15 m in the day and at about 30 m at night. The range of average abundances of postlarvae was from 1,000/m² and 1,000 mg organic matter/m² in August to being nearly absent in December.

Hyperoche mediterranea, a parasitic amphipod, and *Beroë* sp., a potential predator, showed patterns in seasonal abundance similar to that of *P. bachei* postlarvae, except that *H. mediterranea* was absent in winter and spring. The higher frequency of occurrence of endoparasites with larger sized hosts and few multiple infections suggests that the parasites are adapted to prevent overexploitation of hosts. The stomach contents of postlarvae showed a pattern of larger prey in larger ctenophores, and within some prey species increasing frequency of occurrence in larger ctenophores was observed, e.g., *Acartia tonsa*. The diel and seasonal variations in stomach contents were also considered. Prey selection by *P. bachei* may be determined by the following attributes of prey: density, size, avoidance and escapement behavior, strength and protective spination.

Size–specific instantaneous mortality rates, the mean schedule of live births, and somatic growth rates were used to estimate population parameters and compute rates of net production. The highest rate of population growth was 0.02 on a per day basis, which would enable a population doubling in about 35 days. The first 50–100 eggs laid by young postlarvae are most important to replace the population. The mean and range of annual net production by postlarval *P. bachei* are 5.24 and 2.32–7.65 g organic matter per square meter; mean values for eggs and larvae are 0.08 and 0.10 g/m², respectively. The mean annual net production of all stages is 5.4 g/m², with 95% confidence limits for the mean being 4.4–6.5 g/m².

The ecological significance and functional role of *P. bachei* are as: 1) a seasonally dominant carnivorous zooplankter which preys selectively on small crustaceans and may regulate their abundances; 2) a vehicle which provides shelter and nutrition for parasites and; 3) an organism which transfers a substantial amount of organic matter and potential energy in the food web of La Jolla Bight.

Ecological studies may be grouped into four categories, depending on the level of complexity being considered: 1) single individuals, 2) single species populations, 3) communities, and 4) ecosystems. The long–term objective in ecology is the description of ecosystems. More specifically, two important objectives in studies of ecosystems are: the elucidation of complex interactions between species in a food web and the understanding and prediction of the dynamic processes that occur

[1]Scripps Institution of Oceanography, Institute of Marine Resources, La Jolla, CA 92037; present address University of Hawaii, Institute of Marine Biology, Kaneohe, HI 96744.

in this web. To obtain this information, one approach is the investigation of basic trophic relationships among the various developmental stages of different species in the food web (e.g. for herring, Hardy, 1924) and the quantitative measurement of matter or energy transferred along these paths (e.g., for a lake, Lindeman, 1942). From the four categories of complexity I chose to study *Pleurobrachia bachei* A. Agassiz at the single species population level. I have attempted to integrate three basic aspects of the population ecology of *Pleurobrachia* into a study of its quantitative natural history: 1) the structure of its food web, 2) the population parameters and attributes which most affect the population growth rate, and 3) the trophic–dynamic aspect of the quantitative transfer of organic matter. In previous work (Hirota, 1972) the culture and metabolism of *P. bachei* have been described.

Studies on the trophic–dynamics of marine planktonic food webs have concentrated on the measurement of primary production and the factors which influence its level. Mullin (1969) suggested that similar production studies of total zooplankton or of single species are few, because no simple, direct methods exist for the measurement of secondary production in situ. He stated that two basic approaches exist for these studies: the laboratory "carbon balance" study and the population dynamics approach. A somewhat more direct measurement could be made as a modification of the approach used in lakes by Haney (1971). In situ population feeding rates (measured using food particles labeled with isotopes) multiplied by the population gross growth efficiency is the rate of net production. This method has the advantages of being more direct and made in nature, but it is impractical for complex marine plankton communities with their numerous and relatively large, mobile species. It also requires detailed knowledge of factors which affect gross growth efficiency.

Most marine planktonic species are not amenable to culture in the laboratory for entire life cycles, and results of laboratory experiments may fail to represent accurately activity in nature. Present field sampling techniques and variability in plankton studies are often such that it is neither possible to obtain sequential samples from the same target population nor calculate the rates of biological activity. In spite of these difficulties and such severe limitations (Hall, 1964), more and better data are needed in different ecosystems from their functionally distinct component species before a clear understanding of the structure and dynamics of food webs is obtained and generalizations of predictive nature concerning the systems can be made.

Studies on the population dynamics and production of marine zooplankton (reviews by Mann, 1969 and Mullin, 1969) almost exclusively pertain to "herbivorous" calanoid copepods. At present little information exists on the production rates of carnivorous marine zooplankters (McLaren, 1969; Petipa, Pavlova, and Mironov, 1970; Sameoto, 1971), and the study of *Sergestes lucens* (Omori, 1969) is one with the supportive catch data of a commercial fishery. The lack of data for higher trophic levels is in part the result of an inability to culture and maintain delicate or large, mobile forms. Nearly all laboratory data on the long–term metabolism and life cycles of zooplankton species come from successful rearing of one or more generations of facultative herbivorous copepods (see Hirota, 1972 for references). Hamilton and Preslan (1970) and Gold (1971) have cultured ciliate protozoans.

The genus *Pleurobrachia* (Tentaculata, Cydippida) includes about 12 species (see Ralph and Kaberry, 1950 for the most recent summary of the species), some of which may be synonymous. The current taxonomic status of the synonymies in this genus is uncertain, because there are few sets of general characteristics which have been set up as important for the separation of species. In particular, some possibly distinct species have been grouped with the boreal species *P. pileus* O. Müller of the North Atlantic. One of these, *P. bachei,* is the boreal form which inhabits the Pacific coast of North America from Puget Sound to San Diego. This species is believed synonymous with *P. pileus,* based on the works of Moser (1909) and Mayer (1912). However, I agree with Torrey (1904), Bigelow (1912), and Esterly (1914) that *P. bachei* is a distinct and separate species. This distinction is supported by work in progress on the differences between these two forms in both meristic and metric characters (Hirota and Greve, unpubl. data).

Studies of spatial distribution, vertical migration, seasonal variations in numerical abundance, and natural history in the planktonic ctenophores have provided some data on natural populations, but information on population dynamics and rates of production are especially needed. Patterns of the geographic distribution of

Pleurobrachia species and other ctenophores have been described (Moser, 1909; Mayer, 1912), but no attempt was made to relate abundance quantitatively to geographic location. Only a few workers have studied vertical distribution of ctenophores (Esterly, 1914; Russell, 1927; Alvariño, 1967; Rowe, 1971) and only the study of *P. pileus* in Kaneohe Bay, Oahu (Rowe, 1971) could show that diel vertical migration occurs. *Pleurobrachia pileus* in Kaneohe Bay follow the "normal" pattern for zooplankton with the ctenophores living at depth during the day and moving up near the surface at night. However, the vertical displacement of the migrants was only on the order of 10 m because the bay is very shallow. More is known about quantitative seasonal changes in numerical abundance of *P. pileus* (Wear, 1965; Fraser, 1970; Greve, 1971) and *P. bachei* (Esterly, 1914; Parsons, LeBrasseur, and Barraclough, 1970). There are also numerous qualitative reports of ctenophore swarms in coastal waters (Chopra, 1960; Rajagopal, 1963; Fraser, 1970). Fraser (1962, 1970) reviewed the role of ctenophores and salps in marine food webs and their natural history. Greve (1970, 1972) provided laboratory studies of the effects of temperature, salinity, and food on growth of *P. pileus* and a field study (Greve, 1971) of variations in abundance of *P. pileus* and two of their predators, *Beroë gracilis* and *B. cucumis*. These studies did not relate seasonal variations in abundance to rates of population recruitment, growth, mortality, net production, or advection.

In order to describe the quantitative natural history of *P. bachei* as outlined above, it was necessary to sample natural populations and to carry out laboratory experiments. The field work was needed for data on the food web and for demographic purposes, and the laboratory data were used to calculate metabolic rates which could not be measured from field samples. Metabolic rates measured or calculated from individuals reared from eggs to adults in the laboratory were applied to field populations. Preliminary field studies were then made of the variations in abundance of *P. bachei* as a function of distance from shore. The vertical distribution was determined by sampling with opening-closing bongo nets (McGowan and Brown, 1966[2]) while

[2]McGowan, J. A., and D. M. Brown. 1966. A new opening-closing paired zooplankton net. Scripps Inst. Oceanogr. Ref. 66-23. (Unpubl. Manuscr.)

tracking parachute drogues in those locations where ctenophores were most abundant. From the data on water movement and the horizontal and vertical distributions of *P. bachei*, sampling stations and sample depths (the maximum depth to which a net sample is taken) were allocated for a study of spatial and seasonal variations in numerical abundance, standing stocks and net production. Size or stage–specific instantaneous mortality rates were calculated from the observed size–frequency distribution in field samples and development rates calculated from laboratory growth data. Standing stocks per unit area of sea surface were calculated as the summation of the organic weight (ash–free dry weight) of all individuals in a sample multiplied by the ratio of maximum sample depth to the volume of water filtered. The organic weights were estimated from regression equations of bodily weight on bodily diameter. Rates of net production per 24–h day were calculated from the estimated standing stocks of each stage and the stage–specific instantaneous rates of mortality and growth on a daily basis. For a given set of stage–specific instantaneous mortality rates, and using the mean schedule of live births derived from laboratory data, the following population parameters were calculated: T, r, d, b, C_x, which are the generation time, instantaneous rate of natural increase, death and birth rates, and stable age distribution, respectively. More than 12,000 specimens of *P. bachei* were counted and measured during the seasonal study, of which 1,352 postlarvae in 10 size classes contained partially digested food organisms and 1,007 postlarvae contained internal parasites of the hyperiid amphipod, *Hyperoche mediterranea*. Attempts were made to quantify changes in the absolute numbers and the proportions of various prey categories with changes in bodily size of *P. bachei*. A study of the seasonal variation in numbers of parasites, percent hosts parasitized, and the frequency distribution of numbers of parasites per host and percent hosts parasitized at different host sizes is also presented.

GROWTH IN CULTURE AND METABOLIC RATES

Methods

Techniques for the laboratory culture of *P. bachei* at 15°C have been described previously

(Hirota, 1972); culturing has also been done at 20°C to examine the effect of temperature on growth rates. The rates at which different prey species were digested were measured in the laboratory in order to make corrections for predation by *P. bachei* on the most abundant crustaceans during field sampling with nets (Judkins and Fleminger, 1972, discuss feeding by *Sergestes* in nets).

Six ctenophores were cultured from eggs at 20°C and about 20 μg C/liter as prey for the adult ctenophores in order to evaluate the effect of temperature on growth rate (the surface temperature in summer is about 20°C). The basic techniques were the same as described previously (Hirota, 1972, Table 1), except that adult *Paracalanus parvus* replaced *Artemia* nauplii as food for 2– to 3–mm ctenophores. In this manner, it was possible to raise ctenophores without "artificial" foods of any kind and instead raise them on prey species which they utilize in nature. In addition, antibiotics (streptomycin sulfate and penicillin G each at concentrations of 50 mg/liter) were added after 4 wk of culturing at 20°C when several specimens appeared very weak or moribund. When changes in bodily diameter indicated that the last two specimens might also die, the experimental temperature was changed back to 15°C to determine whether or not recovery might occur and whether the mortality effect was due to lethal temperature.

In order to determine whether or not a prey species found in the gut of *Pleurobrachia* sampled with nets was eaten prior to or during capture, a number of observations were made of the rate at which five prey species were ingested and digested after initial entanglement with the tentacles. The time elapsed to achieve one of four scores was recorded during observations with a dissecting microscope through the transparent bodily wall of the ctenophore. These scores are: (4) the prey enters the mouth and is in the distal half of the stomach; (3) the prey is moved into the proximal half of the stomach but no digestion of the prey is indicated; (2) the prey is being digested and assimilated, as indicated by less than 10% of the bodily tissues clearing and the occurrence of prey tissues in the aboral, transverse, and pharyngeal canals; (1) the prey is almost fully digested and assimilated, as indicated by transparent skeletal remains (crustacean exoskeletons are not digested) and the presence of digested tissues throughout the canal network. The elapsed time to achieve a given score was then compared to the maximum time period a prey organism was at risk in the net sample with the ctenophores. This time period is the elapsed time from the start of the tow until preservative was added to the sample jar. Those prey found in the ctenophore stomachs whose score required more time than the maximum period at risk are presumed to have been eaten in nature prior to capture by the net.

Results and Discussion

The growth curve of bodily diameter up to 6 mm at 20°C indicates similar patterns as is the case for 15°C (Hirota, 1972, Figure 1), except that the development rates to the same bodily diameter are 10–15 days faster at 20°C (Figure 1). The other important differences are: 1) very much higher mortality rates at 20°C than at 15°C, 2) 60% mortality despite the addition of antibiotics on day 29, and 3) the recovery and prolonged growth and survival of two specimens after the temperature was lowered to 15°C from 20°C when growth had ceased at 20°C. Note that there is a lag of over a week before the apparent effect of lowered temperature is indicated by a response in bodily diameter. The significance of the effect of temperature on growth rate will be discussed below in relation to the stratification of water temperature in nature, the diel vertical distribution of the ctenophores, and the effect of these distributions on seasonality in the standing stocks and net production of the ctenophores.

Using the data for growth in bodily diameter at 15°C (Hirota, 1972, Figure 1), it is possible to calculate rates of growth in bodily organic weight from regressions of organic weight on bodily diameter (Figure 2). A curve for the mean growth in organic weight and the ranges for weight at a given age and age at a given weight are shown in Figure 3. The mean growth rates are highest from 0.1 to 2 mg (2.5 and 6.5 mm diameter, respectively); the exponential growth rate coefficients on a daily basis are 0.21–0.47. Below 0.1 mg and over 2 mg the exponential growth rates are slower, the values being 0.12–0.17 and 0.04–0.17, respectively. The range for weight at a given age is about tenfold and for age at a given weight about 15 days.

The rates of digestion of five prey species are shown in Table 1. These data show that undigested prey present in ctenophore stomachs (scores 4 and 3) can be ingested during a 0.3– to
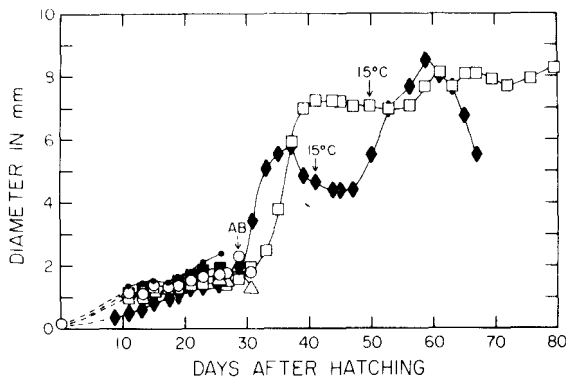
FIGURE 1.—Growth in bodily diameter of *Pleurobrachia bachei* at 20°C, expressed as a function of age in days. Each symbol represents measurements of a different individual. The point indicated by AB refers to the starting date with antibiotic additions and the points indicated by 15°C refer to change of the experimental temperature from a constant 20°C to a constant 15°C. All ctenophores died after the last observation shown for each individual, except that one which was still alive after 80 days.

5-min period at risk while both the predator and prey are being sampled by nets. Partial or fully digested states (scores 2 and 1), however, required more than 9 and 15 min, respectively. Prey of scores 2 and 1 in ctenophore stomachs are, therefore, very likely to have been ingested by ctenophores prior to capture by nets in samples of short duration (i.e., less than 5 min). Only prey of these scores were used in the study of stomach analyses presented below, unless the prey were too small to be retained by the 0.363–mm meshes of the net and, therefore, were not at risk to predation during the sampling. Examples of these smaller prey species not at risk are nauplii of *Acartia* and all stages of *Euterpina acutifrons,* a copepod of 0.7 mm length.

Measurements of the organic weight of six species of "important" planktonic marine crustaceans in La Jolla Bight are given in Table 2. The first four species are copepods and the remainder are cladocerans. Note that for adults, *Labidocera* is tenfold larger than *Acartia* and *Evadne* and about twentyfold larger than *Paracalanus, Corycaeus,* and *Penilia.*

A trend exists in the data for scores 2 and 1 when the respective medians for the elapsed time to achieve these scores are expressed per unit bodily organic weight for each prey species (Table 1). *Labidocera trispinosa* is the most easily digested prey per unit bodily mass although it is the largest. *Acartia* is digested slightly faster than
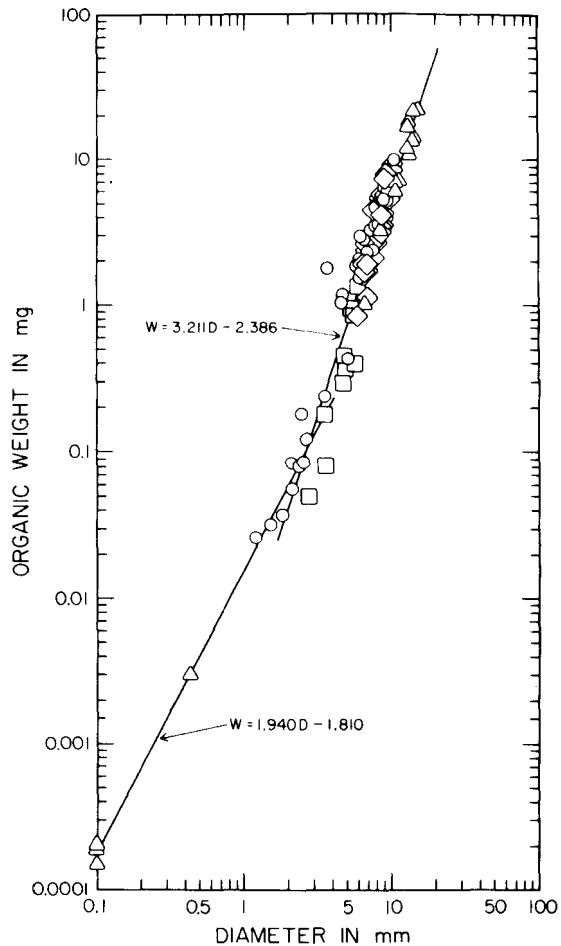

FIGURE 2.—The relationship between bodily organic weight and bodily diameter of *P. bachei* on a double logarithmic scale. The open circles represent data on field-collected ctenophores from La Jolla, Calif.; the triangles represent data on laboratory cultured ctenophores; and the diamonds and squares represent data on ctenophores grown in the deep tank facility at Scripps Institution during experiments 1 and 2, respectively. The lowest four values are calculated from determinations of organic carbon. In the equations the upper line is for ctenophores larger than 3 mm and the lower line for those smaller than 3 mm. In both equations $W = \log_{10}$ (bodily organic weight in milligrams) and $D = \log_{10}$ (bodily diameter in millimeters).

Paracalanus and each of these faster than either *Corycaeus* or *Penilia.* Part of the cause for the delay in digestion of *Corycaeus* and *Penilia* relative to the above–mentioned calanoid copepods is the protective spination. In addition to stout furcal spines, caudal rami, and very sharp projecting corners of the last thoracic joint, *Corycaeus* has a large, smooth cephalothorax which encloses much of the bodily tissues and may retard penetration of digestive enzymes. The spi-

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nation causes great difficulty for the movement of this prey into the proximal half of the gut where digestion occurs. For example, the median time for score 3 of *Acartia* is significantly shorter than the corresponding median of *Corycaeus* as determined by a *U*–test *(P<0.05)*. Similarly, the rigid bifurcate rostrum, caudal spines, and denticulate carapace of *Penilia* are often hooked into the gut wall of the ctenophore and delay passage of the prey to the site of digestion. Contrary to this delay in the passage of *Corycaeus* and *Penilia,* the relatively smooth–bodied calanoids are translocated quite easily by peristalsis of the gut. More detailed studies might indicate differences in the integument to penetration by the digestive enzymes or perhaps differences in the specificity of the enzymes for protein or lipid components of the substrate.

FIELD ECOLOGY OF *P. BACHEI*

Study Area and Previous Plankton Work

The study location is La Jolla Bight (long. 117°20'W, lat. 33°N), including the coastal waters (hereafter coastal waters refers to that area bounded by the shoreline and a line parallel to it out to a distance of about 8 km) south to Point Loma and north to Oceanside (Figure 4). The major physiographic features of the area are: 1) Point La Jolla, which extends about 2 km west of the shoreline at Scripps Institution and forms the southern boundary of La Jolla Bight; 2) two submarine canyons (La Jolla and Scripps Canyons) in La Jolla Bight which bring water over 100 m deep within 2 km of shore; 3) numerous kelp beds located both north and south of Point La Jolla generally in 10– to 20–m depth and extending out to 1 km from shore. The area is not strongly influenced by precipitation and runoff, so that seasonal and annual variations in salinity are within 32–34 ‰ (Fager, 1968). The range of sea–surface temperature is 14–21°C annually and approximates the temperature difference between the surface and 50 m in July (Mullin and Brooks, 1967). The tides are of a mixed semidiurnal type with a diurnal inequality and total daily range that change twice each month. Within a given month the maximum daily tidal range is about 2 m and the minimum about 1 m. Wind velocities are highly variable; storms with wind speeds greater than about 7 m/s generally come from the southwest to the northwest quadrant. Santa Ana winds blow occasion-
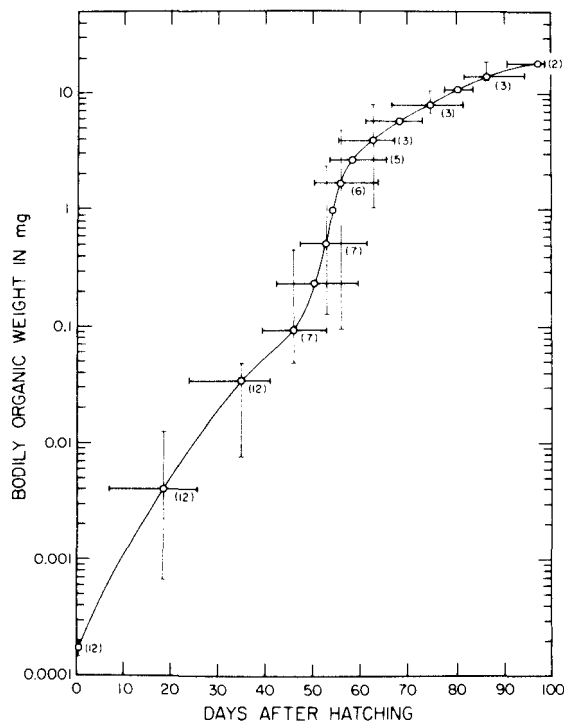

FIGURE 3.—Growth in bodily organic weight of *Pleurobrachia bachei* at 15°C during the second laboratory generation, expressed as a function of age in days. The values for bodily organic weight at different ages were calculated from the observed growth in diameter and a regression of organic weight on diameter. The horizontal and vertical bars indicate the ranges for age at weight and weight at age, and the numbers in parentheses are the number of specimens observed in the data.

ally from the northeast in fall, and diel variations in wind velocities predominate in the east–west directions.

Previous plankton work in the study area include the extensive phytoplankton work of Allen (1928, 1941), the California Cooperative Oceanic Fisheries Investigations programs, and the plankton study off La Jolla by the Food Chain Research Group (Strickland, 1970). In general these previous studies provide basic information on species lists and levels of abundance and variability of phytoplankton, microzooplankton, and macrozooplankton. In these coastal waters, however, very little information is available on the patterns of water circulation, variations in abundance of organisms in relation to variations in the physical parameters (e.g., tidal motion, wind velocities etc.), or the organization and interaction of the species which inhabit this coastal region.

TABLE 1.—Rate of digestion experiments at 20°C for individual adults of five prey species and various sizes of *Pleurobrachia bachei*. Medians and ranges are given for the diameters of the ctenophores used in the trials and for the elapsed time in minutes from the prey entanglement with the tentacles until each score of digestion is achieved. The values in parentheses are the medians for the elapsed time to achieve scores 2 and 1 divided by the bodily organic weight of each respective prey. Refer to the Methods for details.

Diameter					Score of digestion			
	(mm)	Prey	Trials	4	3	2	1
Md	10.9	*Labidocera*	5	1.00	2.67	20	46
W	7.6-12.4	*trispinosa*		0.42-2.84	1.58-8.50	14.5-35	37->60
						(0.23)	(0.53)
Md	6.4	*Acartia*	12	0.50	1.83	15	25
W	2.0-11.7	*tonsa*		0.25-1.50	0.92-3.00	10-29	18-45
						(2.08)	(3.47)
Md	7.2	*Paracalanus*	9	1.00	2.29	12	21
W	2.0-11.7	*parvus*		0.25-2.00	1.00-6.00	9-27	15-37
						(3.16)	(5.53)
Md	7.5	*Corycaeus*	7	0.33	3.0	16	30
W	4.0-10.3	*anglicus*		0.04-1.50	1.0-6.0	9->35	18-37
						(5.3)	(10.0)
Md	8.0	*Penilia*	4	1.83	4.8	>40	—
W	5.4-12.0	*avirostris*		0.42-2.84	0.83->9	21->50	—
						(10.1)	—

TABLE 2.—The mean and range of organic weight of six prey species of *Pleurobrachia bachei*. F, M, A, CV, and J refer to females, males, adults, fifth copepodids and juveniles, respectively.

Prey category		Mean (µg)	Range (µg)	Number of observations
Labidocera trispinosa	F	88	85-94	3
	M	86	83-89	2
	CV	29	—	1
Acartia tonsa	A	7.2	6.2-7.9	8
Paracalanus parvus	A	3.8	3.7-3.8	2
Corycaeus anglicus	F	2.2	—	1
	M	3.4	3.0-3.5	3
Penilia avirostris	A	3.6	3.3-4.0	3
	J	1.2	1.1-1.2	2
Evadne tergestina	A	7.4	6.8-8.2	3

Methods

The three main physical parameters considered in the course of the field studies are current velocity, water temperature, and tidal stage. Current velocities in La Jolla Bight were measured on five occasions between November 1969 and June 1970 by tracking surface floats attached to parachute and "vane" drogues (vane drogues were made of
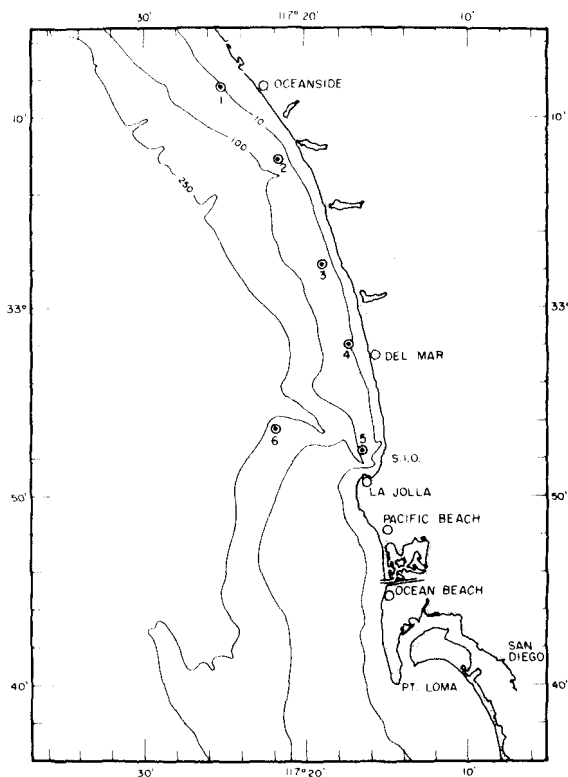

FIGURE 4.—The study area: La Jolla Bight and adjacent waters. Sampling stations 1-5 and 6 are located 1.6 and 10 km offshore, respectively. The juncture of Scripps Canyon with La Jolla Canyon is near station 5. The depth contours are in fathoms.

parachute silk attached to a wooden frame, creating three intersecting planes normal to each other; each plane covers about 9 m²) set at depths in or near the thermocline (about 15-m depth). During the field studies surface temperatures were measured by bucket thermometer to the nearest 0.1°C, and the vertical distribution of temperature was measured by mechanical bathythermograph (BT) or salinity–temperature–depth recorder (STD). Tidal heights for the time of particular events are taken from tide calendars for predicted tides by the U.S. Coast and Geodetic Survey for La Jolla.

For studies of the offshore and seasonal distributions of *P. bachei* two types of nets were used. The net to collect postlarval ctenophores (i.e., ctenophores larger than 0.5 mm in diameter) is a ring net of 0.5 m diameter and 0.363-mm mesh apertures. This net was used for oblique sampling. The second net is a 0.17-m diameter ring net of 0.035-mm mesh apertures equipped with a 20-cm metal collar that attaches the net onto the wire. This net was towed vertically, and it was used for sampling the eggs and larvae of *Pleurobrachia* and the smaller zooplankters which were available as prey but not sampled quantitatively by the 0.363-mesh net. Both nets were equipped with a calibrated TSK (Tsurumi-Seiki Kosakusho) flowmeter[3] to measure volumes of water filtered.

Two studies of the vertical distribution of *P. bachei* were made, the first during 3–6 November 1969 and the second during 22 May–1 June 1970. In both cases, 0.7-m diameter paired, opening–closing bongo nets with mesh apertures of 0.053 and 0.153 mm were used. In each vertical profile of abundance, four to six depth intervals were sampled at 10- to 20-m intervals for shallow depths and at greater intervals below 50 m. Thus, a set of four to six pairs of samples comprised each vertical profile. The volumes of water filtered were between 5 and 50 m³, as determined from calibrations of numerical settings on the net release gear against the calculated cubic meters of water filtered using a TSK flowmeter.

In all cases net samples were preserved with 10 ml of 40% formaldehyde solution, buffered with calcium carbonate, in about 750 ml of seawater. This solution is about 0.5% formaldehyde. Preliminary experiments with preservation of

Pleurobrachia showed this to be the best concentration and type of preservative. Relatively small changes occur in length frequencies of *P. bachei* after 27 mo in this preservative (Table 3).

A preliminary survey of the horizontal, offshore distribution (the distribution of numerical abundance of *Pleurobrachia* in samples taken at increasing distances from the shore) was made on 28 August 1969. Samples were taken at 10 stations with closely spaced intervals out to 11 km from shore off Scripps Institution. Results of this study showed that the ctenophores occurred in highest abundances within 3 km of shore.

Samples were taken in the following manner during the two field studies of the vertical and offshore distributions of *P. bachei* mentioned above. In both studies of vertical distributions, about 10 sets of four to six pairs of samples were taken alongside or between parachute and vane drogues. Each sample set permitted the description of abundances at various depth intervals for one time of the day. In the study of November 1969 the offshore distribution sampling consisted of six transects of stations perpendicular to shore. The transects were about 3–8 km apart, beginning off Del Mar and ending off Point Loma. Each transect consisted of three or more stations located between 1 and 13 km from shore. In the second study the offshore distribution sampling consisted of two transects of seven and nine stations out to 50 km from shore. In all offshore distribution studies replicate samples were taken at each station except in five cases where time prohibited it or second samples were lost.

TABLE 3.—Changes in size-frequency distribution of *Pleurobrachia* with duration in 2% Formalin-seawater preservative. Samples A and B were analyzed 16 and 12 days after sampling, respectively, and a second time after 27 months as indicated in columns A' and B'. The variable indicated is the number of occurrences of each size class. One specimen in sample A was lost.

Mean diameter (mm)	A	A'	B	B'
¼	0	0	1	0
1	10	10	64	69
2	28	24	28	28
3	23	23	17	15
4	12	11	3	1
5	5	4	1	2
6	11	14	4	3
7	5	6	1	3
8	6	8	2	0
9	2	1	1	1
10	2	2	2	2
11	0	4	0	0
12	5	1	0	0
13	2	2	0	0

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[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service.

From 8 March to 1 May 1970 sampling for the seasonal variations in the coastal plankton was done at stations located between Del Mar and Scripps Institution 1–3 km from shore. Results of the study of current velocities during 22 May to 1 June 1970 indicated that the plankton were advected northward on the order of tens of kilometers per week. Therefore from 18 June 1970 to 2 June 1971 the sampling stations for seasonal variations in the coastal plankton were changed to those six stations in Figure 4. Five stations are located 1.6 km from shore about 8 km apart between Oceanside and Scripps Institution, and the sixth station is located about 8 km beyond the station off Scripps. Replicate samples were taken at stations 1–5 with each of the two kinds of ring nets described above. Samples with only the 0.363–mm mesh net were taken at station 6. Analysis of the 0.363–mm mesh net samples, as described below, was carried out on samples at all stations from 8 March through 29 August 1970 (this period includes the seasonal maximum in abundance). From 29 August 1970 to 2 June 1971 mainly samples from stations 1, 3, 5, and 6 were analyzed once it became apparent that the variations between the five stations parallel to shore could be about as well accounted for by variations at stations 1, 3, and 5.

Samples were taken on two occasions for special studies related to the diel variation in predation by *Pleurobrachia*, their stomach contents in net tows of short duration and their selectivity of prey species with which they co–occur. During a field study from 23 to 27 July 1971, five sets of triplicate samples were taken with the 0.5–m net of 0.363–mm mesh in the upper 50 m off Del Mar. Three of these sets were taken at midnight and two sets at midday. All samples were sorted and counted as described below. The ctenophores were measured and the stomach contents identified to determine whether diel variations exist in: 1) the proportion of ctenophores which contain prey and 2) the numbers and kinds of prey which occur in stomachs during the day and at night. This study is important because all other information about the stomach contents of *P.* bachei during the seasonal study were derived entirely from samples taken between 0900 and 1600 h. On 25 August 1970 a pair of samples was taken at the surface with the 0.363–mm mesh net on station 5 at 1500 h. The tows were for 60 s duration and the maximum period which prey were at risk is 95 s. Samples were sorted and counted and the stomach

contents of ctenophores identified for: 1) comparison of these prey species to other data from field samples of longer sample durations and periods at risk, and 2) calculations of the electivity indices of prey on a numerical and organic weight basis. Counts were made of all zooplankters in 2.5% subsamples of each net tow, and the proportions of prey in stomachs and in the net samples were used to calculate electivity indices (Ivlev, 1961).

Whole samples of each of two replicates per station taken with the 0.363–mm mesh net were sorted at 6–12× magnification under a dissecting microscope, and all postlarval ctenophores were counted and measured in polar diameter with an ocular micrometer. These procedures apply to all field samples taken for the offshore distribution, seasonal distribution, and special sets of samples taken for the analysis of diel variations in feeding and prey selectivities. For the sets of samples taken during the seasonal study, postlarvae of one or the other replicate sample selected at random were dissected and the contents of stomachs identified and given one of four scores described above. All specimens were examined if there were less than about 100/sample, but during a few periods of high abundances subsamples of about 50 specimens were taken. For each of 30 sampling dates between 8 March 1970 and 2 June 1971, data on stomach contents of about 100 specimens were obtained, except on those dates with very few specimens captured in all samples lumped together. For these same ctenophores which were measured and dissected, counts were also made of the numbers of larval and early juvenile stages of the facultative endoparastic amphipod, *H. mediterranea*. Also enumerated in these samples of the seasonal study were the numbers of adult and late juvenile *H. mediterranea*, which were not attached to ctenophores, and the numbers of *Beroë* sp.

Each replicate sample of the eggs and larvae of *P. bachei* taken at station 5 with the 0.035 mm mesh net was concentrated to 400 ml by settling overnight, siphoning off the excess water and transferring it to a graduated cylinder. Each of two subsamples of 20 ml was removed by Stempel pipet, examined under 12–25× magnification and the numbers of eggs and larvae counted. Numbers per square meter of sea surface were calculated as ten times the total numbers in both subsamples times the ratio of the sample depth in meters to the volume of water filtered in cubic meters.
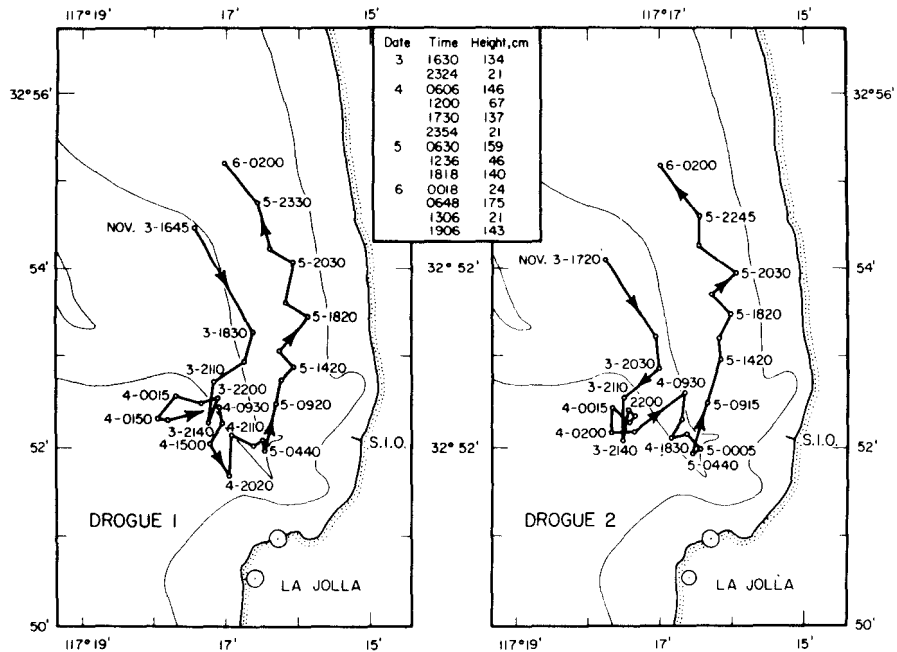
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FIGURE 5.—Trajectories of two drogues during the field study of 3-6 November 1969. Observed positions of the drogues are indicated by the open circles, and the date and time of the triangulation are indicated by the one-four digit sequence of numbers near the circles. The date and predicted times (Pacific standard time) and heights of tides in centimeters are given in the inset.

Estimates of the standing stocks of food available to *P. bachei* were obtained from counts of prey taxa in subsamples of the 0.035-mm mesh net samples at station 3, the centrally located station (Figure 4). These pairs of replicate samples were treated in a manner similar to the counts of ctenophore eggs and larvae, except that counts of all zooplankters were made in a 5-ml subsample of a 500-ml sample. Over 100 specimens were counted in each subsample. The counts of numbers were converted to mass of organic carbon using the data from six species (Table 2) which frequently occur in these waters, data in the literature, and approximations by proportions of body volumes relative to the known mass of species for which data exist.

Counts of ctenophores in samples for vertical distribution studies were made as follows. First, all large ctenophores which could be seen by the unaided eye were removed with pipets from one of the pair of bongo net samples selected at random. When no further specimens could be found by eye, subsamples of 5-12.5% of the whole sample were taken by Stempel pipet or Folsom splitter and examined under 12-25× magnification for all

sizes of ctenophores, including larvae and eggs. The diameters were measured as described above. Numbers per cubic meter were calculated by appropriate corrections for subsample fraction and volume of water filtered.

Results

Physical Parameters and Distribution of *Pleurobrachia*

Patterns in the currents of La Jolla Bight appear to be affected by: 1) the configuration of the coastline (especially in the Point La Jolla–La Jolla Cove complex, 2) the bottom topography and bathymetry in the La Jolla Canyon–Scripps Canyon complex, and 3) the surface tides. During the first field study in November 1969 a pair of drogues drifted toward Point La Jolla, paralleling the axis of La Jolla Canyon during an ebb tide (Figure 5). Both changed directions several times over La Jolla Canyon and made a complete counterclockwise rotation before moving northward nearly parallel to shore. Note that the rotational motion and major changes in direction occur over
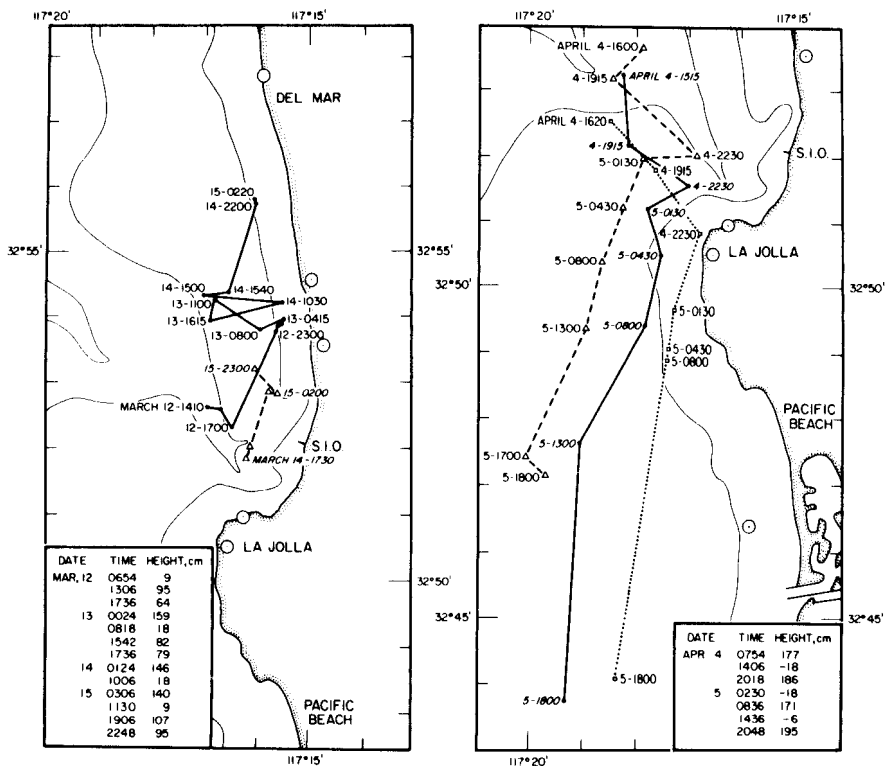
FIGURE 6.—Trajectories of drogues during studies on 12–15 March and 4–5 April 1970. Observed positions of the drogues are indicated by open circles, triangles and squares, and the date and time of the triangulation are indicated by the one–four or two–four digit sequence of numbers near the symbols. The respective dates and predicted times (Pacific standard time) and heights of tides in centimeters are given in each inset.

or near La Jolla Canyon. The surface tides associated with the commencement of the rotational motion were slack ebb tides, and completion of the loops during rotation occurred during flood tides. From 1800 h 3 November until 2300 h 4 November wind speeds were less than 3 m/s with variable direction. From 0240 h 5 November until 0600 h 6 November the winds increased to a steady 3–5 m/s from the south southeast to south southwest. The northward drift of the drogues after 0400 h 5 November may have been a response to changes in the wind velocity. Some changes in direction occurred on the northward drift of the drogues once they were beyond the submarine canyon complex, but these were relatively slight. While the drogues were over shallow water, the mean drifts were slightly onshore during flood tides and slightly offshore during ebbs. The net eastward drift was about 0.3 km and the westward drift about 1 km relative to a line true north at 0400 h 5 November.

During two other drogue studies on 12–15 March and 4–5 April 1970 drogues were tracked for 1 to 2 days. The study of March 1970 provided the best information associating the surface tides with changes in direction (Figure 6). A drogue set in the axis of La Jolla Canyon drifted slowly toward the southeast along the canyon axis until flood tides changed its direction to northeasterly. On the following slack flood tide the drogue slowed and then moved offshore toward the west on the next ebb and smaller flood. The onshore–offshore motions occurred during the following flood–slack–ebb sequences but are not as well associated with the surface tide as in the first cycle. During this drogue study the weather was foggy, especially in the early morning hours, and the winds were less than 3 m/s during the day from the northwest. At night and in the early morning hours offshore winds were about 2–4 m/s. Note that the east–west horizontal translation during a tidal cycle is on the order of 1-2 km. This effect will
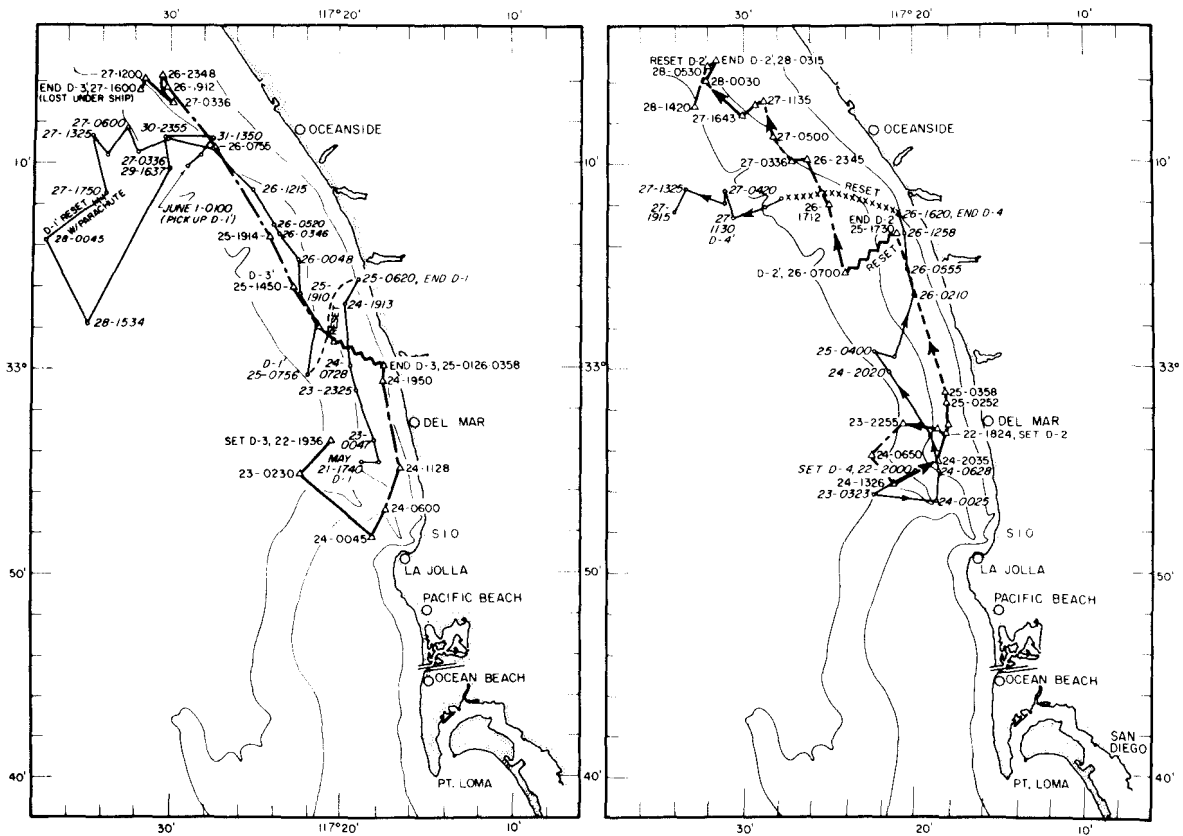
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FIGURE 7.—Trajectories of four drogues during the study of 22 May to 1 June 1970. Observed positions of the drogues are indicated by circles and triangles for each pair of drogues, and the date and time of the triangulation are indicated by the one–four or two–four digit sequence of numbers near the symbols. Reset drogues indicated by primes refer to other drogues placed into the water after ones placed earlier either ran aground or broke down. Refer to the text for further details.

be considered below as one of the physical variables which may affect the offshore distribution of *Pleurobrachia* and present a bias in the sampling program for estimates of ctenophore abundance in the coastal waters. In the study during April 1970 three drogues set in a line about 1 km apart in a north–south direction moved southeast toward Point La Jolla on flood tide and changed direction on ebb tide, moving west or southwest (Figure 6). After moving beyond Point La Jolla all drogues continued toward the south. Note that after 0800 h the two drogues closest to the shore apparently became detached from their surface floats in kelp beds, because only the floats were recovered at the end of the study, 1800 h 5 April. No dramatic changes in direction occurred with changes in the surface tide for the drogues off Pacific Beach. Wind data were not recorded for this study, but the weather reports for 4–5 April indicated easterly

winds at 6 m/s in the morning becoming westerly at 4–7 m/s in the afternoon.

The current velocities measured with drogues in La Jolla Bight for periods up to a week confirmed the presence of a counterclockwise gyre over or nearby the La Jolla Canyon complex (Figure 7). The four drogues moved northward, generally paralleling the shore and finally ran aground or broke down near Encinitas and Carlsbad, seasonal sampling stations 3 and 2, respectively. Drogues which ran aground or lost the subsurface parachute or vane were reset nearby the other drogues. Drogues no. 2 and 3 were reset about 5 km from shore, and they continued to move northward parallel to shore until they were lost. Drogues no. 1 and 4, however, tended to move offshore. Drogue no. 1 made a large counterclockwise loop about 16 km long and returned to cross its original path about 5 days later. Mean
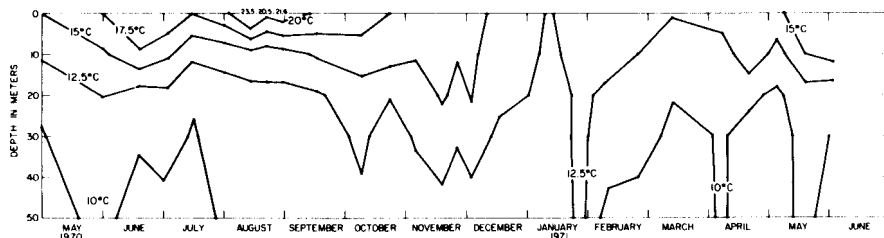
FIGURE 8.—Distribution of water temperature during the seasonal study at stations located 1.6 km from shore.

wind velocities during the study were: southwesterly at 3 m/s from 23 to 26 May, northwesterly at 5 m/s from 27 to 28 May, and northwesterly at 3 m/s from 29 May to 1 June. The range on any given day was 0–7 m/s. No clear pattern of the effect of wind velocity on drogue trajectory was observed.

From these studies the limited data for "near–surface waters" indicated predominantly northerly flow near the coast with some counterclockwise rotational motion in La Jolla Cove and off Oceanside. Some data also showed small scale onshore-offshore motion associated with the surface tidal cycle. South of Point La Jolla the currents on one occasion indicated southerly flow and little east–west motion associated with tidal cycles. The larger scale rotational motion off Oceanside was not associated with a promontory and a submarine canyon complex and remains to be explained by other means.

The water temperature in the upper 50 m for the period from May 1970 to June 1971 was measured by BT casts at stations 1–5. Since the stations were located in water of different depths, only the upper 20 m values were represented by averages for all stations. Data at 30 m were from stations 2, 3, and 5; data at 50 m were only from station 5. Thermal stratification began in May and June and reached maximal development in August and early September (Figure 8). The 12.5°C isotherm rose to the surface in January, and at this time the smallest gradients were found. Note that the annual temperature range at the sea surface was almost identical to the range of temperature in mid–August between the surface and 20 m.

The vertical distribution of *P. bachei* on 3–6 November 1969 (Figure 9) showed three main features: 1) very low abundances below 50 m for those profiles which sampled that deep, 2) the pattern of vertical distribution indicates that *P. bachei*
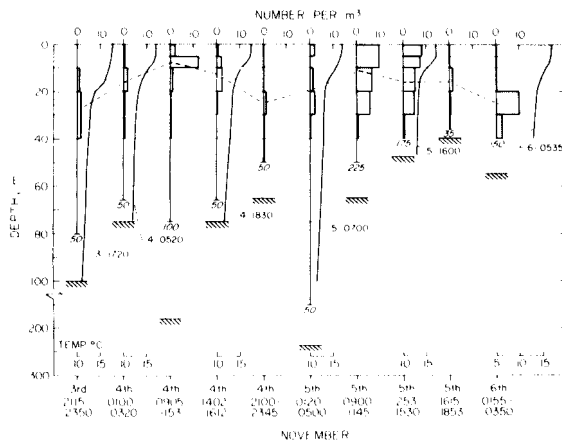

FIGURE 9.—The vertical distributions of *Pleurobrachia bachei* and temperature during the study of 3–6 November 1969. The scale of numerical abundance is given at the top, and the scale of temperature and the time interval required to sample each profile are given at the bottom of the figure. Note that the depth is given with a change of scale below 100 m. The hatched lines below each profile indicate the sea bottom and the numbers at the last sample depth give the approximate numbers of ctenophores per square meter of sea surface. The dashed line between successive profiles connects the centers of gravity of the distributions.

occurred nearer the surface during the day and deeper at night, and 3) the extent of the "vertical migration" as measured by diel vertical displacement of the center of gravity of the population was less than 20 m. The modal class of ctenophore sizes at all depths was 8 mm with a range from 4 to 12 mm. Neither larvae nor eggs were found in these bongo net samples. Vertical separation of different size classes of ctenophores was slight, the 20– to 40–m depth interval consisting of a modal size class at 9 mm and the 0– to 5–m interval consisting of a modal size class at 6 mm. Note that the relatively small vertical movements of *P. bachei* enabled these animals to spend part of the day in or above the thermocline near 17°C and part of the
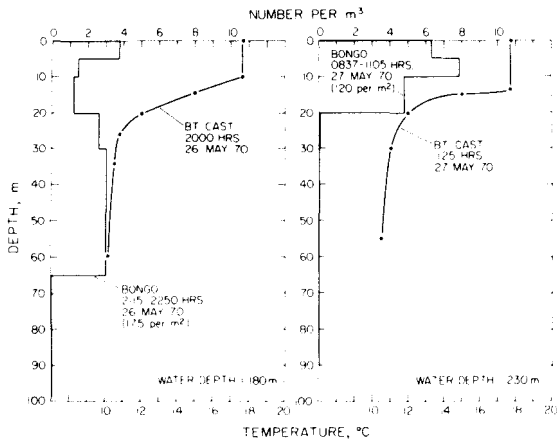
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FIGURE 10.—The vertical distributions of *Pleurobrachia* and temperature during the study of 22 May to 1 June 1970. Profiles are during the evening of 26 May and the following morning. The times of sampling, the depth of the water, and the numbers of ctenophores per square meter of sea surface are also indicated.

night at about 13°C. In addition, individuals may have been displaced from each other horizontally during the migration by currents moving at different velocities at different depths (Hardy, 1935). A physical process of this nature superimposed on the biological activity of diel vertical migration may help account for the observed variations in numbers of ctenophores per square meter. Profiles taken from 0900 to 1530 h 5 November and from 0155 to 0350 h 6 November indicated abundances threefold or fourfold higher than at other times. It is apparent that following a target population with drogues will have limited success over increasingly longer time periods, even for cases in which vertical migration is restricted to shallow depths.

The vertical distribution of *Pleurobrachia* on the evening of 26 May 1970 and the following morning (Figure 10) showed patterns similar to those observed in November 1969, but with more clearly defined vertical migration from about 40 m at night to about 10 m the next morning. Note that very low abundances occurred below 65 m day or night. The size frequency distribution of ctenophores in these samples was more rectangular than in the previous November, with a range of 1–12 mm and the 5–9 mm sizes being most frequent. Again no larvae or eggs were found in these bongo samples, and it is suspected that these smaller, more delicate stages may have been broken during sampling or they did not occur in sufficient abundance to be counted in small subsamples.
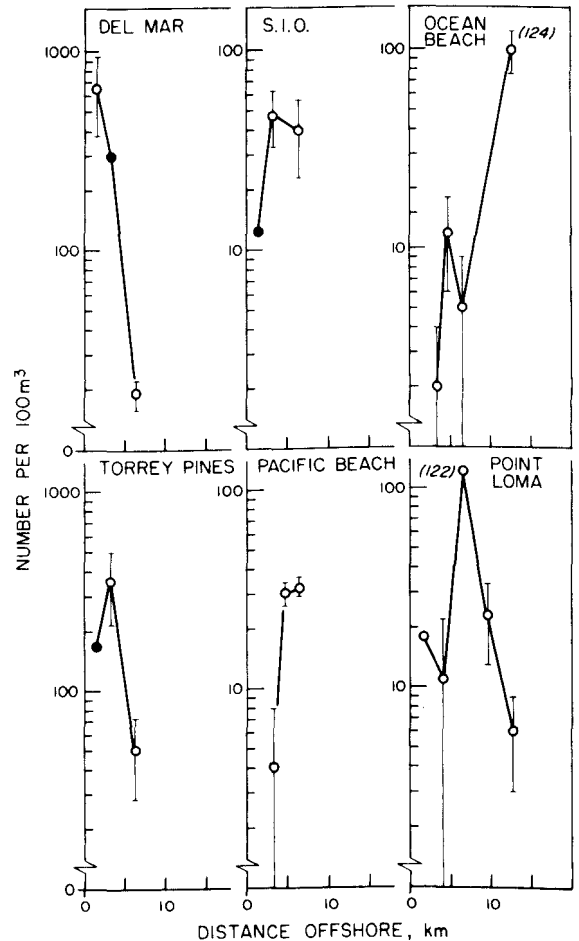
FIGURE 11.—The horizontal, offshore distribution of *Pleuro-brachia* postlarvae on 6 November 1969 at stations along six transects perpendicular to shore. Note the tenfold greater abundance off Del Mar and Torrey Pines and the break of scale in order to account for absence data. The vertical bar represents the range of values for the replicate samples, and dots indicate that the range is less than the size of the dot; the open symbols off Point Loma without any vertical bar are single observations.

Thermal stratification was more pronounced than in November 1969, and these ctenophores experience a 7°C average temperature differential during the course of diel migration.

The horizontal, offshore distribution of postlarval *P. bachei*, as deduced from three field studies, indicated higher abundances at the shoreward stations and lower abundances offshore (Figures 11 and 12). Note that: 1) data are presented on semilogarithmic plots to the same linear scale of distance offshore, 2) there is a tenfold lower abundance scale shift for stations located south of Scripps Institution in Figure 11, and 3) breaks occur in the scale of abundance to account for
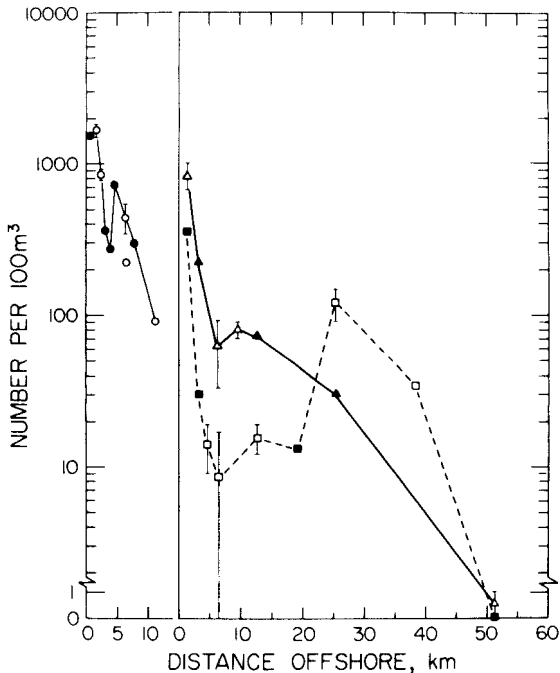
FIGURE 12.—The horizontal, offshore distribution of *Pleurobrachia* postlarvae on 28 August 1969 (circles) and 29-30 May 1970 (triangles and·squares). The profile indicated by the triangles is off Scripps Institution and that indicated by squares is off Encinitas, about 20 km to the north. Note that both distributions are plotted to the same scale of distance as in Figure 11 and that the scale of abundance is broken in order to account for absence data. The vertical bar represents the range of values for the replicate samples, and solid symbols indicate that the range is less than the size of the symbol; open symbols without any vertical bar are single observations.

samples with absences. Shifts were found in the offshore locations of the highest ctenophore abundances at different positions along the coast (Figure 11). All sampling over the six lines of stations was completed between 0700 and 2300 h, 6 November. At the northernmost station at Del Mar, highest values were closest to shore and decreased over tenfold by 6.4 km. Off Torrey Pines, Scripps Institution, Pacific Beach, and Point Loma the observed maxima were located between 3.2 and 6.4 km. The exceptional case was the maximum abundance observed beyond 10 km off Ocean Beach. The surface tides associated with these six lines of stations were slack flood tide at Del Mar and Ocean Beach, slack ebb at Scripps Institution, flood at Pacific Beach and ebb at Torrey Pines and Point Loma (refer to the inset of Figure 5 for the times and heights of tides). The nearshore maximal abundance at Del Mar may

represent the slack flood tide onshore movement of water and ctenophores, while the ebb and slack ebb tides at Torrey Pines and Scripps Institution, respectively may have caused offshore movements of surface water and ctenophores such that the maximal abundances occurred at 3.2 km. After sampling the outer stations off Scripps Institution, a strong southerly wind about 10 m/s generated short period swells 1–2 m high. Increased wind stress and turbulence may have altered the current pattern south of Point La Jolla and added considerable variation to the expected pattern of the distribution. The presence of high abundances of salps in the net tows at stations off Ocean Beach and Point Loma, which were not present north of Scripps Institution, indicated that the water to the south was different in faunal composition than the normal coastal assemblage. On 28 August 1969 and 29–30 May 1970, the offshore distributions indicated a tenfold decrease in abundance in the first 10 km from shore (Figure 12). The maximal abundances between 1 and 2 km were associated with slack flood or flood tides nearing slack flood. The secondary peak at 5 km on 28 August occurred during sampling on midebb tide, and it may

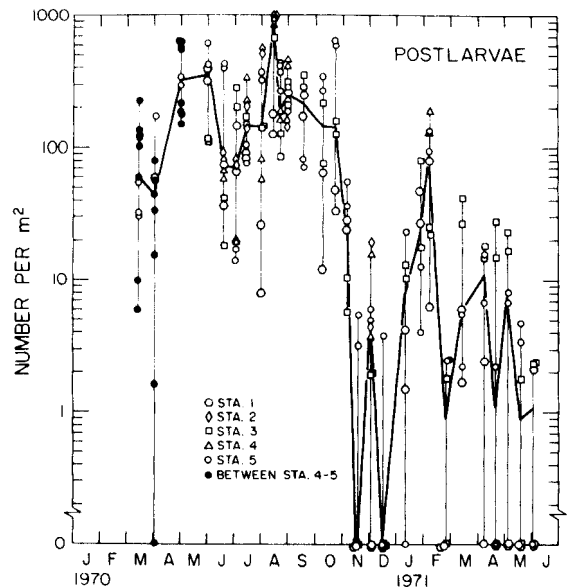FIGURE 13.—Seasonal variation in abundance of *Pleurobrachia* postlarvae from 8 March 1970 to 2 June 1971 at stations located 1.6 km from shore. The solid line connects the medians of each sample date. Note the break of scale to account for absence data. Each type of symbol represents a different station, except for those sample dates prior to May 1970. Refer to the text for details of the field sampling.
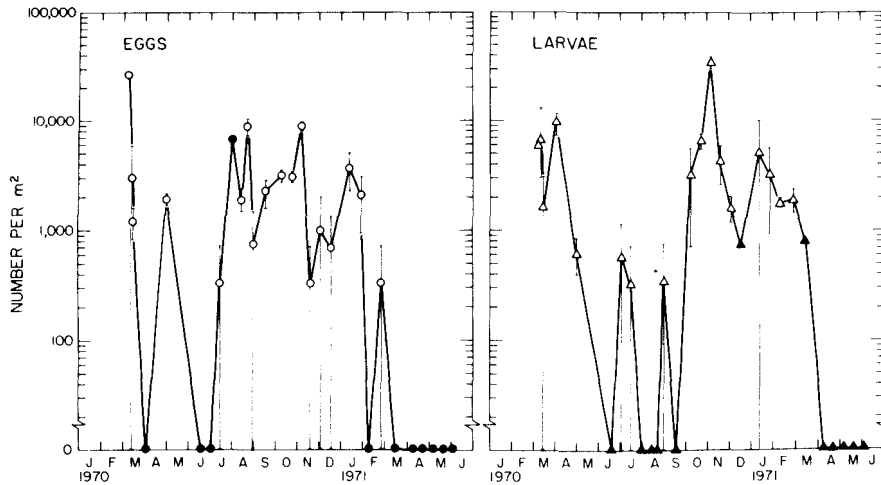
FIGURE 14.—Seasonal variation in abundance of *Pleurobrachia* eggs and larvae from 8 March 1970 to 2 June 1971 at station 5 located 1.6 km offshore at Scripps Institution. The solid line connects the mean of the replicate samples for each sampling date. The vertical bar represents the range of values for the replicate samples, and solid symbols indicate that the range is less than the size of the symbol; open symbols without any vertical bar are single observations.

represent the offshore movement of the high ctenophore abundance while field sampling was taking place. Note the secondary peak in abundance which was 25 km from shore. Deviations from an exponential decay function are perhaps the result of coastal water eddies (Figure 7), which move offshore with their surface–living species and give rise to offshore aggregations in moderate abundance. An important question to resolve is whether or not the expatriated or advected aggregations are able to survive, grow, and reproduce as well in offshore areas as they do in the coastal waters.

Seasonal variations in abundance of *P. bachei* postlarvae, larvae, and eggs on semilogarithmic plot indicated different patterns between these stages in life history (Figures 13 and 14). Recall that egg and larval abundances are based on samples from station 5 only, whereas those of postlarvae are based on the replicate tows of three to five stations. Note the wide range for the median in abundance of postlarvae (Figure 13), which usually was on the order of one–fifth to five times the overall median. In several instances the values from different stations were closer to each other than they were to their respective replicate sample at the same station. This indicates that spatial heterogeneity within a station on the scale of 100 m was often as large as the spatial plus temporal heterogeneity between stations on the scale of 8

km apart in distance and 1 h apart in time to 32 km apart in distance and 5 h apart in time. The 95% confidence limits for the mean of replicate samples at one station is the mean multiplied and divided by 2.15 (determined by two–way analysis of variance estimate of the mean square error using 90 pairs of replicate samples at five stations from 18 June 1970 to 2 June 1971). The 95% confidence limits for the mean of all stations at one sampling date is the mean multiplied and divided by 6.23 (also determined by the two–way ANOVA referred to above). The ratio of the 95% confidence limits for the mean of all stations at one sampling date to that for the mean of replicate samples at one station is 8.4 (the ratio is equal to $6.23^2/2.15^2$). This latter residual variability is comprised of time–dependent physical variations plus spatial variation and is 1.8 times larger than replicate sample error ($1.8 = 8.4/2.15^2$). The seasonal pattern of postlarvae showed high abundances in May to October 1970, low values in November–January and moderate densities in February–June 1971. Note that median abundances in March–June 1970 were one or two orders of magnitude higher than the same interval in 1971. The seasonal distribution of larval abundance was 180^c out of phase with that of postlarvae for most of 1970 (Figure 14). In 1970 larval numbers were low during the summer maximum of postlarvae and highest in November when post-

larvae were in very low abundance. The abundance of eggs was generally the same as that for larvae, except for the absence of eggs in April 1970 and the high abundances of eggs relative to larvae in August–September. There were about 1,000–10,000 eggs/m² in August–September, which are presumed to be spawned by the high abundance of postlarvae. The hatching time of eggs is about 24 h at 15°C, so that the low densities of larvae during this time were the result of large seasonal changes in hatching success, increased mortality rates of larvae, or both, assuming that the observed abundances were not determined mainly by physical processes. The data on seasonal variation in length frequency distributions of postlarvae considered below will provide some information to support the interpretation of increased larval mortality. From the abundance of eggs, larvae, and postlarvae at station 5 it was calculated that on 13 March, 1 May, 31 July, 21 August, 5 November, and 27 January the eggs and larvae made up 89–99% of the numbers of individuals per square meter. On 13 August the eggs and larvae constituted 69% of the total population. The sample dates in which the eggs and larvae made up a very low percentage of the population are those in June 1970 and April–June 1971.

During the seasonal study 18 pairs of replicate samples were taken between 31 July 1970 and 2 June 1971 at both stations 5 and 6, 1.6 and 10 km off Scripps Institution, respectively. The mean abundance of postlarvae per cubic meter was calculated at each respective station on each sampling date, and a U–test was performed on these means to determine whether or not medians of mean abundance over time were significantly different at stations 5 and 6. The null hypothesis is no significant difference, with a one–tailed alternate hypothesis that the median of station 5 is greater than that of station 6. Results indicate significantly greater median abundance at station 5 than at 6 (P<0.025). The median difference is a factor of 4.2 and the mean difference is a factor of 4.8. This result supports the three offshore distribution studies which indicated decreasing abundance with increasing distance from shore. However, the observed decrease in abundance in the first 10 km from shore was about tenfold for the offshore distribution studies and about half this for the seasonal study. The discrepancy of a factor of two is probably real and may be caused by sampling bias in relation to stage of the tide and to seasonal changes in the patterns of currents. The
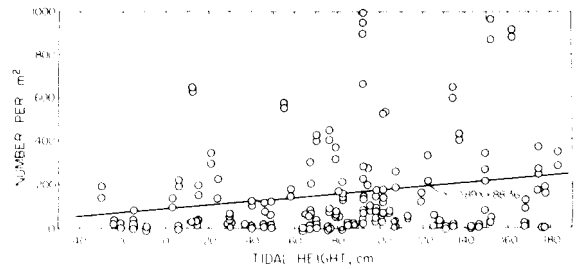
FIGURE 15.—The relationship between abundance of postlarval *Pleurobrachia bachei* and the tidal height. The abundances are in number per square meter of sea surface (Y), and the heights are in centimeters (X) for samples at all stations located 1.6 km from shore. The data are for all stages of the tide.

more accurate measure of variations in abundance with distance offshore should be found in the seasonal comparisons, but more carefully planned sampling could now be carried out to better sort out variations due to small scale tidal motions, larger scale "true" spatial variations offshore, and the effect of other types of motion and the wind on patterns of abundance.

When all of the 180 samples for the seasonal study (15 samples on five sampling dates are excluded from the analysis as five or fewer ctenophores occurred in all samples lumped per date) are plotted against predicted tidal height in centimeters for all tidal stages (Figure 15), the resulting least squares regression is $Y = 0.89X + 88.36$. Y is the number of ctenophores per square meter and X is the tidal height in centimeters. The slope of the line is significantly different from zero in a two-tailed t–test (P<0.01). It is surprising to find a significant positive regression coefficient. The strength of the test is in the many degrees of freedom and the removal of 15 samples which might otherwise tend to pull the line down toward a zero slope because of frequent absence data at any tidal height. This result is unexpected because the tidal currents are probably not the same at different locations along the coast. Variations exist in depth, bottom topography, exposure to wind, strike of the beach, etc. The pattern of circulation will also be differentially affected by spatial and temporal variations in the wind field. The results suggest that over an annual average, abundance at any one time and place of sampling could be affected by as much as a factor of four due to tidal variations alone at locations 1.6 km from shore. This average range due to tidal effects is about the same magnitude as the annual average difference between mean abundances of stations 5
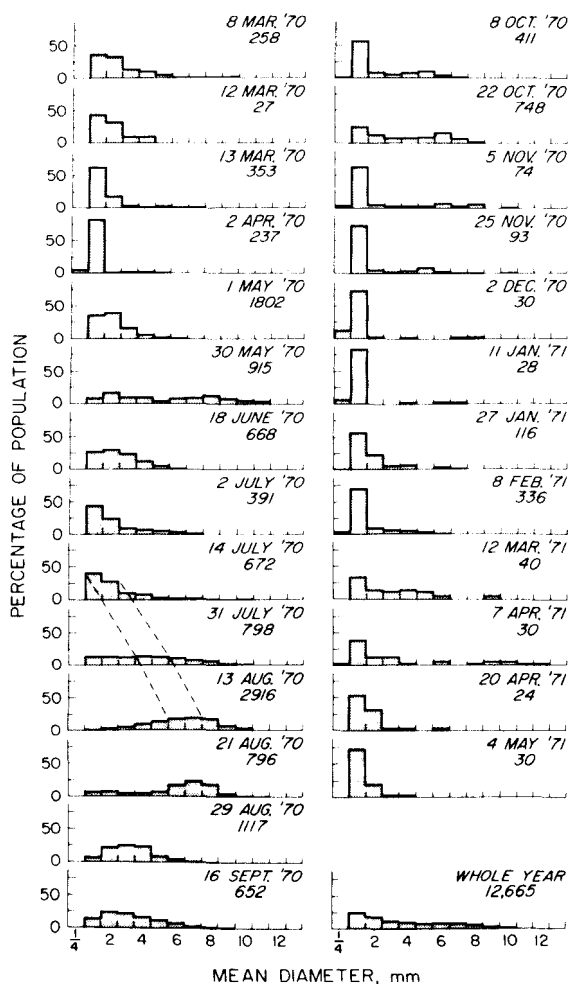
FIGURE 16.—Seasonal variations in the size frequency distributions of *Pleurobrachia bachei* captured by the 0.363-mm mesh 0.5-m net, expressed as the percentage in each size class of total numbers of all sizes on each sampling date. Each histogram is based on all sample data from each respective sampling date. The date and number of individuals measured are given with each histogram.

bility of the 0.363-mm mesh to retain larvae quantitatively. At sporadic intervals the size–frequency distributions show drastic changes, and these are attributed to immigration of individuals in advected water. Between 14 July and 21 August 1971 note the decline in proportion of 1 and 2 mm sizes and a shift in modal class from 1 to 7 mm. During this same period the occurrences of eggs and larvae showed that while up to 9,000 eggs/m² were present in the water, seven of eight samples for larvae indicated none present (Figure 14). Assuming that these changes in size–frequency distribution over the 4-wk period are the result of biological activity rather than sampling error and advective change, it is con-
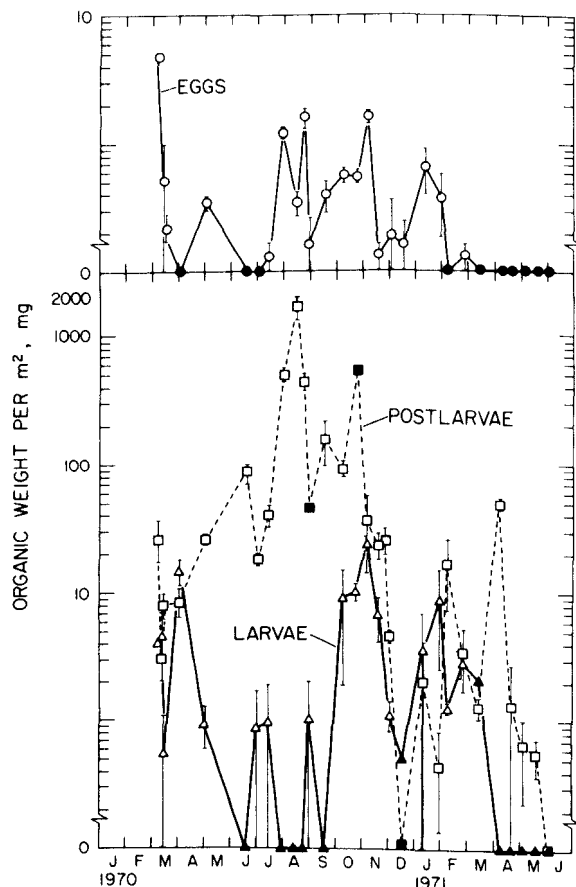
FIGURE 17.—Seasonal variations in standing stocks of postlarvae, larvae, and eggs at station 5. Each type of line connects the respective mean values for the replicate samples at each sampling date. The vertical bar represents the range of values for the replicate samples, and solid symbols indicate that the range is less than the size of the symbol; the open symbols without any vertical bar are single observations.

and 6, whose difference should be less influenced by tidal currents and represents the order of true spatial variation within the first 10 km from shore.

The size–frequency distributions of postlarvae for the 8 March 1970–2 June 1971 period indicate that most of the year the 1- to 2-mm size classes made up the highest proportion of all postlarvae (Figure 16). The lower abundance of the 0.25-mm class relative to the 1-mm class is the result of sampling gear mesh selectivity caused by the ina-

cluded that the ctenophore population was releasing eggs into the water but that the larvae were eaten or died from other causes as fast as they were hatching from eggs. A feedback control mechanism which can account for the presumed high mortality of larvae, high abundance of eggs, and rapid growth of postlarvae is discussed below.

The calculated development rate from 1.5 to 6.5 mm in 30 days from field sample data is about 10 days slower than the growth rates in laboratory cultures at both 15° and 20°C.

Patterns in the seasonal distribution of standing stocks of postlarvae, larvae, and eggs at station 5 (Figure 17) are similar to the respective seasonal variations in numerical abundance. Postlarval values in 1970 increased from March to a seasonal maximum of 1,500 mg organic matter/m² in August, then decreased to a minimum in December. The range over the year for standing stock of postlarvae was about four orders of magnitude. Note that the mean standing stock of larvae was high relative to that of postlarvae in April and November 1970 and the following winter months. Except for a few instances in August and September, the mean standing stock of larvae was about twofold to tenfold greater than that for eggs. The crops for postlarvae were about equal to those of the larvae, except from May to October when they were much greater.

Seasonal Variations in Parasites, Predators, and Prey

Coincident with seasonal variations in the abundance and size frequency distribution of postlarval *P. bachei* are variations in abundance of the hyperiid amphipod, *H. mediterranea* (Figure 18). The data shown are from station 5 off Scripps Institution, but patterns in the seasonal distribution 16 and 32 km to the north (stations 3 and 1, respectively) are essentially the same. Plots of abundance per square meter on a semilogarithmic scale are for postlarval ctenophores, attached endoparasitic larvae and early juveniles of *H. mediterranea*, and unattached free-living late juvenile and adult *H. mediterranea*. The appearance of *Hyperoche* in the plankton is associated with *P. bachei* when the abundance of hosts exceeded about 100 ctenophores/m², which was May–June to November 1970. Prior to June 1970 and after January 1971 *H. mediterranea* was sparse enough to be absent in 6 to 10 samples of
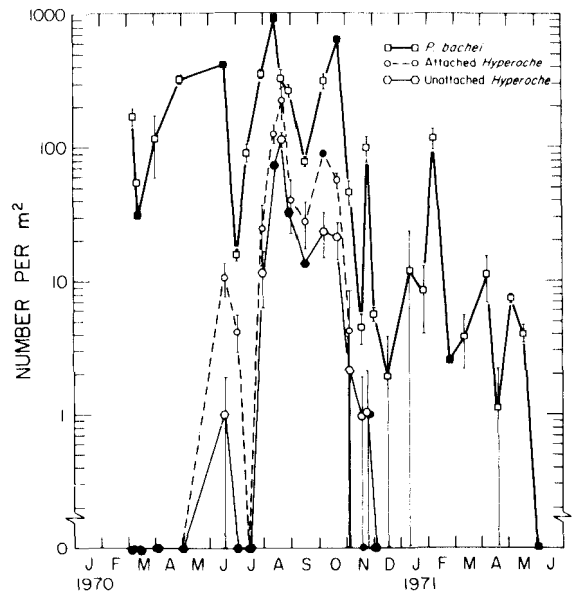
FIGURE 18.—Seasonal variations in numerical abundance of postlarval *Pleurobrachia bachei* and attached (endoparasitic) and unattached (free-living) *Hyperoche mediterranea* at station 5. Values are expressed as number per square meter of sea surface in logarithmic scale, and the lines connect respective means at each sampling date. The vertical bar represents the range of values for the replicate samples, and solid symbols indicate that the range is less than the size of the symbol. *Hyperoche* was absent after December 1970.

15–20 m³ each. Maximal abundance of *Hyperoche* occurred about a week after the ctenophore maximum, and may represent an "overshoot" phenomenon in a density–dependent, parasite–host system. Note that the larger amphipods occurred in highest abundance when most postlarval ctenophores were at 6–8 mm sizes. Little concerning the dynamic aspect of this parasite-host interaction can be deduced from the data because of uncertainties in immigration and emigration over time. In August and September 1969–72 the occurrence of *Hyperoche* in and on *P. bachei* has been noted during plankton sampling. The co–occurrence and relative abundance of these two species is predictable and should follow the same pattern from year to year, with temporal shifts in the maxima and minima, depending on the type of "meterological year" and the sequence of events that occur in the plankton during the increase and decline of the ctenophore summer–fall maximum. The important problems to resolve are where the amphipods occur in the winter–spring months, and whether the observed seasonal pattern of co–occurrence is determined

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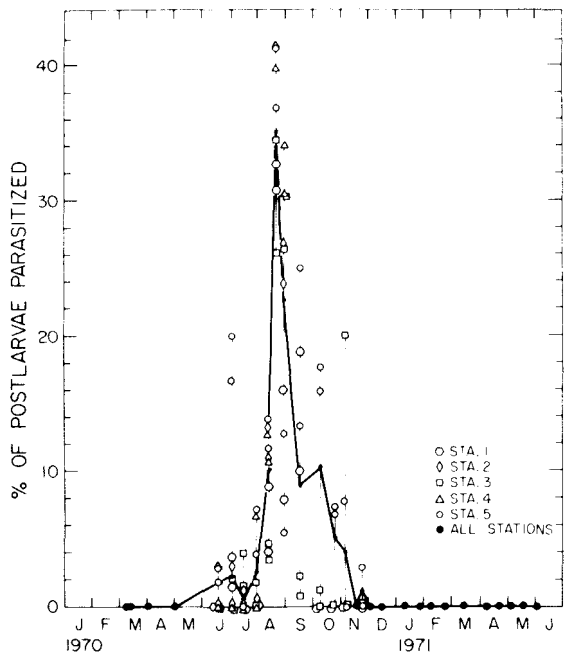
FIGURE 19.—Seasonal variation in the percentage of postlarval *Pleurobrachia bachei* parasitized by *Hyperoche mediterranea* at five stations located 1.6 km from shore. The line connects the mean value at each sampling date, and the various types of open symbols represent different stations.

by a periodic convergence of water types containing *Hyperoche* and *Pleurobrachia*.

Data from all stations during the seasonal study were plotted as the percentage of postlarval *Pleurobrachia* containing one or more *Hyperoche*. The mean percentage over time shows that August was the month of highest percentage hosts parasitized (Figure 19); at this time over one in three postlarvae were infected. The rate of increase of percentage infection appears to be faster than the decrease, although the range of 3 mo time around the maximum was the same for both. The very large variability on some sample dates was more a result of differences in percentages between stations than an artifact of sample size, since several hundred ctenophores were examined per sample date.

The frequency distributions of the percentages of total occurrences and of total numbers of parasites for single and multiple infection and for different sizes of hosts show two interesting results (Table 4). First, there is a central tendency in the percentages of total occurrences of parasites, and in the total number of parasites, with 6–8 mm sizes being the most frequently infected. This re-

sult is caused by the seasonal distribution of parasites in relation to the seasonal distribution of length frequency of postlarval *Pleurobrachia* (see Figures 16 and 18). Note that the 6–8 mm sizes with highest frequency of infection are at the size range for beginning reproduction as adults indicated by results from laboratory cultures. Also notice that only about 1% of all postlarvae in the 1- to 2-mm size classes were parasitized. These are the sizes of ctenophores which reproduce at an early age with small numbers of eggs. Secondly, the distribution of percentages of total occurrences and total numbers of parasites for single infection and multiple infection show a decreasing occurrence of multiple infection, such that over 90% of the occurrences and numbers of parasites are as one, two, or three parasites per host.

Seasonal variations in abundance of *Beroë* sp., a known predator of other ctenophores, show a pattern very similar to that of *P. bachei* (Figure 20). The data plotted are numbers per 2 m² (the sum of numbers per square meter of each replicate sample) at station 5. The distributions show seasonal maximum values in July–October with secondary high abundances in winter months. This pattern of seasonal co–occurrence is similar
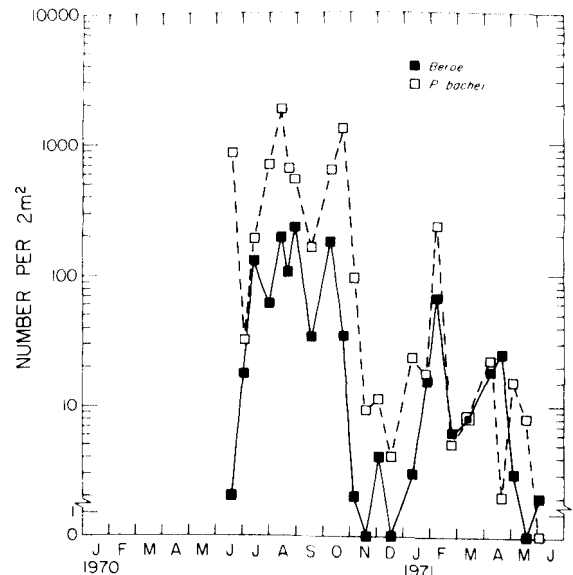

FIGURE 20.—Seasonal variation in the numerical abundance of postlarval *Pleurobrachia bachei* and postlarval *Beroë* sp. at station 5. Values are expressed for simplicity as the numbers per 2 m² (the sum of numbers per square meter in the replicate samples). The range for the mean of replicate samples has been indicated previously (e.g., Figures 13 and 18).

TABLE 4.—The frequency distribution of the number of parasites per host for 14 size classes of postlarval *Pleurobrachia bachei*, the percentage of total occurrences (A) and of total numbers (B) of parasites for each size class, and the percentages of total occurrences (C) and of total numbers (D) of parasites for single and multiple infections. The blank spaces indicate absences.

Mean diameter (mm)	Number of parasites per host									
	1	2	3	4	5	6	7	8	A	B
1		1							0.10	0.14
2	9	2							1.09	0.92
3	42	10	7	1					5.96	6.19
4	100	30	8	1					13.80	13.37
5	82	35	9	3	1				12.91	13.94
6	147	29	11	7	2	1		1	19.66	20.63
7	145	31	10	3			1		18.87	18.21
8	119	36	7	4					16.48	16.22
9	58	14	1	1					7.35	6.61
10	20	6	1						2.68	2.49
11	4	3							0.70	0.71
12	1			1					0.20	0.36
13	1								0.10	0.07
>13		1							0.10	0.14
C	72.29	19.66	5.36	2.09	0.30	0.10	0.10	0.10		
D	51.78	28.16	11.52	5.97	1.07	0.43	0.50	0.57		

to that of *P. bachei* and *H. mediterranea,* except that *Beroë* persists through the year rather than being absent for the winter and spring months. The patterns in the seasonal distribution of *Beroë* and *P. bachei* at station 3 were much the same as at station 5, except that the abundance of *Beroë* was fourfold lower at station 3, and the secondary high abundances of *Beroë* in the winter and spring months at station 5 was not as well defined at station 3.

The partially digested stomach contents of *P. bachei* captured at the surface in tows of short duration (60 s duration, 95 s maximum period at risk to feeding in the net) showed that the same species groups occur as in tows of fivefold longer duration. These species are : 1) copepods—*L. trispinosa, A. tonsa, P. parvus, C. anglicus, E. acutifrons,* and 2) cladocerans—*Evadne nordmanni, E. spinifera, E. tergestina,* and *P. avirostris.* The results provide evidence to support the contention (see results of stomach contents below) that the prey in stomach contents of *P. bachei* captured in tows of short duration are those which were ingested and digested in nature prior to capture by the net. The same species would probably occur in stomachs of *P. bachei* if the ctenophores were pipetted from the sea surface and preserved immediately. Seven species of zooplankton, which were retained quantitatively in the 0.363–mm mesh net as adults, were considered in calculations of electivity indices. In the Ivlev electivity index, $E = (r - p)/(r + p)$, r and p being the proportions of a food item in the stomach and in the environment respectively. *Paracalanus parvus, C. anglicus,* and *E. acutifrons,* which occurred frequently in the stomachs but passed through the net, were not included in the calculations. The results on the basis of numbers show moderate positive selection for *Acartia, Labidocera,* and *E. tergestina;* high positive selection for *E. nordmanni* and *E. spinifera;* and moderate and strongly negative selection for *Penilia* and *Sagitta* (Table 5). The indices on the basis of organic weight show the same trends, but the values for both copepods and *Evadne* are increased somewhat, and that for *Penilia* decreased, due to differences in bodily weights. *Penilia* has a negative electivity and was a slowly digested prey species (Table 1), whereas *Labidocera* and *Acartia* have positive electivity indices and were more rapidly digested. Prey selection by *Pleurobrachia* is more complex than dependence on prey digestibility alone. Data on the stomach contents of *P. bachei* during the seasonal study and observations in the laboratory of avoidance behavior and prey protective mechanisms will be discussed below in the context of prey selection.

In the study of diel variation in feeding, differences in the percentage of ctenophores with

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TABLE 5.—Electivity indices for seven species of zooplankton which are retained by the 0.363-mm mesh net as adults. The range for the mean is calculated from the replicate samples from the proportion of the numbers and the proportion of the calculated organic weight present in the sample and in the stomach of the ctenophores. Refer to the text for further details.

Prey Species	On a numbers basis		On an organic weight basis	
	$\bar{E}$	range E	$\bar{E}$	range E
Acartia tonsa	0.191	0.118-0.264	0.464	0.434-0.495
Labidocera trispinosa	0.130	0.099-0.160	0.413	0.408-0.419
Evadne tergestina	0.244	0.183-0.305	0.506	0.430-0.582
E. nordmanni	0.806	0.748-0.864	0.953	0.936-0.970
E. spinifera	0.770	0.748-0.792	0.776	0.659-0.893
Penilia avirostris	−0.345	−0.300 to −0.391	−0.055	−0.143 to +0.033
Sagitta euneritica	−1.000	−1.000 to −1.000	−1.000	−1.000 to −1.000

TABLE 6.—Diel variation in the percentage of ctenophores which have empty stomachs. The numbers in parentheses are the numbers of specimens examined per sample.

Replicate sample	Midnight station			Midday station	
	A	B	C	A	B
1	70 (27)	62 (40)	75 (8)	69 (16)	62 (32)
2	76 (38)	76 (41)	57 (46)	77 (13)	64 (14)
3	71 (55)	90 (10)	62 (26)	71 (24)	67 (18)

empty stomachs at midnight and midday were small, the medians being 71% and 68%, respectively (Table 6). These medians are not significantly different as determined by a two-tailed U-test ($P>>0.20$). It is concluded that no day–night differences exist in the proportion of the postlarval ctenophores feeding, at least at the time of this study.

The prey categories most frequently found during the diel study in both day and night stomach contents were copepods and cladocerans—*A. tonsa*, unidentified copepods, *P. parvus*, copepod nauplii, *Clausocalanus* spp., *E. tergestina*, *C. anglicus*, *Oithona* spp., *E. acutifrons*, *Oncaea* spp., and unidentified material. In these samples *A. tonsa* was over 50% of all prey by numbers. The species which were present in stomachs of *P. bachei* captured at night include the same groups captured during the day, the larger and deeper-living

copepods, euphausiids and other crustaceans being absent in the stomachs. If redundancy in the presence of prey species day and night (a qualitative aspect) occurs at other times of the year, then the prey species of *Pleurobrachia* could be adequately described by stomach analyses of ctenophores captured during the daytime. However, in quantitative aspect diel variations of percentages of each species may vary. For two of the species most frequently present, *A. tonsa* and *P. parvus*, the results are different. As determined by a two-tailed U-test, there is no significant difference in median percentage *Acartia* of the total number of prey for day vs. night samples ($P>0.20$); however, the same test for *Paracalanus* indicates significant day–night differences ($P<0.05$), there being more frequent occurrences at night than during the day. Further investigation of prey selection by *Pleurobrachia* in relation to time–space distributions of prey and predators is important for understanding the ecology of *P. bachei* but beyond the scope of the present study.

The stomach contents (on the basis of numbers and mass of organic carbon) of postlarval *Pleurobrachia* in 10 size classes over the period 8 March 1970 to 2 June 1971 indicated some patterns in the frequency distribution of prey categories (Table 7). The patterns or trends exist as four types: (I) decreasing frequency with increasing ctenophore size, (II) increasing frequency with increasing ctenophore size, (III) little change in frequency with increasing ctenophore size, and (IV) non-systematic change and low frequency of occurrence for all ctenophore sizes. Examples of each pattern type are: (I) *E. acutifrons*, copepod eggs, *E. spinifera*; (II) *A. tonsa*, *L. trispinosa*; (III) *Oithona* spp., *C. anglicus*, *P. parvus*, copepod nauplii; (IV) *Rhincalanus nasutus*, euphausiid calyptopis, brachyuran zoea, *Sagitta euneritica*.

These results are subject to several sources of bias, three of which are: 1) the occurrence of the stomach contents of ctenophore prey in the stomachs of ctenophores, 2) the numbers of observations per ctenophore size category and the number of total occurrences per prey category, and 3) seasonal variations in the length–frequency distributions of ctenophores and their co–occurrences with prey. The diatom and dinoflagellate prey categories may be biased toward higher frequencies of occurrence if some of these types of organisms which occur in the stomachs of herbivores are released into the gut of a ctenophore during digestion. Fortunately, these

TABLE 7.—Stomach contents over the period 8 March 1970 to 2 June 1971 for 10 size classes of postlarval *Pleurobrachia bachei*. Data are the percentage by numbers (upper value) and by carbon mass (lower value) of each prey category in the stomachs for each size class of ctenophore calculated separately. The first 10 prey categories are given in ascending order of body mass; thereafter the order is by taxonomic group (e.g., copepods, cladocerans, crustaceans, chaetognaths, etc.). The numbers indicated in parentheses below each size class are the number of ctenophore stomachs examined per size class. Total numbers and total carbon refer to values of all prey in each ctenophore size class. Carbon mass is not calculated for protozoans.

Prey category		Size class, mean diameter (mm)									
		1 (189)	2 (211)	3 (235)	4 (190)	5 (158)	6 (150)	7 (105)	8 (68)	9 (24)	>10 (22)
Euterpina acutifrons	%N	20.85	18.33	15.36	15.58	7.41	5.54	4.05	4.00	0	7.06
	%C	9.15	5.56	2.98	3.05	0.80	0.71	0.40	0.23		1.00
Oithona spp.		6.81	3.33	5.03	3.43	4.04	0.98	0.40	4.67	5.17	2.35
		2.18	0.47	0.24	0.14	0.27	0.06	0.01	0.12	0.58	0.17
Oncaea spp.		0.85	2.33	0	1.25	0	0.33	1.21	1.33	0	0
		0.50	0.91	0	0.13	0	0.06	0.15	0.06		
Corycaeus anglicus		4.26	9.33	9.50	8.41	9.76	4.56	5.26	7.33	3.45	14.12
		2.58	9.76	5.25	4.44	3.45	1.80	1 60	0.77	1.43	4.46
Paracalanus parvus		1.70	3.00	4.47	3.43	6.40	3.91	4.86	6.00	5.17	7.06
		2.40	2.22	2.01	1.23	2.11	1.16	1.24	0.67	1.07	2.17
Acartia tonsa		10.64	21.67	25.14	29.91	36.03	47.23	55.87	49.33	60.34	47.06
		39.59	48.04	36.94	39.21	33.66	43.17	37.49	16.80	53.78	37.62
Calanus helgolandicus		0	0	0.28	1.25	1.01	0.65	0.81	0.67	0	1.18
				3.18	7.83	10.14	2.85	4.61	3.26		6.97
Labidocera trispinosa		0	0	2.51	2.49	3.37	2.93	4.45	5.33	1.72	2.35
				29.33	28.44	30.60	37.24	37.50	21.96	10.52	25.08
Metridia pacifica		0	0	0	0	0	0	0	1.33	0	1.18
									4.89		13.94
Rhincalanus nasutus		0	0.33	0	0	0.34	0	0	0	1.72	0
			0.05			4.78				23.90	
Clausocalanus spp.		0	0	0.56	0.62	0.67	0.33	0	0.67	0	0
				0.37	0.27	0.36	0.17		0.06		
Ctenocalanus vanus		0	0	0	0	0	0.33	0	0.67	0	0
							0.09		0.06		
Tortanus discaudatus		0	0	0	0.31	0.34	0	0	0	0	0
					0.45	0.17					
Copepod eggs		14.47	10.67	8.38	4.36	2.69	1.30	0.81	2.00	3.45	0
		6.12	3.20	1.66	0.70	0.33	0.07	0.05	0.09	0.49	
Copepod nauplii		11.91	6.67	3.35	4.05	9.43	4.89	5.67	4.67	3.45	0
		0.78	0.25	0.08	0.08	0.13	0.07	0.06	0.02	0.05	
Unidentified copepods		4.26	4.00	2.79	3.12	2.02	2.28	1.21	1.33	3.45	0
		5.60	3.03	1.27	1.26	0.57	0.64	0.25	0.13	0.96	
Evadne nordmanni		5.96	7.00	6.70	5.61	1.01	4.89	5.26	1.33	8.62	8.24
		16.47	11.12	6.42	4.77	0.60	2.90	2.24	0.27	5.02	4.10
Evadne spinifera		2.13	1.00	0.56	0.31	0.67	0.33	0	0	0	0
		5.88	1.59	0.54	0.26	0.40	0.19				
Evadne tergestina		0.85	1.33	1.96	2.80	1.68	6.84	4.45	0.67	0	1.18
		2.35	2.12	1.87	2.39	1.00	4.06	1.90	0.14		0.58
Evadne spp.		0	2.67	3.91	3.43	0	0	0	0	0	0
			4.24	3.75	2.92						
Penilia avirostris		0.42	0.67	2.51	2.18	3.03	2.93	0.40	1.33	1.72	4.71
		0.56	0.50	1.15	0.88	0.86	0.83	0.08	0.13	0.48	1.11
Podon polyphemoides		0	0.67	0.28	1.25	1.35	0.33	0	0	0	0
			1.06	0.27	1.06	0.80	0.19				
Euphausiid calyptopis		0	0	0.28	0	0	0.33	0	0	1.72	0
				0.46			0.33			1.72	
Cirriped nauplii		0	0	0	0	0.34	0	0	0	0	0
						0.02					
Mysids		0	0	0	0	0	0	0.40	0	0	0
								12.34			
Brachyuran zoea		0	0 ·	0	0	0.34	0.65	0	1.33	0	1.18
						0.96	1.84		1.30		2.79

(Continued)

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TABLE 7.—Continued

Prey category	Size class, mean diameter (mm)									
	1 (189)	2 (211)	3 (235)	4 (190)	5 (158)	6 (150)	7 (105)	8 (68)	9 (24)	>10 (22)
Unidentified crustaceans	3.83	1.67	1.12	1.56	1.35	0.98	0.40	2.00	0	0
	2.52	0.63	0.25	0.32	0.19	0.14	0.04	0.10		
Sagitta euneritica	0	0.33	0	0	0.34	0	0.40	0.67	0	0
		2.14			6.10		0.01	48.88		
Oikopleura spp.	0.42	0	1.12	0	1.01	1.30	0	0	0	0
	2.02		1.83		1.03	1.32				
Echinopluteus, doliolids	0	0	0	0	0	0	0	0	0	2.36
Fish eggs	0	0.67	0	0	0.34	0	0	0	0	0
		2.77			0.53					
Sarcodina	0	0	0	0.31	0.34	0.65	0	0	0	0
Noctiluca scintillans	0	0	0	0	0	0	0.40	0	0	0
Dinoflagellates	0.85	0	1.12	0.31	0.67	1.95	0.81	0	0	0
Diatoms	0	0	0	0.62	0	0	1.62	0	0	0
Unidentified material	9.79	4.33	3.07	3.43	4.04	3.58	1.21	3.33	0	0
	1.29	0.33	0.14	0.14	0.11	0.10	0.02	0.03		
Total numbers	235	300	358	321	297	307	247	150	58	85
Total carbon, µg	178.47	396.48	784.76	791.93	1045.87	1087.39	1215.87	1534.41	209.17	358.80

taxa made up less than 2% of any one category by numbers and less on a mass basis because of their small size. The number of observations per ctenophore size category are similar for classes 1–6, but thereafter they decrease sevenfold. There are few observations in the last two size classes, because these sizes are relatively infrequent and occur in high numbers only during July–August. Some of the larger copepods (e.g., *Calanus, Metridia,* and *Rhincalanus*) occur relatively infrequently in stomachs, perhaps because of their relative rarity and spatial separation from the ctenophores. Other infrequent groups such as fish eggs, cirriped nauplii, euphausiids, etc., may not be spatially separated but are perhaps rare, not selected as prey or are unavailable because of temporal separation during different seasons. Whatever the reasons for the infrequent occurrence of these groups in the stomachs of *Pleurobrachia,* the data for these prey are much less reliable and many more observations are required to establish patterns of occurrence with size of the ctenophore predator. The potential effect of seasonal variations in size–frequency distribution of ctenophores and co–occurrence of prey on patterns of stomach contents is suggested when the annual data are examined separately by sea-

sons. The results indicate that some prey are very seasonal in occurrence, while many are present throughout the year. The seasonal data are given (Table 8) for only those categories which showed strong seasonal variations. The first two prey were most frequent in summer–fall, *E. tergestina* in summer–winter, the next four in fall and the last one in winter–spring. Note the differences in occurrence of three species of *Evadne* regarding seasonal separation and predation by different sizes of *Pleurobrachia.*

When all stomach content data are grouped to include all sizes of postlarval *Pleurobrachia* and prey categories are ordered by rank of occurrence, the results show that *A. tonsa* and *E. acutifrons* account for nearly one–half of all prey items (Table 9). Thereafter, the percentage contribution from each category decreases to less than 1% by the sixteenth category, at which point the cumulative percentage is 94.2%. On a mass basis *Calanus, Labidocera,* and *Sagitta* join *Acartia* as the main large prey items. While these larger items may afford good growth to a few individuals, most of the ctenophore population is being nourished by *A. tonsa, E. acutifrons* and several other species of copepods and cladocerans.

Variations in the standing stock of food avail-

TABLE 8.—Seasonal variations in the stomach contents of ctenophores for eight prey categories. All values are expressed as the number of occurrences per 1,000 stomachs. The seasons spring (SP), summer (SU), fall (F) and winter (W) are groups of three months starting with February 1970 and ending in January 1971; the following spring 1971 is also included. The dashed lines indicate absence of data.

Prey category		Size class, mean diameter (mm)									
		1	2	3	4	5	6	7	8	9	>10
Paracalanus	SP	0	100	154	0	200	0	0	—	0	—
parvus	SU	46	50	52	44	146	67	91	91	91	300
	F	0	22	85	55	79	98	125	26	111	0
	W	33	0	0	182	400	0	125	429	—	500
	SP	0	0	0	83	0	0	0	3,000	333	250
Labidocera	SP	0	0	0	0	0	0	500	—	0	—
trispinosa	SU	0	0	21	0	49	0	45	318	91	100
	F	0	0	66	77	79	88	125	26	0	250
	W	0	0	0	91	0	0	0	0	—	0
	SP	0	0	0	0	125	0	0	0	0	0
Evadne	SP	0	0	0	0	0	0	0	—	0	—
tergestina	SU	0	0	21	44	0	100	0	0	0	0
	F	42	0	47	55	56	167	139	26	0	250
	W	0	364	0	91	0	91	125	0	—	0
	SP	0	0	0	0	0	0	0	0	0	0
Calanus	SP	0	0	0	0	0	0	0	—	0	—
helgolandicus	SU	0	0	0	0	0	33	0	0	0	100
	F	0	0	9	44	34	10	28	26	0	0
	W	0	0	0	0	0	0	0	0	—	0
	SP	0	0	0	0	0	0	0	0	0	0
Evadne	SP	0	0	0	0	0	0	0	—	0	—
spinifera	SU	0	8	0	0	0	0	0	0	0	0
	F	21	43	18	11	22	10	0	0	0	0
	W	33	0	0	0	0	0	0	0	—	0
	SP	0	0	0	0	0	0	0	0	0	0
Penilia	SP	0	0	0	0	0	0	0	—	0	—
avirostris	SU	0	8	0	0	49	100	0	45	0	300
	F	21	22	85	77	79	59	14	26	111	250
	W	0	0	0	0	0	0	0	0	—	0
	SP	0	0	0	0	0	0	0	0	0	0
Podon	SP	0	0	0	0	0	0	0	—	0	—
polyphemoides	SU	0	8	0	0	0	0	0	0	0	0
	F	0	22	9	44	45	10	0	0	0	0
	W	0	0	0	0	0	0	0	0	—	0
	SP	0	0	0	0	0	0	0	0	0	0
Evadne	SP	0	0	0	0	0	0	0	—	0	—
nordmanni	SU	0	58	72	59	0	0	0	0	0	0
	F	62	22	19	0	0	29	14	0	0	0
	W	30	1,000	1,333	909	0	364	1,500	286	—	0
	SP	111	143	538	333	375	1,600	0	0	1,667	1,750

able to *Pleurobrachia* from 18 June 1970 to 2 June 1971 showed a twentyfold range, with high values in May to early November and low values from mid–November to mid–March (Table 10). The food concentrations were about 10–30 mg C/m³ during the summer–fall maxima in numbers and standing stocks of *Pleurobrachia* postlarvae. The decrease in abundance of *Pleurobrachia* during November and December (see Figure 13) was associated with a fivefold decrease in the standing stock of prey. The winter increase of *P. bachei* occurred while food concentration doubled from the minimum in December. The higher food concentrations in May and June do not seem to cause increases in ctenophore abundance.

DISCUSSION

The vertical distribution of *P. bachei* in La Jolla Bight is related to the diel light–dark cycles, but in reverse to the pattern for most migrating zooplankton; the pattern is the result of one or more causes of differing selective advantage to the temporal persistence of this species. Four potential

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TABLE 9.—Rank order in frequency of occurrence by numbers of all developmental stages per prey category in all sizes of *Pleurobrachia* postlarvae and the corresponding estimates of total carbon mass per prey category.

Prey category	Frequency	Percent	μg C	Percent
Acartia tonsa	815	34.56	2,644.23	34.78
Euterpina acutifrons	270	11.45	114.04	1.50
Corycaeus anglicus	180	7.63	225.73	2.97
Copepod nauplii	139	5.89	6.95	0.09
Copepod eggs[1]	129	5.47	49.47	0.65
	(1,649)			
Evadne nordmanni	122	5.17	256.20	3.37
Paracalanus parvus	101	4.28	108.80	1.43
Unidentified	89	3.77	8.90	0.12
Oithona spp.	83	3.52	15.99	0.21
Unidentified copepods	62	2.63	62.00	0.82
Evadne tergestina	61	2.59	128.10	1.68
Labidocera trispinosa	58	2.46	2,085.54	27.43
Penilia avirostris	45	1.91	45.00	0.59
Unidentified crustaceans	34	1.44	17.00	0.22
Evadne spp.	33	1.40	69.30	0.91
Oncaea spp.	19	0.81	8.86	0.12
Dinoflagellates	17	0.72	—	—
Calanus helgolandicus	14	0.59	355.00	4.67
Evadne spinifera	14	0.59	29.40	0.39
Podon polyphemoides	12	0.51	25.20	0.33
Oikopleura spp.	12	0.51	43.20	0.57
Clausocalanus spp.	8	0.34	11.74	0.15
Brachyuran zoea	6	0.25	60.00	0.79
Diatoms	6	0.25	—	—
Sagitta euneritica	4	0.17	822.4	10.82
Sarcodina	4	0.17	—	—
Metridia pacifica	3	0.13	125.0	1.64
Rhincalanus nasutus	3	0.13	100.2	1.32
Euphausiid calyptopis	3	0.13	10.80	0.14
Fish eggs	3	0.13	16.50	0.22
Ctenocalanus vanus	2	0.08	2.00	0.03
Tortanus discaudatus	2	0.08	5.40	0.07
Cirriped nauplii	1	0.04	0.2	0.003
Mysids	1	0.04	150.0	1.97
Echinopluteus	1	0.04	—	—
Doliolids	1	0.04	—	—
Noctiluca scintillans	1	0.04	—	—
Total	2,358		7,603.15	

[1]The frequency value refers to the number of groups of copepod eggs and the value in parenthesis below it refers to the total number of eggs.

TABLE 10.—Seasonal variations in the calculated standing stocks of prey for *Pleurobrachia* at station 3.

Sample date	Mean (mg C/m³)	Range (mg C/m³)
18 June 1970	10.9	10.8–11.0
14 July	10.7	10.4–11.1
13 August	15.5	6.0–25.0
29 August	17.8	16.4–19.1
22 September	27.8	20.2–35.4
5 November	15.7	13.4–17.9
18 November	5.8	3.4– 8.1
16 December	2.7	2.6– 2.8
11 January 1971	6.8	3.7– 9.9
8 February	6.0	2.2– 9.7
12 March	5.2	5.1– 5.3
4 May	58.4	52.2–64.6
2 June	9.3	9.3– 9.4

advantages of migration to *P. bachei* are the ability to: 1) seek locations and depths with favorable food types and concentrations, 2) seek locations and depths with few predators and parasites, 3) avoid lethal or near–lethal surface temperature after the downward migration at night and increase the rate of development by living in warmer water during the day, and 4) maintain the pattern of high abundance close to shore and decrease the chance of drifting offshore. No data have been collected on quantitative changes in the abundance of prey and predators with *P. bachei* during vertical migration; such information would enable qualitative evaluation of the effect of these changes on the pattern of vertical distributions. Limited data from the study of diel changes in the species composition of prey in stomachs of ctenophores indicated no major changes between day and night, although

Paracalanus occurred more frequently in stomachs of ctenophores captured at night. Another major study would be required to quantify changes in the temporal and spatial co–occurrence of *Pleurobrachia* with their prey and predators. The data on vertical and seasonal distribution of *P. bachei* and the thermal stratification of water; the failure of laboratory cultures at 20°C; and growth experiments in the deep tank facility at 14.5° and 19.5°C are interpreted to indicate that vertical migration for this ctenophore is beneficial for survival and would optimize the rates of development and increase of bodily mass. A constant temperature of 20°C was detrimental to survival and growth of bodily weight (Figure 1), relative to conditions at 15°C. It is suspected that in August when the ctenophore abundance is highest and the maximum thermal stratification occurs, vertical migration from the surface to 20–m depth increases the chance of survival by lowering the ambient temperature at night by nearly 10°C. In addition, the detrimental effect of high temperature on somatic growth may be decreased and the ctenophores develop at some rate intermediate to the rate at 12° and 22°C. Growth experiments using the deep tank facility in which stratification of temperature is made to simulate conditions in nature might support some of these speculations. Alternatively, laboratory growth experiments could be made in which temperature is varied with a semidiurnal period. Another complication in these experiments, if they are to simulate conditions in the field, is the co–occurrence of the parasite *Hyperoche* and its possible temperature–dependent effect on the growth and survival of *P. bachei*.

A consequence of diel vertical migration in the

coastal waters off southern California is the potential effect on the horizontal, offshore distribution of a species. Stevenson (1958)[4] summarized some wind data for the Newport Beach to Los Angeles Harbor area, which show that in the sea breeze–land breeze diel variation of wind velocity there is a stronger sea breeze component from the west–northwest quadrant during the afternoons and a more variable and weak wind in the mornings. Robert Arthur has suggested that a possible result of the diel variation in wind velocity and the observed pattern of vertical migration in *P. bachei* may in part account for the maintenance of high ctenophore abundances close to shore. By living in the wind–mixed layer during the day with a westerly–northwesterly sea breeze, ctenophores are moved shoreward. At night through the early morning hours the weaker land breeze moves the surface waters offshore, but by living deeper at night the net offshore movement of ctenophores should be relatively smaller than the shoreward displacement. The frequent stranding or grounding of drogues nearshore suggests a net onshore movement of water. One mechanism of horizontal, seaward transport is the rip currents, but these are probably important only a few hundreds of meters seaward of the surf zone and are dependent on the size of sea swells. It is not known how important stranding is as a source of mortality to *Pleurobrachia*, but in summer months *Pelagia* (Scyphozoa) are frequently stranded on La Jolla beaches and are broken apart in the surf zone. Other macrozooplankton, such as salps and *Velella*, periodically occur on the beach and in waters near the shore. It is not clear what cues or mechanisms the ctenophores use to maintain their distribution to within 1 km of shore without most being washed into the surf and killed. A number of net tows taken near the end of Scripps Institution pier and just seaward of the surf zone indicate absence of *P. bachei*.

The estimates of abundance of *P. bachei* at fixed stations located alongshore 2–3 km from the shoreline are subject to variability in time and space from several causes. At a single station the abundance will be affected by: 1) spatial heterogeneity and patchiness on the scale of 100–m horizontal distance and 20– to 50–m depth over the course sampled during a tow, 2) the stage of the tides and the tidal current velocity (see Figure 15), and 3) the water temperature stratification and near–surface drift due to the wind. The magnitude of replicate sample error is one–half to twice the mean, and the variability in abundance due to the presumed horizontal motion generated by the tides and wind for the annual average is about the same as replicate sample error.

For estimates of abundance on a given sampling date at stations 1.6 km from the shore at different locations along the coast, "true spatial" variability exists in addition to replicate sampling error and aliasing due to physical effects of tides and the wind. It is difficult to sort out quantitatively the separate error components due to physical effects and true spatial effects alone, because the time period for the physical effects to bias sampling (about 6 h) is about the same as that required to move through space and sample different stations. Variability around the mean of all stations at one sampling date includes variations due to replicate sampling error, variations due to physical effects, and variations due to true spatial differences. The relative magnitudes of these components of variation estimated from the 95% confidence limits of the two–way analysis of variance and the regression of abundance on tidal height are: 1) the 95% confidence limits about the mean of all stations at a given time of sampling is the mean multiplied and divided by 6.23, 2) the 95% confidence limits about the mean of replicate samples is the mean multiplied and divided by 2.15, 3) the range of the expected abundance from the regression equation over the observed values of tidal heights is four-fold, or a range of about one–half to twice the overall annual mean, and 4) the residual true spatial variation calculated by difference is the mean multiplied and divided by 1.45 (i.e., $6.23^2 = 2.15^2 \times 2^2 \times 1.45^2$). In terms of the relative contribution of these three components to the total variability, the values are 2.2:1.9:1 for replicate sampling error, physical effects, and true spatial variation, respectively. The relative contribution of replicate sampling error vs. physical plus true spatial variations to the total variability of all stations on one sampling date is 1:1.8. These results from a sampling program not designed specifically to separate each effect suggest that physical effects on sampling bias and the replicate sample error are important relative to real spatial differences of abundance between stations equidistant from shore. A synoptic sampling program with two or

more ships would better enable separation of the total variability into variations from time–dependent physical effects, true spatial differences, and replicate sample error. It is indeed discouraging that confidence limits for the mean of replicate samples could not be reduced below about one–half to twice the mean, even with a *t* value based on 90 degrees of freedom. Zooplanktologists may continue to be plagued with the inability to reduce field sampling variability much below this level, given reasonable time and manpower limitations and no significant changes in sampling methodology. Because of their large size and lack of rapid escapement, postlarval *P. bachei* are as easy to sample accurately as any zooplankter is likely to be.

Seasonal changes in abundance of *P. bachei* postlarvae observed in La Jolla Bight during my study (Figure 13) agree with the earlier work of Esterly (1914) off San Diego and work by Parsons et al. (1970) in the Strait of Georgia, British Columbia (the values reported in the Strait of Georgia work are numbers of *Pleurobrachia* plus *Philidium* per cubic meter). These two studies showed that seasonal maxima occurred in July or August; high densities were from June to September and lower values and absences were observed from October to March. Esterly (1914) noted that *P. bachei* were more abundant at temperatures above 18°C than below; they were especially abundant at about 19°C in August. He also noted that although *P. pileus* and *P. bachei* are similar in morphology, their distributional pattern and temperature optima are widely different. In the Atlantic *P. pileus* was abundant at lower temperatures during the year (<15°C); in the Pacific the reverse seemed to be the case.

Seasonal studies of *P. pileus* in Wellington Harbor, New Zealand (Wear, 1965) and the North Sea region (Russell, 1933; Fraser, 1970; Greve, 1971) show that it differs from *P. bachei* in the season of maximal abundance. In Wellington Harbor *P. pileus* was dominant in the winter plankton, and it was the most variable planktonic species. *P. pileus* was absent in February-March, rare (1-10/20- min tow) in April-May, and December-January, common (20–100/tow) in June and September–November and abundant (500–1,000/tow) in July-August (note that this is the winter in New Zealand). Critical temperature for the occurrence of *P. pileus* was between 15° and 16°C. When the temperature fell below this level, *P. pileus* occurred in great abundance; in

early summer at temperatures above 16°C they were rare or absent. In the North Sea off Plymouth, *P. pileus* occurred in a bimodal seasonal distribution with early summer (May–June) and fall (October) maxima (Russell, 1933). In the North Sea near Helgoland *P. pileus* occurred with a May–June maximum at 10–15°C and a less distinct fall peak (Greve, 1971). Long-term mean seasonal distributions in the Scottish North Sea showed a clear November maximum with a less distinct secondary mode in June (Fraser, 1970); however, the month of the seasonal maximum can be as early as July–August in "abnormal" years compared to the expected fall maximum of normal years. Highest numerical abundance of postlarval *P. pileus* in the North Sea was on the order of 10–20/m^3 (Fraser, 1970; Greve, 1971). This is about the same as the maximum of 40/m^3 I found for *P. bachei* postlarvae, but through most of the year the population of *P. bachei* was dominated by numbers of larvae and eggs. Contrary to the annual or biannual spawning patterns of *P. pileus* in the North Atlantic (Fraser, 1970), *P. bachei* produced eggs throughout the year except for spring and some summer months.

Important differences exist between *P. pileus* and *P. bachei* in addition to the pattern of seasonal distributions and the surface temperature at the season of maximum abundance. Patterns in the seasonal co-occurrence of *Beroë* with *Pleurobrachia* and the parasitism of each *Pleurobrachia* species are different for *P. pileus* and *P. bachei*. In the North Sea, *P. pileus* occurred in patterns of seasonal abundance which were 180° out of phase with the abundance of *Beroë* (Russell, 1933; Greve, 1971). In La Jolla Bight abundances of *P. bachei* and *Beroë* sp. generally increased and decreased in phase without time lags. The seasonal patterns for the co-occurrence of *Beroë* with *P. pileus* and *P. bachei* suggest that *Beroë* and other predators may overexploit *P. pileus* temporarily to decrease the population abundance seasonally, whereas *Beroë* and *P. bachei* appear to co–occur in a less intense predator–prey association. In the North Sea, *P. pileus* were parasitized by nematodes (Greve, 1971) and cercaria of *Opechona*, a trematode (Fraser, 1970). In La Jolla Bight, *P. bachei* were parasitized by *H. mediterranea*. Farther to the north *Hyperoche mediterranea* is replaced by *H. medusarum* (Bowman, 1953), and *P. bachei* is parasitized by this species in waters off northern

California (Brusca, 1970).

Off southern California, the strongest equatorward surface flow occurs during spring and summer, and south of Point Conception the semipermanent cyclonic eddy produces a northward inshore circulation (Wyley, 1966). Beneath the California Current, the undercurrent is a subthermocline poleward flow of water of relatively high temperature and salinity; for example in August 1966 the undercurrent at lat. 31°N, long. 177°W was close to the continental slope, being about 20 km wide and 300 m thick (Wooster and Jones, 1970). This undercurrent below 200 m surfaces well inshore of the main stream in late fall and early winter when northerly winds are weak or absent (Reid et al., 1958).

The seasonal distributions of *P. bachei* in La Jolla Bight showed some features which are consistent with seasonal changes in the vertical movement of the California undercurrent (also called the Davidson Current). Postlarvae decreased by over two orders of magnitude from the end of October through December, and reappeared at moderate abundance in late January and February. For larvae and eggs, the timing and magnitude of the winter decrease were about the same, but the frequency of absences was less than for postlarvae (see Figures 13 and 14). Another variable associated with the presumed winter shoaling of the undercurrent is the fivefold decrease in prey standing stock from early November to the middle of December (Table 10). A subsurface current which rises to the surface in winter is expected to contain relatively low crops of animals and plants, and poleward advection of water from the south should cause decreases in abundance of *Pleurobrachia*.

Studies of stomach contents of *P. pileus* in the Scottish North Sea (Fraser, 1970) and in Kaneohe Bay, Oahu (Rowe, 1971) indicate that this ctenophore is predominantly a crustacean feeder, especially of copepods, cladocerans, and cirriped nauplii. In the Scottish North Sea, *P. pileus* fed about 80% of the time on *Acartia, Calanus, Evadne,* invertebrate eggs, *Temora longicornis, Oithona,* unidentified copepods, cirriped larvae, *Spiratella,* and *Podon.* In Kaneohe Bay 75% of the prey were nauplii of barnacles and copepods and the appendicularian *Oikopleura longicauda* (Rowe, 1971). The evidence indicated that *Pleurobrachia* very rarely fed on fish eggs and larvae. The North Sea study included seasonal and annual data, the differences between which

Fraser attributed to differences in the composition of the plankton rather than prey selectivity by *Pleurobrachia.*

The gut contents of *P. bachei* in La Jolla Bight generally agree with the results for *P. pileus* in that they fed: 1) predominantly on crustaceans, especially copepods; 2) very rarely on fish eggs and larvae; and 3) on a broad spectrum of organisms some of which appear seasonally for only limited periods. The major difference between the results from the three study areas is that in Kaneohe Bay *Pleurobrachia* fed on relatively few prey categories, the number being about one–fifth that in my study and the North Sea study. The three most frequent foods on a numerical basis were: 1) barnacle and copepod nauplii, *Oikopleura* and other copepods in Kaneohe Bay; 2) *Acartia, Calanus,* and *Evadne* in the Scottish North Sea, and 3) *Acartia, Euterpina,* and *Corycaeus* in La Jolla Bight. Both studies of *P. pileus* gut contents considered the postlarvae as a homogeneous group. I have treated the postlarvae of *P. bachei* as being made up of 10 separate size classes to show that some changes do occur in prey frequency during ontogeny (Table 7). All studies of ctenophore gut contents have been inadequate to describe quantitatively the developmental stages of prey species eaten by different life history stages of ctenophores, including the larvae. Great difficulties and amounts of work would be required for such a study (each copepod species has 13 developmental stages counting the eggs). Many important biological interactions probably occur during different developmental stages during ontogeny, yet we know very little about them.

Feeding rate experiments with 9– to 10–mm diameter *P. bachei* (Bishop, 1968) have shown differences between mean ingestion rates of copepodids of *Epilabidocera amphitrites* and *Pseudocalanus minutus; P. bachei* also fed at a faster rate on copepodids and adults of *P. minutus* than on their nauplii. These results showed that rates of feeding depend on prey size and other differences between the same stages of different prey species and between different developmental stages of one species. The study of feeding behavior of *P. pileus* indicated that this ctenophore regulates its feeding rate by changing the average size of the tentacles in response to different concentrations of *Artemia* nauplii (Rowe, 1971).

During laboratory culturing and rate of digestion of prey experiments, differences were observed in: 1) the avoidance and escape behavior of

prey, 2) the protective spination of various species, 3) the strength and sensory acuity of larger zooplankters, and 4) the active search patterns of "setting out" tentacles by the ctenophore. Each of these four factors in addition to other variables, which are determined by the relative abundance and movement of species in nature, have some bearing on the selection of prey by *Pleurobrachia*. The first consideration is time–space co-occurence of prey with the ctenophore. Since the ctenophores are neritic and mostly live close to shore in the upper 50–60 m, they will occur with surface–living holoplanktonic and meroplanktonic species, only coexisting with deeper-living, migratory species at night. Secondly, the ctenophores will most frequently encounter the most abundant organisms in numbers per unit volume. Size and swimming activity of the prey are also important to determine the chance of encounter with the tentacles. Bodily length determines the likelihood of retention of a given organism by the tentacle net, and swimming activity determines how often the prey will encounter a given ctenophore if swimming in a random manner. Rowe (1971) has shown, using *Artemia* nauplii, that the instantaneous feeding rate of *P. pileus* follows the form for effusion of an ideal gas; this requires the assumption that prey move about randomly. However, I have seen *P. bachei* make at least three different types of settings of its tentacles in apparent attempts to alter the pattern of search for prey: 1) a double helix set like two interwoven corkscrews perpendicular to a level surface with the body at the uppermost end, 2) a pair of spirals parallel to a level surface with the ctenophore body at the outer end of the spiral, and 3) linear and curved sets which are placed at different angles with respect to the vertical and with the ctenophore body either heading up or down. The types of tentacle settings may be adaptive responses to the nonrandom swimming patterns of different zooplankton species, some of which move more in a horizonal or a vertical plane. It is at this point that animal behavior becomes very important. Species which co–occur with *Pleurobrachia* and are relatively abundant (up to several hundred per cubic meter) are not necessarily eaten by this ctenophore, because these potential prey probably use their sensory acuity and locomotive power to avoid danger. One outstanding example is *S. euneritica*, a species which is very fast and difficult to catch compared to most zooplankton; it had a highly negative electivity index (Table 9). Assuming that a prey organism has just made contact with the ctenophore tentacles, three possible outcomes have been observed in the laboratory for different species: 1) the prey is too strong and breaks away from the tentacle hold; 2) the prey provides a strong escape response, becomes further entangled and is eaten; and 3) the prey provides little or no escape response, remains nearly motionless and "plays dead," often being dislodged from the tentacle hold and not eaten. A species which is too powerful for *P. bachei* to capture is *H. mediterranea*. The adults of this amphipod can break away from the entanglement and also have the ability to exploit the ctenophores as a predator. Prey which provide a strong, "calanoid escape response" are almost always further entangled by swirls of the tentacle branches and are eaten. The immediate struggling and pulling away appears to signal the ctenophore of a successful prey capture, much as I would expect that a spider detects the impact and vibrations of the prey struggling on its web. The copepods such as *Acartia, Labidocera, Calanus,* etc., exhibit strong escape responses when stimulated by contact or approaching danger. Two prey species were observed to exhibit the motionless or "play dead" response. These are *C. anglicus* and *P. avirostria. Penilia* is also one of the species which has a negative electivity index or is taken less frequently than in proportion to abundance in the water. Once the prey is brought to the mouth of the ctenophore, the next limitations are the configuration of the prey body and appendages plus the protection from external spination. Bodily shapes such as those of *Sagitta* and zoea larvae of Porcellanidae (a family of crabs) create difficulties for their ingestion by *Pleurobrachia*. Large *Sagitta* must be bent in half and ingested at the middle section first (observations are from the laboratory work; gut contents from field sampled ctenophores show that this event is very infrequent). The long anterior and posterior spines of the porcellanid zoeae prevent full ingestion and digestion entirely, although the prey probably do not survive the capture. Many other decapod larvae possess stout spines and very thick exoskeletons (e.g., *Emerita* larvae), which prevent ingestion and would retard digestion as well. Some brachyuran zoeae which have dorsal and lateral spines have been observed to cut open the ctenophore gut wall during ingestion. Recall that brachyuran zoeae only make up 0.25% of the total number of prey in ctenophore guts (Table 7).

DEMOGRAPHY AND NET PRODUCTION

Methods

Computations of stage–specific instantaneous mortality rates (hereafter referred to as mortality rates or mortalities) were made in order to use these values in other calculations to estimate population parameters and rates of net production. Mortalities were calculated using field data on stage frequencies treated as a composite of all samples taken on each sampling date and laboratory data on rates of development, with temperature and food concentrations being similar to average values observed in the field study area. The growth or development rate data are from laboratory cultures at 15°C and 35 μg C/liter food concentration. The mortalities were computed by a computerprogram (Fager, 1973) which solves an equation to fixed level or error by a specified number of iterative calculations.

$$\bar{N}_{x+1}/\bar{N}_x = t_x (1 - e^{-Mt_{x+1}})/t_{x+1} (e^{Mt_x} - 1). (1)$$

The variables t_x and t_{x+1} are the duration of development in days for stage x and $x+1$, respectively; variables $\bar{N}_x$ and $\bar{N}_{x+1}$ are the numbers of each stage in the composite divided by the respective duration of development. The mortality rate on a per day basis from stage x to stage $x+1$ is M; for an organism with continuous growth, such as a ctenophore, a "stage" is a size category. Positive mortalities can be calculated only when $\bar{N}_x$ exceeds $\bar{N}_{x+1}$. Implicit in the calculation are the assumptions that: 1) successive stages of the organisms were born during a period of constant recruitment and 2) successive stages have lived together in spatial proximity, or emigration is balanced by immigration in the water parcel.

The life table calculations were based on the estimated mortalities for different time periods of field sampling and the mean schedule of live births from laboratory cultures at 15°C. The equations used to calculate population parameters and stable age distributions are from Birch (1948).

The rate of net production per day of each developmental stage is a function of the numbers and weights of the animals and their instantaneous rate of tissue growth and of mortality on a per day basis; the rate of net production by a species population of a given age structure is simply the sum of the rates for each stage. These rates are calculated from the equation of Ricker (1958), which relates the rate of net production to the mean daily standing stock and the rates of growth and mortality.

$$NP_i = G_i B_i (1 - e^{G_i - M_i})/(M_i - G_i) = G_i \bar{B}_i .(2)$$

In this equation G_i and M_i are the mean exponential coefficients or mean instantaneous rates of growth and mortality of the ith stage on a per day basis. The variables B_i and $\bar{B}_i$ are the calculated standing stocks per sample in milligrams organic matter per square meter of the ith stage at the beginning of the day (B_i) and the average over a 24–h period ($\bar{B}_i$). This function equates the rate of net production per day for the ith stage (NP_i has units of milligrams organic matter per square meter over a 24-h period) to the instantaneous rate of tissue growth times the standing stock at the beginning of the day (the beginning of the day is the time a field sample is taken) corrected for differential increases due to tissue growth and differential decreases due to mortality. For further details refer to the work of Ricker (1958) and Mullin and Brooks (1970). Note that the rate of net production per day is actually an average value, because it is calculated using means for growth and mortality rates.

The rates of net production for postlarvae and larvae of *P. bachei* were calculated according to Equation (2) above. No values for mortality rates of eggs were calculated, but the hatching time of eggs at 15°C is about 24 h. In calculation of the net production of eggs per day, it is assumed a steady state in the standing stock of eggs with a hatching time of 24 h. This is equivalent to the assumption that the rate of net production of eggs per day is equal to the standing crop at the time of sampling the eggs.

From calculations of the net production per day of postlarvae for each replicate sample at each station, the mean value and the variance of the mean are calculated according to standard parametric statistics. At a given station, the total amount of organic matter produced over some interval of time, $\wedge t$, equals the product of the mean rate per day and the time interval in days. For calculations of the annual net production (ANP), it is assumed that the mean rate per day on a given sampling date at one station applies linearly over an interval of time equal to the sum of one–half

the period between the given sampling date and the previous sampling date plus one–half the period between the given sampling date and the next following sampling date.

The ANP equals the sum of all net production increments over the year.

$$\text{ANP} = \underset{t_n = 1}{\overset{t_n = n}{\text{SUM}}} \overline{NP}_{t_n} (t_{n+1} - t_{n-1})/2. \qquad (3)$$

In the equation t_n refers to the nth sample date, $\overline{NP}_{t_n}$ refers to the mean rate of net production per day on the nth sample date, and ANP is the mean value of the annual net production for any life history stage being considered. For the first and last sampling dates of the year, the mean rates per day were applied over one–half the following sampling date interval and one-half the previous sampling date interval, respectively. Calculations using Equation (3) were carried out separately for postlarvae, larvae, and eggs at station 5 off Scripps, and the total for all life history stages is the sum of the annual values for the eggs, larvae, and postlarvae at that station. ANP was also calculated at stations 1, 3, and 6 for postlarvae only.

The variance of the mean value of the ANP at a given station was calculated as the product of the variance of the mean rate of net production per day and the square of the time interval over which it was applied, summed for all time intervals during the year. The equation was derived from the variance formula of a dependent variable which equals the product of two independent variables (net production over a time interval, $\triangle t$, equals the product of the mean net production per day and $\triangle t$), by solving for the square of the differential of net production over a time interval $\triangle t$. The covariance term is zero since the daily net production and time interval between sampling dates are independent. The term for the square of the mean daily net production multiplied by the variance of $\triangle t$ is presumed to be small, because sampling during the year was within a few hours at the same time of the day for all sampling dates.

$$\text{Var}(\overline{\text{ANP}}) = \underset{n = 1}{\overset{t_n = n}{\text{SUM}}} \text{Var}(\overline{NP}_{t_n})(t_{n+1} - t_{n-1})^2/4. \quad (4)$$

The symbols are as given above in Equation (3), and Var $(\overline{\text{ANP}})$ and Var $(\overline{NPt_n})$ refer to the var-

iance of mean annual net production and the variance of mean daily net production on sampling date t_n, respectively.

Results

During the field study from 8 March 1970 to 2 June 1971, 100 mortality values were obtained for postlarvae and larvae. On any one sampling date it was not possible to calculate mortality values for all size classes, especially with small sample sizes in older stages. Therefore, the mortalities from all sample dates were grouped into seven time periods and seven size classes (excluding eggs) in order to obtain an estimate of mortality for each class over time. The mortalities were grouped according to the subjective criterion that medians of a group would differ from any other by at least 50%. The mortalities for size classes were set by the comparisons of mean numbers per class between successive classes.

For the time period of 1 May to 18 June 1970 a life table calculation is given in Table 11. The mean hatching success of eggs is 94%. The l_x values are the probability that an individual born will survive to the beginning of each age interval. The instantaneous mortality rates which were used to construct the l_x schedule are as follows: 1) 0.170 for larvae of age 1–19 days, 2) 0.021 for stage 1–2 mm postlarvae of age 19–45 days, 3) 0.150 for stage 3–4 mm postlarvae of age 45–53 days, 4) 1.047 for stage 5 mm postlarvae of age 53–54 days, 5) 0.572 for stage 6 mm postlarvae of age 54–55 days, 6) 0.378 for stage 7–8 mm postlarvae of age 55–63 days, and 7) 0.260 for stage 9–13 mm postlarvae of age greater than 63 days. These mortality rates were applied equally for each age interval over the duration of the respective stages. Note that up to age 53 days (4.5 mm) the first 45 live births give a net reproduction of 1.0405 (60% of the total), enough to replace the population. The next 53 live births add 23% of the total net reproduction. The enormous potential reproductive capacity at age 61–63 days and older is not fully realized because of the miniscule numbers which survive to this age. These results show the great importance of early reproduction in size classes 1–2 mm toward the net reproduction.

The population parameters and stable age distributions in May–June and three other time periods, each with its own schedule of survival and the mean schedule of births, are shown in Table 12. For the 1 May to 18 June period, the observed

TABLE 11.—The life table for *Pleurobrachia bachei* during 1 May–18 June 1970 based on laboratory growth and reproduction data at 15°C and calculated mean rates of mortality for this period. The symbols dx, 1_x, b_x and x represent the age interval in days, survival to the beginning of the age interval, the numbers of live births during the age interval, and the pivotal age, respectively.

dx	1_x	b_x	$1_x b_x$	$1_x b_x x$
0-1	1.0000			
1-3	.9400			
3-5	.6691			
5-7	.4762			
7-9	.3390			
9-11	.2413			
11-13	.1717			
13-15	.1222			
15-17	.0870			
17-19	.0619			
19-21	.0441			
21-23	.0423			
23-25	.0405	1	0.0405	0.9720
25-27	.0388	0		
27-29	.0372	0		
29-31	.0357	1	.0357	1.0710
31-33	.0342	0		
33-35	.0328	0		
35-37	.0315	0		
37-39	.0302	0		
39-41	.0290	0		
41-43	.0277	6	.1662	6.9804
43-45	.0266	15	.3990	17.5560
45-47	.0256	3	.0768	3.5328
47-49	.0189	13	.2457	11.7936
49-51	.0140	4	.0560	2.8000
51-53	.0103	2	.0206	1.0712
53-55	.0077	53	.4081	22.0374
55-57	.00152	102	.1550	8.6800
57-59	.00071	8	.0057	.3306
59-61	.000336	53	.0178	1.0680
61-63	.000158	353	.0558	3.4596
63-65	.000074	325	.0240	1.5360
65-67	.000044	302	.0133	.8778
67-69	.000026	204	.0053	.3604
69-71	.000015	557	.0084	.5880
71-73	.000009	298	.0027	.1944
73-75	.000006	960	.0058	.4292
75-77	.000003	1026	.0031	.2356
77-79	.000002	1319	.0026	.2028
		R_o = 1.7481		85.7768

mean age distribution in field samples was 66.7% eggs, 20.0% larvae, 8.7% 1- to 2-mm postlarvae, and 4.7% all other stages. The field age distribution is unlike the stable age distribution in that the proportions of eggs and larvae are reversed and the proportion of late stages is sevenfold higher than in the stable age distribution. The population growth rates (r) in other time periods predict decreases of population abundance from 8 March to 2 April ($r = -0.105$) and increases in 14 July to 21 August ($r = 0.020$) and in October ($r = 0.0115$). Eggs and larger ctenophores were again more frequent, and larvae less frequent in the field during July–August than calculated for the stable age distribution.

For postlarvae the mean rate of net production per day for all stations located 1.6 km from the shore (Table 13) followed the seasonal variation in the standing stocks. The maximum rate of net production on 13 August, 212 mg organic matter m^{-2} day^{-1}, was about 20% of the standing crop. About two–thirds of ANP occurred during August. The variance of the mean ANP is quite large, but since the confidence limits for the mean are determined by standard deviations, the 95% confidence interval for the mean ANP is 4,200–6,280 mg organic matter m^{-2} yr^{-1}.

Mean ANP of postlarvae at stations 1, 3, and 5 (1.6 km from shore) and at station 6 (10 km from shore) are given in Table 14. Note that "annual" net production at the stations 1, 3, and 5 are for 0.956 yr and at station 6 for 0.84 yr; these values were not corrected to a full year by proportion, because statistical tests based on variances would not be valid. Tests for differences of variances (F–ratio) and means (t–tests) between stations 1, 3, and 5 were made. The variance of station 3 was significantly different from that of stations 1 and 5 ($P<0.01$), but the variances of stations 1 and 5 were not different from each other ($P>0.05$).

The difference between means of all pairs of contrasts for stations 1, 3, and 5 are significant ($P<<0.01$). The net production at station 6 located 10 km from shore off Scripps Institution was about

TABLE 12.—Summary of population parameters for *P. bachei* during four time periods in 1970. The symbols R_0, r, T, B, b, d and C_x refer to net reproduction, instantaneous rate of population growth, generation time, finite birth rate, instantaneous birth rate, instantaneous death rate and stable age distribution respectively. The percentages of eggs (E), larvae (L), 1-2 mm, and $\geq$ 3 mm stages are given in that order for the stable age distribution.

Time period	R_0	r	T	B	b	d	C_x
8 Mar.-2 Apr.	0.0058	-0.105	49.0	0.2485	0.2617	0.3667	—
1 May-18 June	1.7481	0.0115	48.6	0.2348	0.2328	0.2213	23.3 *E* 69.0 *L* 7.0 1-2 mm 0.7 $\geq$ 3 mm
14 July-21 Aug.	2.9271	0.020	53.7	0.248	0.248	0.228	24.6 *E* 69.3 *L* 5.6 *1-2 mm* 0.5 $\geq$ 3 mm
8-22 Oct.	1.7565	0.0115	49.0	0.2348	0.2328	0.2213	Same as 1 May–18 June

TABLE 13.—Seasonal variation of the mean rate of net production per day ($\overline{NP}t_n$ is in mg organic matter $\overline{m}^2$ day^{-1}) for postlarval *Pleurobrachia bachei* at stations located 1.6 km from shore in La Jolla Bight. The mean annual net production is given as the sum of the mean rate per day multiplied by the appropriate time interval, $\triangle t$; the variance of the mean annual net production is also given. Note that the sum is for 0.956 yr.

Sampling date	Number of samples	$\overline{NP}t_n$	$\overline{NP}t_n(\triangle t)$	Var $(\overline{NP}t_n)\triangle t^2$
18 June 1970	10	5.188	36.316	270.5065
2 July	10	5.356	69.628	216.5228
14 July	10	9.080	131.660	639.0759
31 July	10	38.396	575.940	35,286.5025
13 Aug.	10	212.287	2,229.014	102,152.1706
21 Aug.	8	70.454	563.632	11,169.1520
29 Aug.	10	22.712	295.256	2,370.3264
16 Sept.	6	21.416	428.320	2,824.7200
8 Oct.	6	10.843	195.174	7,217.9748
22 Oct.	6	41.882	586.348	91,135.2960
5 Nov.	6	1.775	23.962	141.4260
18 Nov.	6	0.350	4.725	7.4322
2 Dec.	10	0.114	1.596	0.7291
16 Dec.	10	0.0003	0.006	0.0003
11 Jan. 1971	6	0.321	6.741	14.4207
27 Jan.	6	0.962	13.468	87.1612
8 Feb.	8	1.745	25.302	102.6440
25 Feb.	6	0.240	3.840	4.9306
12 Mar.	6	1.148	24.108	221.5584
7 Apr.	6	1.018	20.360	48.4800
20 Apr.	6	0.202	2.727	2.8978
4 May	6	0.061	0.854	0.1764
18 May	6	0.044	0.638	0.1051
2 June	6	0.002	0.015	0.0004
SUM			5,239.63	253,914.2097

sevenfold lower than that at station 5 (1.6 km off Scripps Institution) and fivefold lower than the mean for all stations located 1.6 km from shore. For these comparisons, the production at station 6 was extrapolated to 0.956 yr. The net production of larvae and eggs at station 5 contributed only about 3% of the sum of net production of eggs, larvae, and postlarvae at that station.

For stations 1, 3, and 5 the annual mean ratio of the net production per day of postlarvae to their mean daily standing stock ($\overline{B}_i$ of Equation (2)) are 0.197, 0.196, and 0.211, respectively. The mean ratios are based on 32, 43, and 54 observations for stations 1, 3, and 5, respectively. There are no significant differences between the variances (F-ratio tests) of all paired contrasts of stations ($P > 0.05$). There are no significant differences between all paired contrasts of station means ($P > 0.50$). The overall annual mean ratio at these three stations is 0.202, with 95% confidence limits for the mean being 0.187–0.217. Thus, the ratio of production to biomass on the day of maximal production was no greater than the annual mean.

In order to estimate the food chain efficiency (defined for any trophic level L as the steady state ratio of yield to predators at level $L+1$ to the net production of trophic level $L-1$) of the transformation of materials or energy by trophic levels, the two parameters stated above must be known: 1) the net production of potential food at level $L-1$ and 2) the yield to predators from the level L, which in steady state is the total net production of level L minus losses to decomposers. This concept can be extended to include more than three trophic levels, e.g., the square root of the ratio of ingestion by secondary carnivores to net primary production might be termed the equal transfer efficiency of herbivores and primary carnivores.

In practice it is very difficult to accurately "measure" the secondary production of the entire herbivore trophic level in the sea, and such data are not available in my study area. Further, the estimates of net production by *P. bachei* could not be partitioned into the fractional losses to decomposers and as yield to predators. Therefore, two simplifying assumptions were made in calculating the transfer efficiency for the macrozooplankton of La Jolla Bight: 1) all of the net production by *P. bachei* resulted in yield to predators and none to decomposers and 2) the efficiency was constant and equal from the primary producer level through the first–order carnivore level of *P. bachei*. Given these limiting assumptions, the efficiency calculated is referred to as the "equal transfer efficiency." Thus, if net production data were not available for trophic levels between primary producers and the trophic level of in-

TABLE 14.—Summary of "annual" net production (ANP) values (in mg organic matter $\overline{m}^2$ time^{-1}) of *Pleurobrachia bachei*, at four stations in La Jolla Bight. The value at station 6 is for 0.84 yr; all other values are for 0.956 yr. The standard deviation of ANP for each respective value is also given. Values are for postlarvae unless otherwise specified. The mean production for larvae and eggs at stations 1-5 were calculated assuming that the same fraction of production would be as larvae and eggs at all stations as at station 5.

Station	Number of sample dates	ANP	SD
1	24	2.320	104
3	24	4.320	377
5	25	7.650	125
		144 Larvae	18
		111 Eggs	6
6	17	950	85
Mean of station 1-5	24	5.240	504
Mean of station 1-5 plus eggs and larvae	24	5.240	
		99 Larvae	
		76 Eggs	
		5.415	504

terest, a general equation to calculate equal transfer efficiency for n transfers is

$$ETE = (NPL/NPP)^{1/n} \qquad (5)$$

In the equation ETE is the equal transfer efficiency, NPL is the net production of trophic level L (which is equal to ingestion by level $L+1$), NPP is the net primary production, and n is the number of transfers from primary producers (the zeroth trophic level) through trophic level L. This equation was derived from the works of Schaefer (1965) and Ryther (1969). The equal transfer efficiency calculated in this manner for $n>2$ says nothing about the efficiency of a given trophic level, but only the equal efficiency of all trophic levels from primary producers through trophic level L.

The equal transfer efficiency from primary producers through *P. bachei* was calculated using estimates of annual net primary production in the coastal waters of southern California, ANP of *P. bachei*, and the weighted mean number of transfers from primary producers through *P. bachei*. The mean number of transfers was calculated from the percentage contribution from each of 21 prey categories to the total numbers of prey (these 21 categories are 98% of the total numbers of prey in the stomachs of *P. bachei* over a year) and best guesses as to the number of transfers from primary producers to each of the 21 prey species. The mean and range of ANP by all stages of *P. bachei* extrapolated to 365 days (5,700 and 8,300–2,500 mg organic matter) were converted from units of organic matter into organic carbon by taking 50% of the organic matter as organic carbon. The mean and range of annual net primary production (400 and 600–200 g C $\overline{m}^2$ yr^{-1}) were estimated from the mean and range of the rates per day in southern California coastal waters (Eppley, Reid, and Strickland, 1970; W. Thomas, pers. commun.) and multiplication by 365. The expectation of the number of transfers from primary producers through *P. bachei* is 2.3 with an upper limit of the estimate equal to 2.5. These fractions occur because species of animals often do not fall into a single trophic level, and this is in fact the case with *P. bachei*; some of its prey organisms are herbivorous and some are themselves carnivorous. The equal transfer efficiency was calculated and presented in a matrix for the means and ranges of the three variables stated above (Table

TABLE 15.—Calculations of the equal transfer efficiency in percent for different numbers of transfers from primary producers through *Pleurobrachia*, given the observed range and mean of annual net production of *P. bachei* and the estimated range and mean of annual net primary production in g C $\overline{m}^2$ yr^{-1}. In each group of three values, the first is for the highest value of ctenophore net production (4.1 g C $\overline{m}^2$ yr^{-1}), the second is for the mean (2.8 g C $\overline{m}^2$ yr^{-1}) and the third is for the lowest value (1.2 g C $\overline{m}^2$ yr^{-1}).

Net primary production	Number of transfers		
	2.0	2.25	2.5
200	14.3	17.8	21.1
	11.8	15.0	18.1
	7.7	10.3	12.9
400	10.1	13.0	16.0
	8.4	11.0	13.7
	5.5	7.6	9.8
600	8.3	10.9	13.6
	6.8	9.2	11.7
	4.5	6.3	8.3

15). Note that the range of equal efficiency is found on the diagonal from the lower left to the upper right of the table. The overall central value is an equal efficiency of 11%. This efficiency of transfer involves phytoplankton, herbivores, and those primary carnivores on which *P. bachei* feeds, *P. bachei*, and the predators and parasites of *P. bachei*. This efficiency equals the nth root of the ratio of ingestion by predators of *P. bachei* to net primary production.

DISCUSSION

Life table parameters of *P. bachei* show adaptive value in the interdependence of the schedule of births and the rates of development and mortality on population growth. Early reproduction makes a very important contribution to net reproduction and population growth rate, but only in relation to the rates of development and mortality. The larvae have relatively high rates of mortality and lower rates of growth compared to other stages. The 1- to 2–mm postlarvae have the lowest rate of mortality and grow slowly, but they are able to reproduce at an early age and thereby contribute an important fraction of net reproduction. The 3- to 7–mm stages have very rapid tissue growth (instantaneous rates of 0.21–0.47) but do not contribute many young to the population. Instead, these larger stages are important to net production of organic matter because of their rapid growth and high abundance in summer. The stages larger than 8 mm are able to produce enormous numbers of young, but few survive to

this size in nature. Regulation of population growth rate would be very sensitive to changes in mortality rates during production of the first 50–100 young and again during the production of the several hundred young by later stages.

The seasonal occurrence of *H. mediterranea* and the frequency distribution of single and multiple infections and of the percentage of cases for different stages of hosts show two kinds of patterns that are related to life history episodes: 1) the parasites do not often attack the 1– to 2–mm stage postlarvae which are important to net reproduction as discussed above and 2) the parasites occur mainly as one or two individuals per host and most frequently in 6– to 8–mm postlarvae. The early stages of parasites infect the larger hosts more frequently than the smaller hosts because of seasonal availability and perhaps also because of the ability of the larger hosts to better accommodate the extra metabolic burden. The "strategy" of the parasites appears to be infection of larger hosts with few young to provide sufficient food and shelter during their development, but not overexploit each host with too many parasites. The larger stages of hosts are buffered against local extinction by adult parasites, because suitable hosts become more difficult to locate the faster they die. The total ctenophore population has some protection from overexploitation of postlarvae by parasites and other predators in the presence of relatively large numbers of eggs and larvae and the ability of young postlarvae to reproduce soon after development to 1–mm size.

The calculated population growth rates of *P. bachei* indicate that the minimum time for a population doubling is about 35 days (0.693/0.02). This suggests that rapid increases of *Pleurobrachia* observed on a time scale less than a month are probably due to gross advective change if reference of a "bloom" is made to total abundance of all stages. However, the growth in bodily size of *Pleurobrachia* from 2 mm to 6–7 mm diameter may occur in about 2 wk, and this may account for the visual impression of a bloom. Regarding individual and potential population growth rates the salp *Thalia democratica* as another macrozooplankter, is much faster than *P. bachei* (Heron, 1972a, b).

The statistical treatment of variances for mean net production per day describes precision of the estimates, which probably is not the same as inaccuracy in the estimates. For example, it is questionable whether growth rates in the laboratory under constant temperature, food concentration, and food type are accurate estimates of the rates in nature. Variation during a day in ambient conditions appear to be at least as important or more important than the average condition (e.g., temperature). The rates of tissue growth and mortality both depend on the duration of development within a stage, and they are not fully independent variables although they are treated as such in Equation (2). Another error ignored in the statistical treatment is the variance of the standing stock calculated for each replicate sample. I assumed in the calculation of the net production per day for each replicate sample at one station that the variance for the best estimate of the crop is negligible compared to the deviations between the best estimates from the regression equations for each sample. The net production per day for each replicate sample is based on the mean rates of growth and mortality and the best single estimate of the standing crop.

The variance for the mean value of the ANP depends on the variance of the mean net production per day and the square of the time interval over which the rate is linearly applied (Equation (4)). Assuming that the data on net production per day would have a Poisson distribution (variance equals the mean), reasonably small 95% confidence limits for the annual net production (ANP±ANP/10) are obtained with replicate samples if each of ten sampling dates is spaced evenly during the year. The limits are relatively insensitive to whether the seasonal distribution of production is rectangular and continuous, rectangular and discontinuous, or triangular and discontinuous. The important considerations to minimize the confidence limits for the mean annual production are: 1) the number of observations per sampling date, 2) the number of sampling dates, and 3) the time interval between sampling dates in relation to the seasonal maximum abundance and rate of production. The number of observations per sampling date is determined by the number of replicate samples and the number of stations. More stations and replicate samples improve the accuracy in estimating the mean and should decrease the variance of the overall mean for a given sampling date. The number of sampling dates minus one is the number of degrees of freedom for the *t*–statistic which is multiplied by the standard deviation of the mean to give one tail of the confidence limit. The time interval between sampling dates will affect the variance for the net

production over a given period as the square of the interval; therefore, sampling should be carried out on a regular basis without long intervals between dates unless previous information is available on the seasonal distribution of production and the relationship between means and variances.

Three parameters can influence the magnitude of net production by *P. bachei* in addition to errors in the estimation of abundance: 1) water temperature, 2) food supply, and 3) parasitism. In the first two cases, it would appear that for the observed range of temperature and food supply in the study area temperature is more important than food supply. A 10°C range of surface temperature over the year or the temperature change experienced during a postulated 20–m vertical migration in August (see Figure 8) should affect the rate of growth in length and weight and survival. Data are not sufficiently good for quantitative statements about the effect of vertical migration during August on rates of tissue growth, net production, and population growth. The case for the effect of food supply on rates of net production is somewhat better than for temperature. Rates of growth in the laboratory at 15°C are essentially the same for ctenophores cultured on *Acartia* at 35 μg C/liter and 500 μg C/liter. The rates of growth in length and weight at 14.5°C and 1-2 μg C/liter of mixed natural food organisms indicated that the postlarvae grow about as well as at tenfold higher food concentrations. From field samples in which the calculated food concentration was about 10 μg C/liter growth rates in the laboratory and from the field size frequency distributions agree within ±20% of the mean rate. It appears therefore that *P. bachei* postlarvae are very efficient at the extraction of prey from the water at very low concentrations. The estimates of gross growth efficiency showed that over one–half of the food ingested was incorporated into somatic tissues. Perhaps the "passive" feeding mode of these carnivores allows them to have a very low threshold for the commencement of feeding activity, especially since the area of the tentacles is very large in relation to the bodily size of the ctenophore, and relatively low metabolic expenditure is generated while waiting for prey to contact the tentacles.

The estimates of ANP by *P. bachei* are also inaccurate, because no corrections were made for effects of parasitism by *Hyperoche* on rates of tissue growth and duration of development. Since the occurrence of parasitism and high rates of production both were in August (two–thirds of the

ANP was in August), correction may not be trivial. It is not possible to make a quantitative estimate of the error based on any data, but the following sources of error must be considered: 1) the standing stock, B_i, was overestimated by the amount of ctenophore tissue in the volume that the parasites occupy; 2) the instantaneous rate of tissue growth, G_i, was overestimated by the difference between the instantaneous growth rates of nonparasitized and parasitized ctenophores; 3) the instantaneous rate of mortality, M_i, was overestimated by the difference between the durations of development of nonparasitized and parasitized ctenophores (see Equations 1 and 4) the total loss of ctenophore tissue (due to mortality of all types and to ingestion of tissue by parasites that does not result in mortality) in one time increment was underestimated by that fractional amount of tissue removed from the mean standing crop during the time increment by parasitism. Overestimation of the standing stock of ctenophores due to presence of parasites is believed to be negligible, especially since only one or two parasites were present in 92% of all cases (Table 4). For given values of standing stock and rates of growth and mortality (e.g., B_i = 100 mg/m², G_i = 0.2, and M_i = 0.5), the effect of additional tissue loss due to parasitism on the rate of net production is relatively small (ca. 10%) for instantaneous rates of parasitism up to 50% of the rate of mortality. The mean net production per time interval was overestimated. The actual extent of the overestimate can not be evaluated without more information on the effect of parasitism on ctenophore growth.

The ratio of net production per day to mean standing crop during the day for all postlarvae is the biomass–weighted mean instantaneous rate of tissue growth (Allen, 1971), assuming that growth and mortality rates are exponential. The similarity of mean values between stations 1, 3, and 5 is due partly to the bias of having used only the growth rates at 15°C throughout the year, but the range between stages of the mean exponential growth rate is at least tenfold. Some of the consistency in ratios of production to mean standing stock is due to similarity in the length frequency distributions between stations and relative contribution of different stages to the total crop. The overall annual mean production to standing stock value of 0.202 indicates that net production per day is 20% of the mean daily standing stock. This value is within the range of values summarized by Mullin (1969), but is quite high considering the

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relatively large size of postlarvae (e.g., over 10 mg organic weight).

The 11% overall mean in the equal transfer efficiency is surprisingly close to the values of ecological efficiency measured in the laboratory (Silliman, 1968; Slobodkin, 1968); food chain efficiency is the same as ecological efficiency if all food available to a consumer level is ingested (the range for ecological efficiency is generally accepted to be 5–20%). The stability and convergence characteristics of these efficiencies must be set by two boundary conditions: 1) the minimum net production and food required to just replace the component species within a trophic level and 2) the age–structure weighted maximum gross growth efficiency of the component species within a trophic level. The upper limit is set by the physiological maximum gross growth efficiency of each developmental stage weighted over all stages and species in proportion to their relative abundance. In this regard the adults of *P. bachei* are very efficient (60%) at converting food ingested into somatic tissues, and this is probably near the upper limit of gross growth efficiency. Low ecological efficiency is found in species populations dominated by older, slowly growing individuals with low growth efficiency and low rates of mortality (Mann, 1965). In nature it would seem unlikely that food chain efficiency through several successive trophic levels could vary widely. For example, a low efficiency through producers to herbivores means that less net herbivore production would be available to first–order carnivores, all else being equal. Under these circumstances the efficiency through herbivores to first–order carnivores should also be low, because the carnivores must search a larger volume or area to feed and this decreases growth efficiency. Conversely, a high efficiency through producers to herbivores should perpetuate a high efficiency through herbivores to carnivores, unless the age or size distributions of herbivores which yields high net production from producers is not conducive to maximize the efficiency through herbivores to first–order carnivores (i.e., the herbivores are predominantly younger stages which are not available to those stages of carnivores which possess the highest growth efficiency).

There is some evidence from lakes and from theoretical considerations of growth patterns that food chain efficiency is at least in some cases determined by growth efficiency of component species in a food chain and their metabolic flexibility in response to size and abundance of prey (Kerr and Martin, 1970; Kerr, 1971). In complex marine systems considerable effort must be expended before the predator–prey interactions are described and the metabolic rates and efficiencies are measured. Meanwhile, an explanation based on sound theoretical grounds is needed to show why the food chain and ecological efficiencies tend to converge on 10% and have a relatively small range from about 5 to 20%.

SIGNIFICANCE OF *P. BACHEI* IN THE PLANKTON

The coastal waters of southern California represent an ecotone which includes the boundary of land and sea. It is influenced strongly by physical processes and the biota in the water from several sources. The relatively shallow depths within the first 2–3 km from shore emphasize the interdependence and coupling of the benthic and planktonic communities. The benthic community depends on the planktonic community for some of its food supply and for removal of the least fit individuals of those meroplanktonic larvae released by benthic animals. The plankton community receives some of its food in the form of meroplanktonic larvae, and the benthic community returns the materials removed from the water in the form of regenerated nutrients, detritus, and decomposing tissues. It is not surprising, therefore, that *Euterpina* and *Oithona* are the prey of young stages of newly settled juvenile garibaldi, *Hypsypops rubicunda* (Clarke, 1970) and also of *P. bachei*.

The pattern of high standing stocks of different trophic levels and intense biological activity within the first 5–10 km from shore is probably associated with the high regeneration rates of nutrients and high productivity in shallow water (Anderson and Banse, 1961) and life history adaptations of coastal water species to exploit highly productive zones. The short generation times of microcopepods, parthenogenesis in cladocerans and spined eggs of *Acartia* are some adaptations to enable rapid exploitation of favorable conditions in the plankton. The coastal waters may be compared to a chemostat. The rates of dilution by physical forces vary in time and space, but the specific growth rates of the organisms plus their refugial seed stocks and immigrants enable them to persist over time. The quasi–continuous change

in the physical–chemical habitat of the coastal waters prevents the formation of a stable, time–independent assemblage of organisms, although the system appears to be basically composed of the same recurrent species in seasonally varying proportions. Occasionally expatriates from oceanic, southern waters, and northern waters appear (e.g., *Candacia, Eucalanus attenuatus, Tortanus discaudatus, Velella,* etc.). The transients are joined by some organisms which appear seasonally in this area during spawning migrations (e.g., gray whale, squid, grunion).

The regulation of population size in *Pleurobrachia* is postulated to be through density–dependent feedback meahanisms proposed by Greve (1972), in which the prey of larger ctenophores (e.g., adult stages of copepods) are detrimental to survival of the small ctenophore larvae. Balance in the abundance of predators and prey is conferred by selection of larger copepods by the larger ctenophores (Bishop, 1968), but with dependence of ctenophore larvae on copepod nauplii for food supply and low abundance of adult copepods for their survival. A high density of copepod nauplii and low density of copepod adults would favor occurrence of ctenophore larvae and early postlarvae. As both prey and predators grow the roles of predator and prey become reversed to some extent. The large ctenophores may nearly deplete the water of large copepods to satiate their metabolic demands, but this condition is unstable, because the larger ctenophores will become food limited. The population size will not increase greatly because few adult copepods are available to produce eggs, and the nauplii which are hatched from eggs are needed for food of larval ctenophores. If the abundance of postlarvae should increase and some threshold is exceeded, the ctenophore population also becomes vulnerable to density–dependent predation by *Beroë* and other predators and infection by parasites.

All organisms in nature consume food, recycle materials through excretion (and exuviation), and are themselves consumed. In this regard the functional role or ecological significance of a species population is closely related to its relative abundance and rates of turnover. *Pleurobrachia bachei* is a dominant carnivorous zooplankter during summer and fall in the coastal waters off San Diego. Its functional role can be divided into three parts: 1) a predator which regulates the abundance of small crustaceans (copepods and cladocerans) and removes least fit individuals, 2) a vehi-cle which provides shelter and nutrition for parasites such as *Hyperoche,* and 3) an organism which transfers and transforms material and potential energy in the planktonic food web. As a predator, the role of selective removal of prey is an important factor for both the evolution of size, shape, behavior, etc. in the coastal water species and for regulating the abundance and species composition of prey. *Pleurobrachia bachei* is not unique as a planktonic form in providing shelter and nutrition for co–occuring species; salps are exploited in a similar manner by copepods, except that details of the life histories differ (Heron, 1969). As a seasonally dominant carnivore, *P. bachei* is also undoubtedly an important species which transfers organic matter and potential energy to higher trophic levels in the food web of La Jolla Bight.

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