ECOLOGY OF <u>PARATHEMISTO</u> <u>LIBELLULA</u> AND <u>P. PACIFICA</u>
(AMPHIPODA: HYPERIIDEA) IN ALASKAN COASTAL WATERS

by

Bruce L. Wing

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ABSTRACT OF THE THESIS

The planktonic amphipods <u>Parathemisto</u> <u>libellula</u> and <u>P</u>. <u>pacifica</u> co-exist in coastal waters from southeastern Alaska (56° N) to the south-eastern Chukchi Sea (70° N). Observations on distribution, reproductive cycles, diets, metabolism, and starvation tolerance contribute to under-standing this case of congeneric coexistence.

Samples were collected monthly from September 1969 to October 1970 in southeastern Alaska, from May to September 1969 in the southeastern Bering Sea, and in September-October 1970 in the southeastern Chukchi Sea. Respiratory metabolism and starvation tolerance were studied in winter-caught amphipods from southeastern Alaska.

Both species consistently occurred above 300 m in southeastern Alaska. In the southeastern Bering Sea, their distributions were sepa-rate, with <u>P</u>. <u>libellula</u> restricted to an area where summer bottom temperatures were less than 8.0° C. The <u>P</u>. <u>pacifica</u> found in the Chukchi Sea were probably expatriates from the Bering Sea.

In southeastern Alaska, <u>P</u>. <u>libellula</u> has a 1-year life cycle. Broods are released in early May. Juveniles initially live in the sur-face 50 m, but by late June (at a size of 10 mm) they migrate vertically. By late October they have a daytime depth of 200-300 m. Males mature in late winter at 19-21 mm and females at 21-25 mm.

In southeastern Alaska, <u>P</u>. <u>pacifica</u> reproduces throughout the year with a strong peak in early May. Juveniles initially live in the surface 50 m. Adults and subadults migrate vertically to a daytime depth of 100-200 m. Summer growth is rapid, and maturity is attained in 6-8 weeks at

a size of 4.5-6.5 mm. Generation time lengthens in winter to 8-12 weeks, and size at maturity increases to 6.0-7.0 mm. Diets of the two amphipods are similar. About half the food items were calanoid copepods, and 30% were compound-eyed crustaceans (primarily euphausiids and amphipods). Parathemisto pacifica were more cannibalistic than P. libellula.

The temperature coefficient (Q_{10}) for respiratory metabolism of P. libellula is 3-5 at temperatures below 5.0° C, and near 2 at temperatures above 10.0° C. At 7.5° C, the respiration rates for animals tested had a bimodal distribution--not all animals changed their metabolism at the same rate and/or temperature. Respiration rate-weight relationships are not affected by temperature. Respiration rates are inversely correlated with salinity between 30.7°/oo and 32.4°/oo. This relationship may serve to maintain a constant metabolic rate during vertical migration.

The Q_{10} for respiratory metabolism of P. pacifica is near 2 at temperatures below 5.0° C; thus, P. pacifica cannot lower metabolic requirements during the winter as well as P. libellula.

Parathemisto libellula endured starvation for 56 days and P. pacifica for 36 days at 6-7° C.

Annual cycles of temperature and food in Alaskan coastal waters impose conditions outside optimum physiological ranges but within the tolerance of both species. Temperatures above 8.0° C may impose higher metabolic demands upon P. libellula than can be fully supported by the available food. Winter food may be inadequate for the metabolism of P. pacifica. Parathemisto libellula is better adapted to winters than P. pacifica, and P. pacifica better adapted to summers than P. libellula; consequently, in either time of year neither deominates long enough to exclude the other.

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ECOLOGY OF PARATHEMISTO LIBELLULA AND PARATHEMISTO PACIFICA (AMPHIPODA: HYPERIIDEA) IN ALASKAN COASTAL WATERS

I. INTRODUCTION

Hyperiid amphipods of the genus Parathemisto are major contributors to the biomass and trophic structure of temperate and high latitude marine zooplankton communities (Dunbar, 1957; Bowman, 1960). They are frequently the third most abundant holoplankters in temperate and high latitude regions, ranking behind copepods and euphausiids (Bowman, 1960). In the offshore waters of the North Pacific, and in the southern Bering Sea, P. pacifica is the most abundant planktonic amphipod, comprising 55-87% of the amphipod populations in the upper 200 m (Sanger, 1973, 1974). In Arctic waters, P. libellula predominates and supplants the euphausiids as a key species of the trophic system (Dunbar, 1946). Both P. libellula and P. pacifica are abundant in the inshore waters of southeastern Alaska (Wing and Reid, 1972), although in that area, the lysianassid amphipod, Cyphocaris challengeri, appears to be the predominant planktonic amphipod (Wing, unpublished data on file Auke Bay Fisheries Laboratory).

Because of their abundance, relatively large size (5-50 mm length at maturity), swarming habits, and tendency to reside at shallow depths, the various Parathemisto species are an important but variable component in the diets of fish, birds, seals, whales (Bigelow, 1926; Phillips, 1964; Dunbar, 1957; Lambert, 1960; Dell, 1963; LaBrasseur, 1966; Gray and McHardy, 1967; Carlson, 1968; Bedard, 1969; Nemoto and Yoo, 1970; Kawamura, 1970) and other marine forms such as pasiphaeid shrimps. As carnivores, they may compete seriously with fish as well as invertebrates for smaller

herbivorous plankton, or may prey directly on the larvae of commercially utilized fish and invertebrates. The biology of the North Pacific Parathemisto and the relationships of the various species of Parathemisto to their environment and to each other are poorly known. Each species probably responds differently to changes in the ecosystem, and may have significantly different roles in the ecosystem. This study was undertaken to define some of the environmental factors which may control the abundance, distribution, and interrelationships of P. libellula and P. pacifica in the coastal waters of Alaska. Emphasis is on material from the inside waters of southeastern Alaska, with supplementary information from the Bering and Chukchi Seas.

Four species of Parathemisto occur in Alaskan coastal waters. Parathemisto abyssorum Boeck, appears to be restricted to the Arctic Ocean, where it is common along the Beaufort Sea coast (Cobb and McConnell, 1974), but is has not been observed in the Chukchi Sea south of Barrow, Alaska (Bowman, 1960). Parathemisto libellula (Lichtenstein) is widely distributed from the Arctic Ocean to the southern Bering Sea (Bowman, 1960) and in the inside waters of southeastern Alaska (Wing and Reid, 1972). Only a single record for P. libellula in the Gulf of Alaska has been reported (Bowman, 1960). Parathemisto japonica Bovallius appears to be limited to subarctic water of the western Bering Sea, and rarely occurs in the southeastern Bering Sea (Sanger, 1974). Parathemisto pacifica Stebbing occurs in Alaskan waters from the southern Chukchi Sea (Wing, 1974) through the Bering Sea, Gulf of Alaska (Bowman, 1960) and inside waters of southeastern Alaska (Wing and Reid, 1972). The range of P. pacifica extends southward to Baja California (Bowman, 1960).

Previous investigations on northeastern Pacific hyperiids have been limited mostly to taxonomic and distributional studies. Bowman (1960) comprehensively reviewed the taxonomy and geographical distribution of the North Pacific and Arctic Parathemisto species, and gave particular attention to the seasonal distribution, development, and reproductive cycles of P. pacifica off the California coast. Van Arsdale (1967) examined the seasonal and depth distribution of P. pacifica off the Oregon coast. Sanger (1973, 1974) reported on the fall abundance of P. pacifica offshore from Washington and British Columbia and the summer abundance in the southeastern Bering Sea. Wing and Reid (1972) gave limited data on the seasonal abundance of P. libellula and P. pacifica in Auke Bay, southeastern Alaska. Aside from these reports and the primarily taxonomic early literature cited therein, the biology of the northeastern Pacific species of Parathemisto must be inferred from studies on other Parathemisto species and/or areas considerably distant from the northeastern Pacific.

In addition to many taxonomic and geographic distribution studies, some investigations have considered the reproductive and developmental cycles of Parathemisto spp. in the Arctic, North Atlantic, and Southern Oceans. Generally, these investigations have found high Arctic species such as P. abyssorum and P. libellula to have a 2-year life cycle with a small amount of overlap between generations, resulting from a few individuals maturing in less than 2 years (Bogorov, 1940; Dunbar, 1946, 1957). Mid-latitude populations of P. abyssorum have a 1-year life cycle (Hoffer, 1972), and low-latitude species such as P. gracilipes and P. gaudichaudii have multiple, overlapping generations and year-round

reproduction, although strong seasonality may be evident in the intensity of reproduction (Bowman, 1960; Siegfried, 1965; Kane, 1966; Evans, 1968). The high Arctic forms may die after first reproduction (Dunbar, 1946, 1957); and heavy adult mortality may occur in mid-latitude populations (Hoffer, 1972). However, at lower latitudes significant numbers of adults survive to reproduce more than once (Bowman, 1960).

Environmental temperatures have been correlated with geographical and vertical distribution of some species, as well as with generation time and size at maturity (Hurley, 1955; Bowman, 1960; Kane, 1966; Evans, 1968). The salinity differences between oceanic and neritic waters may influence the distribution of several species (Bowman, 1960).

The behavior of Parathemisto spp. has been poorly studied. Some species have been observed to migrate diurnally--P. gracilipes (Russell, 1925) and P. japonica (Chebanov, 1965). Diurnal migration is not evident in P. pacifica (Van Arsdale, 1967; Sanger, 1974); or possibly occurs only seasonally (Bowman, 1960). Two species, P. gracilipes and P. gaudichaudii, are known to form dense swarms at the surface at the time of brood release (Gray and McHardy, 1967), during which time a large variety of fish, whales, etc. feed extensively on these species.

Physiological investigations concerning Parathemisto spp. are limited to a very few observations of respiration rates of P. gaudichaudii (Conover, 1960, as Euthemisto compressa) and P. libellula (Ikeda, 1970, as Euthemisto libellula), and the demonstration that P. gaudichaudii may assimilate dissolved organic compounds (McWhinnie and Johanneck, 1966). Nakai (1942) gives limited data on the protein, fat, and ash content of a species of Parathemisto (probably P. japonica). Dietary requirements

of Parathemisto are poorly known, although they are generally recognized
to be carnivorous (feeding primarily on copepods), occasionally
cannibalistic and possibly consuming some phytoplankton (Bigelow, 1926;
Dunbar, 1946; Bowman, 1960). A portion of the present study has been
directed toward experimental examination of the influence of temperature
on the metabolism of P. pacifica and P. libellula, and in this
connection, a limited amount of data on lipid contents was obtained.
Information on the diets of P. libellula and P. pacifica over the course
of a year were obtained from stomach analyses.

II. STUDY AREAS

Three geographical areas are considered in this study: the northern portion of southeastern Alaska, Bristol Bay of the Bering Sea, and the southeastern portion of the Chukchi Sea (Figure 1). Because a full year of monthly observations were available from southeastern Alaska, and only a single season's data were available from the Bering and Chukchi Seas, the three areas are given unequal treatment. Southeastern Alaska receives the most attention, and the Bering and Chukchi Seas are treated very briefly. Within southeastern Alaska, two sites have served as the primary oceanographic stations fro the collection of Parathemisto libellula and P. pacifica together with pertinent environmental data. The Auke Bay Monitor station was selected to represent the smaller bays and inlets, and the False Point Retreat station was chosen to represent the large deep channels. Both stations are readily accessible from the Auke Bay Fisheries Laboratory of the National Marine Fisheries Service.

Auke Bay (lat. 58°21.9'N, long. 134°40.0'W) is 19.3 km northwest of Juneau, Alaska, and 130 km from the open waters of the North Pacific. As the site of the Auke Bay Fisheries Laboratory, it has received the attention of a variety of published and unpublished investigations since the late 1950's. These include temperature records (Williamson, 1965), amino acid-phytoplankton relationships (Bruce, 1969; Shell, 1971, 1974), a nutrient-phytoplankton model (Curl et al., 1971; Iverson, 1971), wind-driven circulation-phytoplankton relationships (Kirk, 1972; Iverson et al., 1973), seasonal zooplankton concentrations (Wing and Reid, 1972), and descriptions of the seasonal oceanographic cycles (Bruce and McLain, in prep.). Additionally, a number of other papers not concerned specifically with Auke Bay biota have included notes on the

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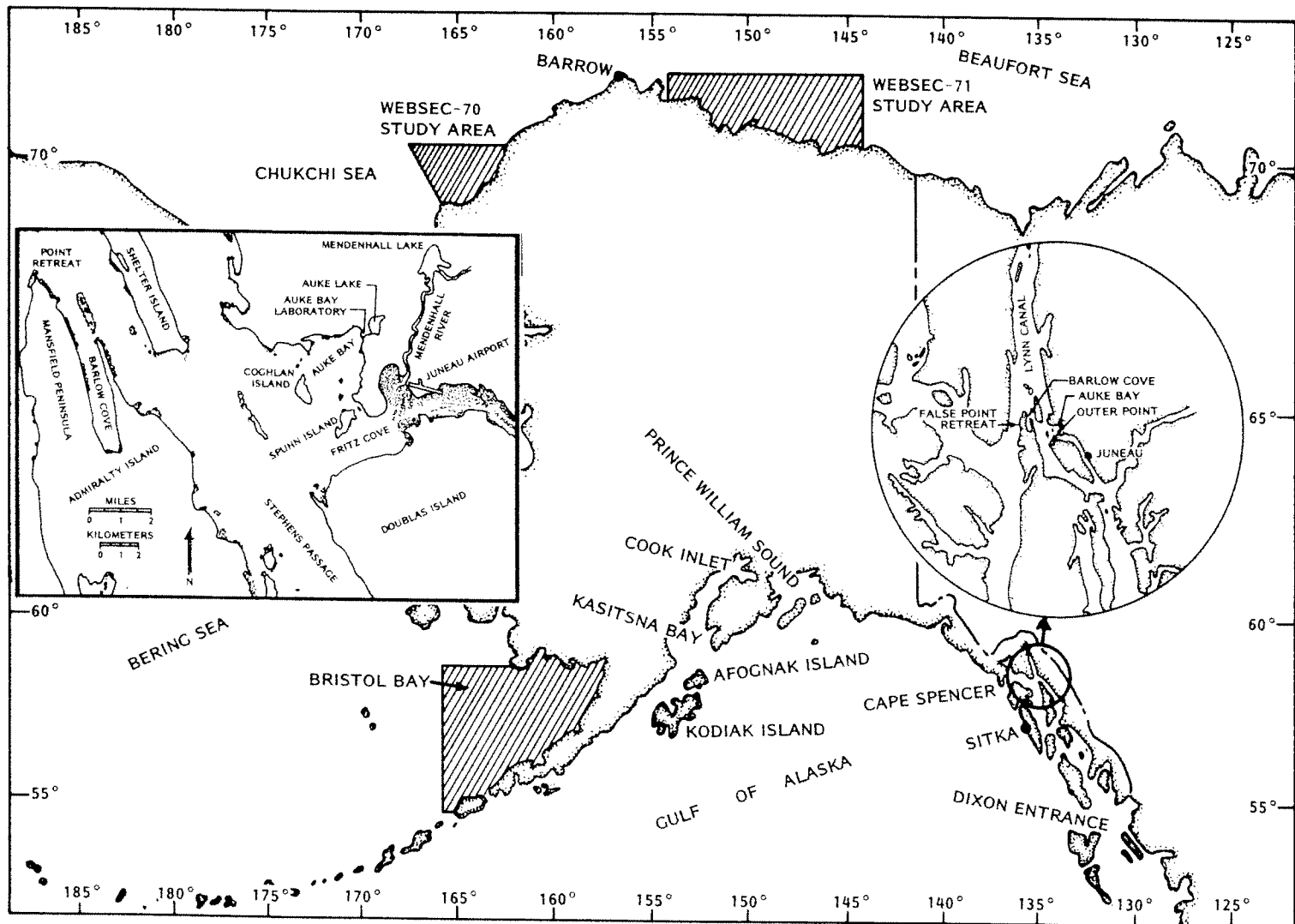
Figure 1.--Map of Alaska showing areas and locales discussed in text

fauna (Ricketts and Calvin, 1952; Merrell, 1970; Quast and Hall, 1972; Carlson and Haight, 1972). Auke Bay is probably the most studied small bay in Alaska.

False Point Retreat (lat. 58°22.2'N, long. 134°59.1'W) 45 km northwest of Juneau lies on the northwest tip of Admiralty Island at the southern end of Lynn Canal. As an area representative of the large deep channels of southeastern Alaska, it has received sporadic attention from several investigations on the physical oceanography of southeastern Alaska (Williamson, 1965; Rosenberg, 1966; Packard, 1967; McLain, 1969; Coughenower, 1972; Curl et al., 1972). With exception of McLain's study, these investigations have been conducted mostly in the late spring and early summer; consequently little information is available on the seasonal oceanographic cycles of the deeper channels. Information on the temporal variation in species and abundance of the biota consists mostly of unpublished observations on the phytoplankton, zooplankton, and nekton gathered by the National Marine Fisheries Service (on file at Auke Bay Fisheries Laboratory).

Historically, Bristol Bay in the southeastern corner of the Bering Sea has been the site of intensive fisheries for salmon, halibut, herring, crabs, shrimp, etc. by the United States, Canada, Japan, and Russia. Because of these fisheries, Bristol Bay and the rest of the Bering Sea have received the attention of numerous and varied oceanographic investigations, extending back to the turn of the century (Grier, 1941; Favorite, 1974). However, the ecology of Parathemisto spp. in the area has not received attention beyond documentation of their presence.

The northern limits of Parathemisto pacifica are not well recorded (Bowman, 1960). During the fall of 1970, I had an opportunity to collect

zooplankton in the southeastern part of the Chukchi Sea at which time a few P. libellula and P. pacifica were taken. This is the area between lat. 70°20'N and lat. 68°54'N (Icy Cape south to Cape Lisburne) covered by the first Western Beaufort Sea Ecological Cruise (WEBSEC-70). The WEBSEC program attempted to provide an integrated physical, chemical, geological, and biological description of the area during the onset of winter conditions. Physical and chemical oceanographic characteristics of the area and a review of past oceanographic surveys of the southern Chukchi Sea are given in Ingham et al. (1972). The methods for and results of the zooplankton sampling have been presented by Wing (1974).

III. METHODS

Field Sampling Program

Field operations were conducted as a series of monthly samplings in southeastern Alaska using the Auke Bay Fisheries Laboratory research vessel Murre II, an 80-foot power barge equipped for oceanographic and biological research. The Auke Bay Monitor and the False Point Retreat stations were occupied on successive days at mid-month; and weather and time permitting, night samples of zooplankton were also taken. At each sampling, routine surface meteorological observations were recorded and Nansen bottle casts were made for temperature, salinity, nutrient, oxygen, and chlorophyll a concentrations. In Auke Bay, the sampling depths were 0, 1, 5, 10, 20, 30, 40, and 50 m over a bottom of 55 m. At False Point Retreat, additional temperatures and water samples were taken at 75, 100, 150, 200, 250, 300, 400, 500, and 600 m. Chlorophyll a samples were taken only to 50 m at both stations. Secchi disk and submarine photometer casts were made whenever current conditions and functional equipment allowed. Upon completion of physical observations and chemical sampling, a bathythermograph cast was made to determine depth of the seasonal thermocline and the maximum depth of the first zooplankton sample.

Biological sampling consisted of a 3-minute surface tow with a 1/2-m 0.076 mm (#20) mesh NORPAC plankton net for qualitative phytoplankton samples, and vertical tows for zooplankton with a 1/2-m 0.505 mm (#0) mesh NORPAC net. Zooplankton samples were taken by lowering the net open, cod end first, at approximately 60 m per minute and retrieving at approximately 40 m per minute. Because functioning closing devices were not available, the vertical tows were made from predetermined depths to the surface. The shallower samples were always made first and the net thoroughly rinsed

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between tows to reduce between-tow contamination. At False Point Retreat, the normal sequence of zooplankton tows was thermocline or 15 m to surface, 50-0 m, 100-0 m, 200-0 m, 300-0 m, 400-0 m, 500-0 m, and 600-0 m. In Auke Bay only three samples were usually taken: thermocline or 15 m to surface, 50 m to surface, and a qualitative oblique tow of approximately 3 minutes duration from 50 m to surface.

Day samples in Auke Bay were normally taken between the hours of 1000 and 1100. Because of longer running time and more time required to obtain the physical and chemical data at greater depths, daytime samples at False Point Retreat were normally taken between 1430 and 1630. When possible, night sampling was done the following evening or the following day after completion of the False Point Retreat day sampling. Night sampling at False Point Retreat began approximately 2 hours after sunset and consisted of vertical tows for zooplankton first. After the vertical night tows were completed, and if weather and time permitted, I made two 1/2-hour tows with a 1.8-m (6-foot) Isaacs-Kidd midwater trawl, one each at 125 m and at 15-20 m, in the hope of obtaining larger catches of amphipods for use in laboratory physiological studies. After completion of night work at False Point Retreat, the Murre II returned to the Auke Bay Fisheries Laboratory. Night samples in Auke Bay were taken en route to the laboratory, usually about 0200.

Samples taken during the field operations were treated variously according to the purpose of their collection. Water samples taken for oxygen determination were immediately fixed for Winkler analysis, while the samples taken for nutrients were immediately frozen for later determination of PO_4-phosphate, NO_3-nitrogen, and SiO_2-silicon. Chlorophyll a samples were filtered through 0.45-micron HA millepore filters and placed in a desiccator.

Subsequent chemical analyses were performed at the Auke Bay Fisheries

Laboratory by the Oceanographic Investigations staff using the methods

recommended by Strickland and Parsons (1968).

Phytoplankton and zooplankton samples were preserved in 3% seawater

formalin within 10 minutes of collection. After 3 to 10 days of fixation

in formalin, the zooplankton samples were washed in tapwater and then

transferred to 40% isopropyl alcohol for sorting and permanent storage.

A few specially collected samples were frozen immediately upon collection

for lipid analyses.

Dates of sampling and the types of data successfully recorded are

presented in Tables 1 and 2. All physical and chemical data have been

submitted to the National Oceanographic Data Center, Washington, D.C.

Results of the oceanographic observations and a summary description of

the oceanography of northern southeast Alaska are presented in Chapter

III.

Laboratory Treatment of Field Collections

After transfer to 40% isopropyl alcohol, the zooplankton samples

were sorted for Parathemisto spp. All Parathemisto were removed from the

samples, identified to species, tallied by cruise and sample, and then

stored in separate vials for later analysis of size, sex, and foods

eaten. The remaining zooplankton were not enumerated, but a

listing of all species in each sample was recorded, and the samples saved

for future investigations.

Size composition and sex determinations were done after approximately

2 years storage. This procedure assures that all shrinkage would be complete,

and no errors imparted by differing degrees of freshness of sample

(Ahlstrom and Thrailkill, 1963). Measurements were made by straightening

TABLE 1.--Summary of oceanographic observations at False Point Retreat, southeastern Alaska, September 1969 to February 1971   (x indicates observations completed, - indicates not completed)

| Date | Observations of surface weather | Profiles of-- | | | | | | | | No. plankton samples | | | |
		Temperature	Salinity	Submarine light	NO$_3$	PO$_4$	SiO$_2$	O$_2$	Chlorophyl-a	Surface phytoplankton	Zooplankton Day	Zooplankton Night	Isaacs-Kidd midwater trawl
1969													
16 Sept.	x	x	x	-	x	x	-	x	x	1	5	-	-
14 Oct.	x	x	x	x	x	x	-	x	x	1	5	-	-
14 Nov.	x	x	x	x	x	x	-	x	x	1	6	6	-
16 Dec.	x	x	x	x	x	x	x	x	x	1	9	-	-
1970													
22 Jan.	x	x	x	x	x	x	x	x	x	1	8	8	-
11 Feb.	x	x	x	x	x	x	x	x	x	1	9	8	2
17 March	x	x	-	x	x	x	x	x	x	1	8	9	1[a]
14 April	x	x	x	x	x	x	x	x	x	1	9	8	1
8 May	x	x	x	x	x	x	x	x	x	1	9	-	-
15 June	x	x	x	x	x	x	x	x	x	1	9	9	2
21 July	x	x	x	x	x	x	x	x	x	1	8	8	1
12 Aug.	x	x	x	(b)	x	x	x	x	x	1	8	8	-
10 Sept.	x	x	x	x	x	x	x	x	x	1	8	-	-
20 Oct.	x	x	x	x	x	x	x	x	x	1	9	8	-
1971													
10 Feb.	x	x	x	-	x	x	-	(b)	x	1	8	-	-

[a]One sample was also taken in a light-baited trap.

[b]Data are of doubtful validity.

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TABLE 2.--Summary of oceanographic observations in Auke Bay, southeastern Alaska (Auke Bay monitor stations), August 1969 to February 1971 (x indicates observations completed; - indicates not completed)

Date	Observations of surface weather	Profiles of --								No. plankton samples		
		Temperature	Salinity	Submarine light	NO_3	PO_4	SiO_2	O_2	Chlorophyl-a	Surface phytoplankton	Zooplankton Day	Zooplankton Night
1969												
22 Aug.	-	-	-	-	-	-	-	-	-	-	1	3
17 Sept.	x	x	x	-	x	x	-	x	x	x	2	-
15 Oct.	x	x	x	x	x	x	-	x	x	x	4	-
13 Nov.	x	x	x	x	x	x	-	x	x	x	3	3
17 Dec.	x	x	x	x	x	x	x	x	x	-	3	3
1970												
20 Jan.	x	x	x	x	x	x	x	x	x	x	3	3
12 Feb.	x	x	x	x	x	x	x	x	x	x	3	3
20 March	x	x	-	x	x	x	x	x	x	x	2	2
13 April	x	x	x	x	x	x	x	x	x	x	3	3
6 May	x	x	x	x	x	x	x	x	x	x	3	-
16 June	x	x	x	x	x	x	x	x	x	x	3	-
20 July	x	x	x	x	x	x	x	x	x	x	3	3
11 Aug.	x	x	x	x	x	x	x	x	x	x	3	3
9 Sept.	x	x	x	x	x	x	x	x	x	x	3	-
21 Oct.	x	x	x	x	x	x	x	x	x	x	3	2
1971												
9 Feb.	x	x	x	-	x	x	-	x	x	x	3	-

the animal along a scale graduated in 1-mm increments under a dissecting microscope at magnifications of 10-40X. Total body length was taken as the straight line distance from the anterior margin of the head to the tip of the third uropods. Large _Parathemisto libellula_ were measured to the nearest 0.5 mm, and the lengths of small P. libellula and most P. pacifica were estimated to the nearest 0.1 mm. The sex of adult and subadult amphipods was determined on the basis of antennal characteristics. No attempt was made to determine the sex of small juveniles.

Some losses of samples occurred because of dehydration during storage, but when possible, stomach contents of approximately 50 individuals of each species from each set of day and each set of night samples were used for stomach content analysis. If less than 50 animals of a species were taken during a given month or remained after dehydration losses, all specimens were used. Otherwise, the sample or combination of samples approximating 50 specimens were utilized. In a few months, where the catch of _Parathemisto libellula_ by vertical tows was very low, supplementary material was drawn from Isaacs-Kidd midwater trawl catches.

To obtain the stomach contents, the amphipods were dissected under a microscope at magnifications of 10-40X, by separating the head from the metasome from the dorsal side. The foregut and midgut were then removed, usually intact, with all contents. This eliminated much of the potential contamination due to organisms being entrapped among the ventral and oral appendages. Stomach contents were then mounted in water on a microscope slide, teased apart, and examined at magnifications of 30-40X with a dissecting microscope, and at 100-250X with a compound dark-phase microscope. Food items were identified by general categories on the basis of hard or indigestible parts such as appendages of copepods, amphipods,

euphausiids, and other crustaceans; hooks and jaw parts of chaetognaths; or setal clumps from polychaetes. If the parts led to species recognition, this was recorded. Beyond the observation as to whether the foregut and midgut were full or nearly empty, little attempt was made to quantify the amount of food in the stomachs.

Methods for Physiological Studies

Parathemisto spp. have rarely been maintained in laboratories for extended observations or experimental studies. Kane (1963) held P. gaudichaudii for observation of early development, and Galt and Whisler (1970) kept P. pacifica for investigation of the sporulation and development of the parasitic ellobiopsid Thalassomyces marsupii. Other attempts at maintaining Parathemisto consisted of short-term shipboard observations (Conover, 1960; Ikeda, 1970; McWhinnie and Johanneck, 1966). Between January 1970 and March 1973, I kept subadults and adults of P. libellula and P. pacifica in the Auke Bay Fisheries Laboratory wet laboratory for experiments on the relationship of temperature and metabolic rates. Maintenance of the amphipods in the laboratory provided opportunity for observations on molting rates, starvation tolerance, feeding behavior, and response to light and physical agitation in addition to the experimental studies on oxygen consumption rate. The experimental work was done during the winter between the months of November and early May, when only subadult and adult P. libellula were available in sufficient numbers for replicate experiments. Attempts to maintain juvenile Parathemisto during the late spring and summer months were not successful. The schedule of collections for physiological material and observations made are presented in Table 3.

TABLE 3. --Summary of _Parathemisto_ collections for physiological studies

Date	Location	Method and depth of capture	Species	Number	Laboratory observations on:
1970					
20 Jan.	Auke Bay	1/2-m NORPAC net, surface tow	P. pacifica	4	Laboratory survival
11 Feb.	False Point Retreat	2-m Isaacs-Kidd midwater trawl, 15-20 m	P. libellula	21	Starvation tolerance, feeding behavior, molting
20 March	False Point Retreat	Light trap, 18-20 m; 2-m Isaacs-Kidd midwater trawl	P. pacifica P. pacifica P. libellula	5 16 1	Starvation tolerance, feeding behavior, molting, brood release
1971					
10 Feb.	False Point Retreat	1-m NORPAC net, 200-300 m	P. pacifica P. libellula	12 18	Feeding behavior, molting, brood release, respiration rates
28 May	False Point Retreat	60-cm bongo net, 300 m	Parathemisto spp. (juveniles)		Laboratory survival, feeding behavior
29 Dec.	Barlow Cove	2-m Isaacs-Kidd midwater trawl, 85 m	P. pacifica P. libellula	1 11	Respiration rates, feeding behavior
1972					
11 Feb.	Outer Point	2-m Isaacs-Kidd midwater trawl, 75 m	P. pacifica P. libellula	10 50	Respiration rates, feeding behavior, molting
22 March	Barlow Cove	2-m Isaacs-Kidd midwater trawl, 90-120 m	P. pacifica P. libellula	4 5	Respiration rates Feeding behavior
23 March	Barlow Cove	2-m Isaacs-Kidd midwater trawl, 40-50 m	P. libellula	150	Brood release, brood survival
17 Nov.	Outer Point	60-cm bongo net, 25-50 m	P. pacifica P. libellula	20 200	Respiration rates, feeding behavior, molting
18 Dec.	Outer Point	1-m NORPAC, 25 m	P. pacifica P. libellula	1 200	Respiration rates, feeding behavior, molting

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Maintenance of Parathemisto in the Laboratory

Amphipods used for experimental purposes were captured by three methods. An experimental plexiglass light-baited trap which previously had proved effective in capturing Parathemisto pacifica, mysids, and positively phototropic hydromedusans took less than five amphipods per set in the winter of 1970; consequently its use was abandoned in favor of towed nets.

NORPAC standard nets with 0.505-mm mesh were used on three occasions; 60-cm Bongo nets with 0.505-mm mesh were used twice; and a 6-foot Isaacs-Kidd midwater trawl was used six times to collect amphipods for laboratory experiments (Table 3). For these collections, tows were made for periods of 10-30 minutes at suspected depths of amphipod concentrations. Longer tows were judged undesirable because of potential net injury to the amphipods. As soon as the net was brought aboard, the catch was placed in a large tray with fresh seawater and active amphipods were sorted out. The amphipods were placed in 1-gallon containers of fresh seawater for transport back to the laboratory. With 25-50 amphipods per container, a battery-powered aerator was employed to prevent oxygen depletion. The temperatures were maintained either by replacement with new cool seawater or by leaving the containers on the open deck when air temperatures were the same as water temperatures.

In the laboratory, the animals were placed in individual glass containers with 300-500 ml of seawater cooled to the temperature of collection. On occasions when more amphipods had been collected than there were individual containers available, 5-10 amphipods were held in 4-liter flasks and 1-gallon jars. Separation of individuals was necessary to prevent cannibalism. The containers were kept in four flow

tables with water flows adjusted to maintain temperatures near 5° C for the reserve stocks, and at temperatures up to 12° C for animals being acclimated for experiments at temperatures above incoming seawater temperatures. Two chilled water baths were used to acclimate animals for experiments below ambient seawater temperatures. Three of the flow tables and the water baths were covered to keep the amphipods in darkness. The fourth flow table and the amphipods held in it were exposed to erratic light-dark cycles coincident with other activities in the wet laboratory.

It was necessary to change water in the holding flasks at least once a week, and preferably twice a week to remove uneaten food, and to prevent a buildup of excretory products, contaminating algae, and bacterial growth. Clean containers were used at each water change. While in the laboratory, the amphipods were checked daily; temperatures were recorded; and excess food, casts, and dead amphipods were removed.

The amphipods were fed at least once a week. When available, living zooplankton were offered as food. These zooplankters consisted of copepods, euphausiids, small gammarid amphipods, barnacle nauplii, crab zoeae, chaetognaths, and fish larvae. If live food was not available, small pieces of sea urchin, mussels, clams, scallops, herring, sole, tanner crab, frozen euphausiids, or frozen brine shrimp were offered as food. Because the amphipods seemed unable to search and locate food, it was necessary to feed each animal individually by placing nonliving food on the end of a glass probe and touching the amphipod's legs with the food. Once the amphipod had taken the food, the probe was withdrawn.

Although the above methods for maintaining zooplankton in the laboratory were admittedly crude and far from ideal, the Parathemisto proved to be hardy animals. With care, specimens were kept alive in

excess of 80 days (Table 4).

Measurement of Oxygen Consumption Rates

Oxygen consumption rates, an indirect measure of the metabolic rates of whole animals, were used to determine the response of Parathemisto libellula and P. pacifica to changes in environmental temperatures. All measurements were made with a 14-flask Gilson respirometer (Gilson, 1963) using 15-ml flasks. The standard preparation for experiments with P. libellula was one amphipod per flask in 10 ml of freshly aerated seawater, equilibrated to the desired experimental temperature. A saturated KOH solution (0.3 ml) and filter paper wick in the center well provided for CO_2 absorption. To correct for the mechanical variability of the particular respirometer used, at least four control flasks were included in each experiment.

With the exception of a series of experiments made to determine the possible effect of variations in technique, all measurements were made in the dark, with the shaker set for 80 cycles per minute. Readings were taken at hourly intervals for 4-8 hours with at least 45 minutes equilibration allowed before closing the valves to begin readings.

To evaluate possible influence of experimental techniques, experiments were performed on the same group of animals with and without the shaking in the dark, and with and without shaking in bright light. The light source was provided by a 100-watt frosted incandescent bulb placed 60 cm above the respirometer. At this time, the water bath of the respirometer was filled with an aquamarine antifreeze (Goodyear) solution for use in experiments near the freezing point of seawater, although the actual experiments were run at 4° C. During this series of experiments, one set was performed during normal daytime working hours

TABLE 4. --Summary of maximum survival times of Parathemisto libellula and P. pacifica in the laboratory

Date of capture	Number	Temperature at which captured (° C)	Range of holding temperatures (° C)	Maximum days survival
		Parathemisto libellula		
11 Feb. 1970	21	3.5	5.4 to 10.2	90
20 March 1970	1	3.5	6.3 to 7.8	46
10 Feb. 1971	18	2.2 to 2.8	-0.6 to 10.2	82[a]
29 Dec. 1971	11	3.5	-1.6 to 4.5	49[a]
11 Feb. 1972	50	3.5	-1.8 to 10.8	31[a]
22 March 1972	5	3.6	3.8 to 15.5 ⎤	
23 March 1972	150	3.6	3.8 to 15.5 ⎦	70[a]
17 Nov. 1972	200	4.6	3.5 to 18.0	40[a]
18 Dec. 1972	200	3.4	3.6 to 10.0	82[a]
		Parathemisto pacifica		
20 Jan. 1970	4	3.0	7.8	10
20 March 1970	16	3.5	6.6 to 9.6	53
10 Feb. 1971	12	2.2 to 2.8	-0.6 to 7.5	83[a]
28 May 1971	4	4.5 to 5.5	4.5 to 16.0	33
29 Dec. 1971	1	3.5	-1.5 to 3.6	42[a]
11 Feb. 1972	10	3.5	-1.8 to 4.5	26
22 March 1972	4	3.6	3.7 to 4.0 ⎤	
23 March 1972	5	3.6	3.7 to 4.0 ⎦	14[a]
17 Nov. 1972	20[b]	4.6	3.5 to 9.8	13[a]
18 Dec. 1972	1	3.4	4.5	1

[a]Death by accident or deliberate termination of work. Data are not indicative of longevity in the laboratory.

[b]Juveniles.

and another at night to test for possible day-night differences in respiration rates.

To determine metabolic rates at given temperatures, the water baths in which the amphipods were held were brought to temperature by increments of 1° C per day. Once the experimental temperature had been reached, the animals were held at that temperature for at least 24 hours before respiration rates were measured. When possible, the animals were held for an additional 7-10 days for a repeated measurement. At the end of each experiment, the condition of each animal was recorded, and it then was carefully returned to a numbered holding container for possible use in later experiments at other temperatures. Records kept for each amphipod were: (1) length of time in captivity; (2) length of time allowed to acclimate to the experimental temperature; (3) date of molt; and (4) date of death. Salinity and temperatures during the experiment were recorded. Wet and dry weights were obtained either after death or at the termination of an experimental series.

Weight and length data for all experimental animals, and for several lots of animals which died before use in experiments, were taken for the purpose of determining weight-length relationships of nonpreserved material. Wet weights were not always recorded immediately upon the death of the amphipod. When it was not possible to take weights immediately, the animals were frozen and held until these data could be recorded. Length measurements of the fresh or thawed amphipods were made in the same manner as described for lengths from preserved material, except that both Parathemisto libellula and P. pacifica were measured only to the nearest 0.5 mm. Wet weights were taken on carefully blotted individuals placed in pretared glass or polyethylene weighing bottles.

Weights were measured to the nearest 0.01 mg using a Metler Model B6 microbalance. After wet weighing, the amphipods were retained in their weighing bottles, and placed in a lowered atmosphere desiccator for drying at room temperature. Desiccant (silica gel and/or calcium carbonate) was changed every 3-4 days, and the amphipods were dried for a minimum of 2 weeks before dry weights were taken.

To facilitate the statistical analyses of the relationships of weight, temperature, salinity, days in captivity, days allowed for acclimation, days before or after molt, and days before death to the observed oxygen consumption rates, all data were entered on computer punch cards. The BioMedical Computer Programs for data description and plots (BMD 02D) and for stepwise regressions (BMD 02R) were used with various subsets of data to examine specific questions. Statistical analyses of the results of experiments performed to test experimental techniques were made on the raw 6-hour oxygen consumptions using paired t-tests for mean differences and F-tests to examine variances.

IV. OCEANOGRAPHIC ENVIRONMENT OF PARATHEMISTO IN SOUTHEASTERN ALASKA

Summary of the Oceanography of Southeastern Alaska

Although several authors have published on the oceanography of southeastern Alaska, there are few observations covering the yearly cycle or giving multiple-year sequences of data suitable for describing or evaluating deviations from normal conditions. With the exception of a 4-year sequence of surface temperatures for 1959-63 (Williamson, 1965), assessment of normal conditions must be based on observations over one season, and at best over a single year. The topography, general circulation, and heat budgets of the major channels and inlets have been described on the basis of single cruises or short seasonal studies (Packard, 1967; Coughenower, 1972) or with a small amount of year-round physical oceanographic data (McLain, 1969). Likewise, most of the descriptions of oceanographic conditions in the smaller bays and inlets are the results of quick surveys or short seasonal studies (Barnes et al., 1956; Powers, 1963; Hood et al., 1969; Curl et al., 1971; Iverson, 1971; Kirk, 1972; Barr and Knull, 1973; Iverson, Curl, O'Connors, Kirk, and Zakar, 1974). The only small bay to have been treated for a full year or more is Auke Bay (Bruce, 1969; Bruce and McLain, in prep.).

The following summary of oceanographic conditions and cycles in southeastern Alaska has been drawn from the literature noted above, as well as from unpublished data on file at the Auke Bay Fisheries Laboratory. The major channels will be discussed first, followed by a description of conditions in Auke Bay. Oceanographic conditions at False Point Retreat and in Auke Bay from September 1969 to February 1971 will be treated following the general summary.

Topographically the major bodies of water in southeastern Alaska may be considered as interconnected fjords, having developed as flooded glacial valleys of a major fault system. The mean depth of these large fjords is 350 m, and the maximum is 840 m (Packard, 1967). Sill depths generally exceed 50 m, even at the entrance to the smaller side inlets and bays, which may account for infrequency of anaerobic bottom conditions (Barr and Knull, 1973). In similar areas of British Columbia and Norway, anaerobic bottom conditions occur with some regularity. Typically the major channels and inlets have a classic U-shaped cross section with precipitous sidewalls and relatively flat mud bottoms. Depths exceeding 100 m less than 0.5 km from shore are more the rule than the exception.

Southeastern Alaska as a whole may be considered as a complex of positive estuaries (McLain, 1969), having a continuous low-salinity seaward transport at the surface and a deep inflow of high-salinity water. Surface salinity varies seasonally, the lowest salinities occurring in the summer when glacial and river runoff are maximum. Runoff is low in the winter, and surface salinities rise due to the combination of lesser freshwater input and increased evaporation rates associated with high winds and low temperatures. In the summer, salinities at the heads of inlets and bays may be as low as $5^\circ/_{oo}$; but may rise to $30\text{-}32^\circ/_{oo}$ in the winter. Seasonal salinity changes are most extreme at the surface and decrease with depth. The seasonal pycnocline forms in the late spring and averages 10 m; but may extend to 30 m in the late summer. Below the pycnocline, salinities vary from a summer low of about 30°_{oo} to a winter high of $32^\circ/_{oo}$ in the upper 200 or 250 m. Below

250 m, little seasonality is evident, with salinities averaging $33.3°/_{oo}$

at 300 m and $33.8°/_{oo}$ at 600 m.

The seasonal variations in the temperatures of the major inlets,

like those of salinity, decrease with depth. Surface temperatures are

highly dependent upon local geography and local meteorology. Winter

surface temperatures are usually 3-4° C (but may reach an extreme low

of -1.0° C in some areas), while summer temperatures are near 10° C

(Williamson, 1965). The seasonal thermocline usually coincides with the

seasonal pycnocline at 10-30 m. Below the pycnocline and above 100 m,

the winter low is near 4° C and the summer high 6-7° C. Below 100 m

the temperatures are uniformly 4-5° C.

The smaller bays and inlets of southeastern Alaska have a varied

topography and show less uniformity in oceanographic conditions than the

major channels. Not only do the seasonal changes have a greater

magnitude, but the timing of events within the bays differs greatly from

bay to bay, and between bays and adjacent channels. Data collected in

1972 (unpublished) indicate that the more southerly and western bays have

an earlier spring and a later fall than the northerly bays or those closer

to the mainland, and that the bays in general have earlier springs and

later falls than the channels.

Auke Bay, because of the past attention it has received, serves as an

oceanographic model for the smaller bays. Seasonal oceanographic

patterns of Auke Bay have been summarized by Wing and Reid (1972), and

by Bruce and McLain (in prep.). The area has a northern maritime climate--

cool and damp with few periods of either dry or warm weather. Annual

precipitation is 138.7 cm per year, with maximum in October (20 cm), and

minimum in February (7 cm). Cloud cover exceeds 70%, with clear-sky

periods over 2 weeks duration being rare. Clear weather, most frequent in

midwinter, is accompanied by high northerly winds and extreme low

temperatures. Air temperatures range from -25° C to 30° C, with the

lowest monthly average in January (-3° C) and the highest in July (13°C).

Winds are predominantly from the south and west, and are generally less than

8.3 knots. However, storms often pass to the south of Auke Bay so that storm

winds appear to be mostly from the southeast. The winter clear periods

bring high north winds, often exceeding 42 knots in the unprotected channels

which drain through mountain passes from the interior of British Columbia

and Yukon Territory. However, Auke Bay is protected from most winds.

Day length (sunrise to sunset) varies from 6.5 hours in late December

to 18.2 hours in late June.

The meteorology of the are strongly influences the seasonal and

within-season patterns of salinity, temperature, and nutrients in Auke

Bay (Iverson, 1971; Kirk, 1972; Curl et al., 1971; Iverson, Curl, and Saugen,

1974). Salinity is strongly influenced by the freshwater runoff from three

small streams draining directly into the bay, and from the Mendenhall River,

which enters the adjacent Fritz Cove. Surface salinities may be low as

$12^°/_{oo}$ in midsummer, and reach a late winter maximum near $31^°/_{oo}$, while

bottom salinities remain near $31^°/_{oo}$ the whole year. A seasonal pycnocline

extending from near surface to 10-30 m exists from late May until late

September. Within this seasonal pycnocline, the salinities average

$25.5^°/_{oo}$. Water temperatures are strongly influenced by air temperatures,

insolation, and local wind conditions. Maximum surface temperatures of

10-12° C occur in July, although the top meter may reach 17° C on calm

sunny days. Below the pycnocline the summer temperature may reach 6-7° C

at a depth of 55 m. Winters are characterized by isothermal conditions of 2-3° C. However, in midwinter, the top meter or so of water may occasionally have temperatures of -1.5° C, and surface freezing may occur near shore and in the mouths of freshwater streams.

The density structure of Auke Bay is controlled by the temperature and salinity cycles. From December to early April (a period of low runoff, strong cooling, and strong wind mixing) there is little or no stratification. Although increased warming and increased runoff in late April initiate the formation of the pycnocline, late storms may mix the bay until mid or late May. The pycnocline strengthens and deepens through the summer. Often a secondary pycnocline will form in the top 5 m during periods of high runoff, high insolation, and low winds. With the advent of cooling and frequent storms in late September and October, the summer stratification is rapidly lost. Wind and insolation are believed the most important factors controlling mixing in Auke Bay. Although the mean 4-m tidal range and its associated currents augment mixing, they are not sufficient to break down the strong summer stability of Auke Bay (Bruce and McLain, in prep.).

Circulation in Auke Bay is of the classic positive estuarine form, with a freshened surface outflow and a more saline bottom inflow. During the periods of low freshwater input, circulation is weak, but the wind and tide conditions continue to maintain water exchange with the outer passage. Surface currents in the bay are strongly dependent upon local wind conditions, but there is a general outward flow of 5-50 cm/sec at the mouth of the bay. Net current circulation is counterclockwise, with water entering from the southeast and passing out on the southwest side of the entrance most of the time, although alternating tidal flows are

evident in the small passages between islands and the mainland.

The oxygen and nutrient cycles of Auke Bay are typical of high-latitude areas. During the winter, dissolved oxygen concentrations average 6 ml/l throughout the water column. After the summer pycnocline has formed, the surface layers have dissolved oxygen concentrations generally above 8 ml/l, and occasionally during the spring phytoplankton blooms, over 12 ml/l. Below the summer pycnocline, dissolved oxygen concentrations decline but remain above 3 ml/l. Lowest oxygen concentrations at the bottom occur in September and October, and are probably the result of biological and chemical decomposition of the summer accumulation of animal and plant detritus.

The cycle of inorganic nitrate, phosphate, and silicate follows a seasonal pattern, with highest concentrations in November and December (30 µg at NO_3^{-1}/l; 3 µg at PO_4^{-3}/l; 65-70 µg at SiO_4^{-4}/l). Nutrient concentrations remain high until mid March or early April when the first spring phytoplankton blooms occur. Once the spring blooms begin, and the seasonal stratification is initiated, concentration of nutrients in the surface layers decrease rapidly to annual minimums (0.05 µg at NO_3^{-1}/l; 0.2 µg at PO_4^{-3}/l; 2.0 µg at SiO_4^{-4}/l). A similar but less extreme decrease occurs below the pycnocline. Short-term fluctuations of nutrient concentrations caused by recycling of the nutrients in situ have been attributed to zooplankton grazing, bacterial activity, and chemical hydrolysis (Bruce, 1969). Nitrates appear to be regenerated less rapidly than phosphates and silicates, and remain almost completely depleted through much of the summer. Summer phytoplankton productivity levels in Auke Bay appear to be sustained by the utilization of dissolved organic nitrogen sources (Bruce, 1969).

Phytoplankton productivity closely follows the nutrient, stratification, and insolation cycles. From late October through March, productivity as determined by chlorophyll a concentrations is low (less than 0.5 µg chlorophyll a/l). Productivity increases with increased insolation in April and peaks with the first evidence of stratification in late April and May (14 µg chlorophyll a/l). Nutrient, depletion lowers productivity during the summer, although lesser blooms occur (2.5 µg chlorophyll a/l) at 10- to 20-day intervals depending upon rates of nutrient recycling and extent of wind mixing. Late summer and fall strong phytoplankton blooms may occur in September and October. The magnitude and timing of these late blooms are quite variable, and are dependent on the mixing of deep and surface water by early storms.

The primary productivity of Auke Bay is mainly due to diatoms. The succession of diatom species is not fully known, although they are the major component of the spring and fall phytoplankton blooms and most of the summer blooms. Twenty-two species of diatoms, several dinoflagellates, and a few silicoflagellates have been recorded in the bay (Williamson, pers. comm.). Thalassiosira nordenskioldii usually comprise 80-90% of the spring bloom populations, while Skeletonema costatum, Coscinodiscus spp., Fragillaria spp. and Chaetoceros spp. contribute heavily to later blooms. Dinoflagellates, especially Ceratium spp. and Peridinium spp., as well as microflagellates, are often abundant between diatom blooms and are occasionally the major component of some summer blooms. During the winter, the most commonly encountered phytoplankton are Biddulphia aurita, Melosira dubia, and a variety of Chaetoceros, Coscinodiscus, and Ceratium species.

Oceanographic Conditions at False Point Retreat
September 1969-February 1971

Oceanographic cycles of the major inlets and channels described above were based on data collected primarily in the spring and summer seasons. The major weakness of McLain's (1969) year-round data is that very few observations were made below 200 m. In the present study, I was able to obtain monthly observations to depths of 600 m for 15 cruises between September 1969 and February 1971. The present section is a summary of these observations.

Temperatures

Temperature profiles from the False Point Retreat data show strong seasonal changes in the upper 75 m, modest seasonal changes between 75 and 300 m, and weak or perhaps no seasonality below 300 m (Figure 2). Surface temperatures were highest in August 1970 (12° C), and lowest in late winter (3.5° C, March 1970; 2.3° C, February 1971). The greatest thermal changes with depth occurred in the top 20 m during the summer when a normal profile was present, and in the winter when an inverse profile was observed. Annual warming began in April at the surface and gradually extended downward until September, when cooling began at the surface. At the onset of fall cooling (September 1969), the seasonal summer surface thermocline had a maximum depth of 100 m and a bottom temperature of 4.8° C. In August 1970, the bottom of the summer surface thermocline was at 75 m with a temperature of 5.6° C. By February, the surface 75-100 m was nearly isothermal with water temperatures of 3.7-3.8° C in 1970 and 2.3-2.5° C in 1971.

From 75 or 100 m down to between 250 and 300 m, the seasonal warming lags behind the surface almost 5 months. Within the 100- to 300-m
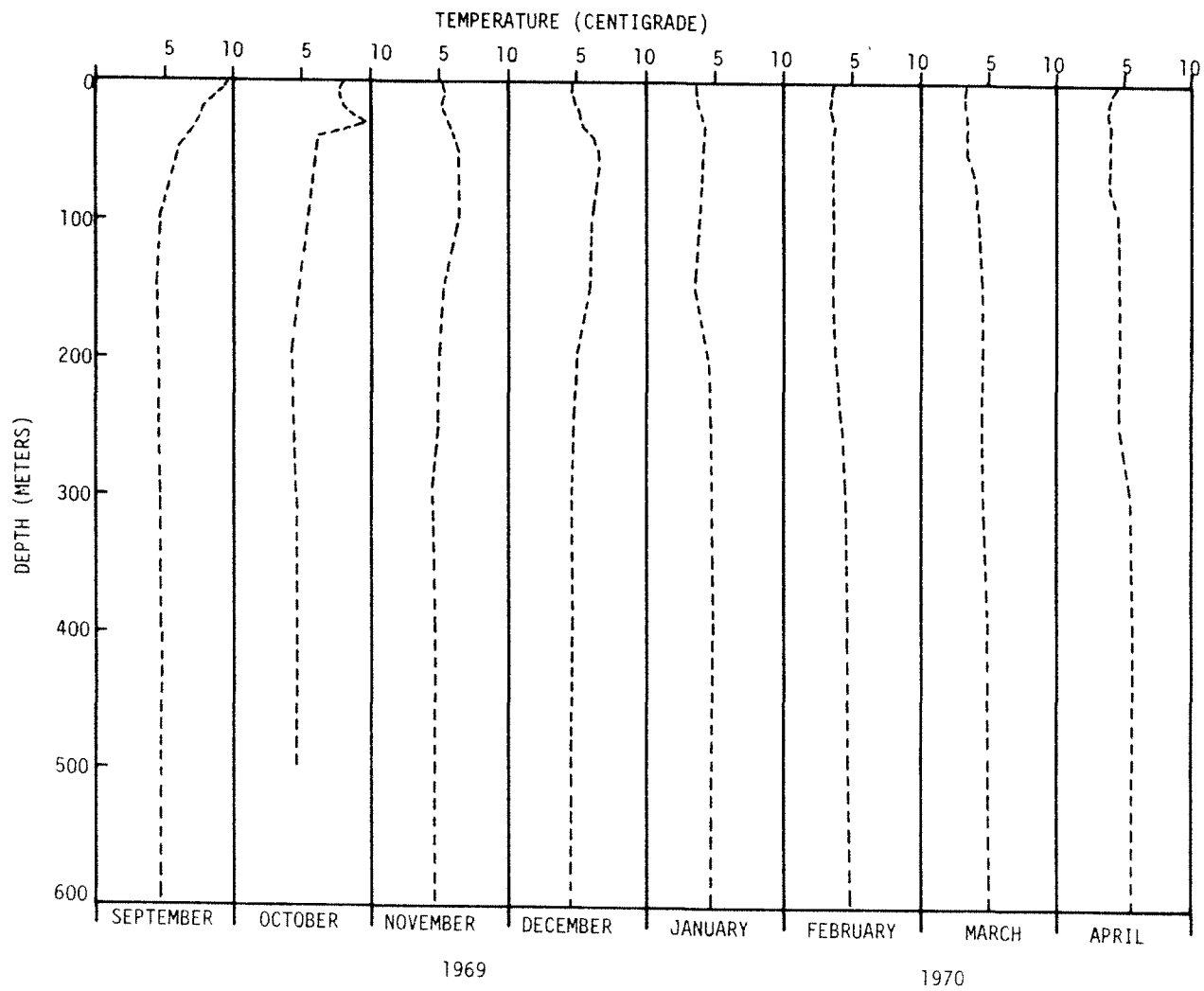
Fig. 2.--Monthly variation in vertical distribution of temperatures at False Point Retreat, Alaska, September 1969 to February 1971

Fig. 2.--Continued

33
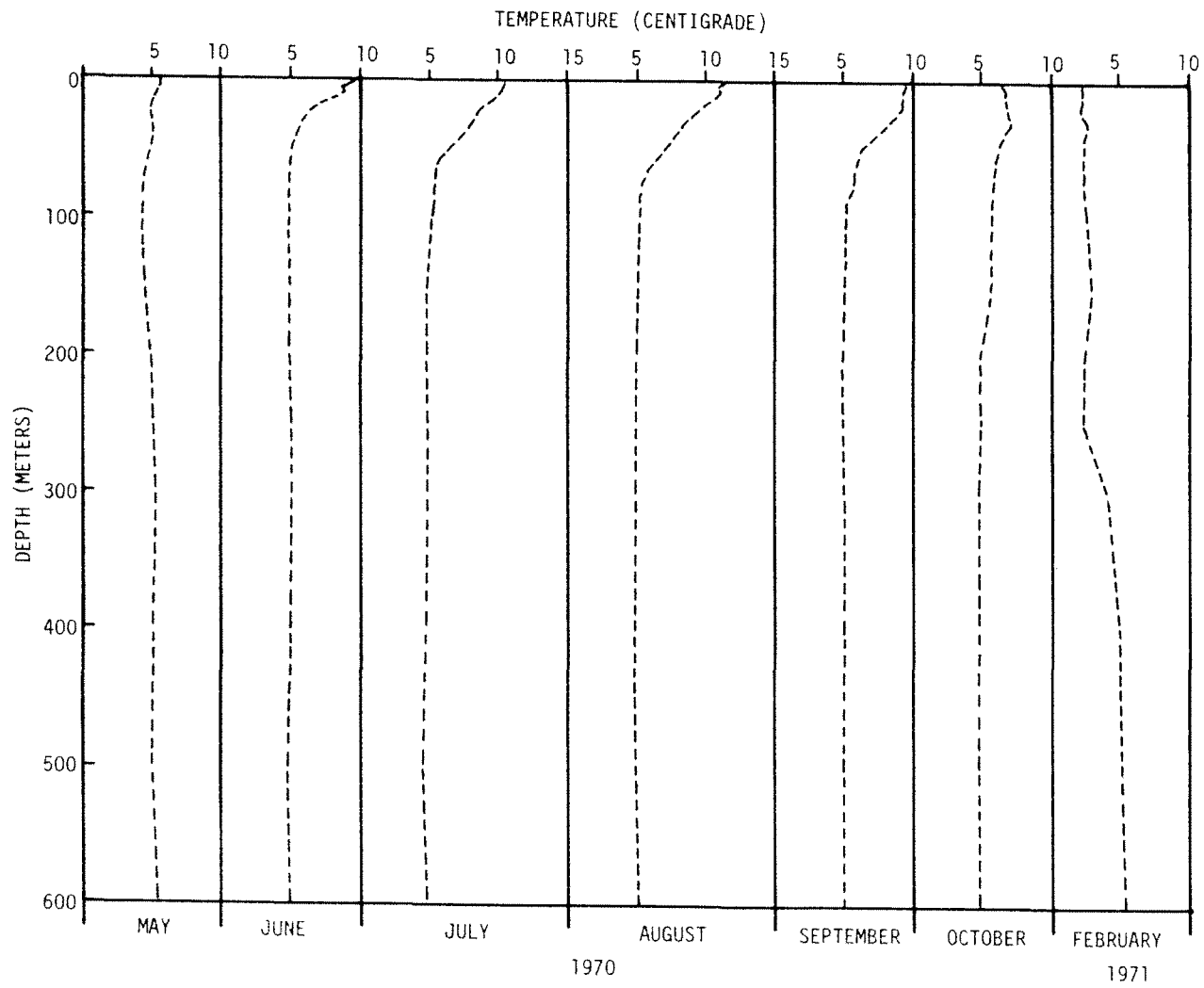
layer temperatures were highest in December (4.8°-6.1° C). In January and February, downward mixing of cold surface waters with temperatures of 3.5° C in 1970 and 2.5° C in 1971 was evident to at least 250 m.

Below the 300-m depths, temperatures varied very little with depth, and only over about a 1° C range through the year. The highest temperatures (5.6° C) were observed in April 1970, and the lowest (4.7° C) in October 1969. These deep temperatures are about 0.5° C higher than previously reported means. It appears likely that the thermal characteristics of the bottom portion of this water column are in large part dependent upon events removed some distance from False Point Retreat. In this regard, it should be pointed out that the circulation of the deep waters of the Alaskan channels has not been invesitgated. Possibly during exceptionally cold winters, local thermal circulation would affect the waters below 300 m at False Point Retreat.

Salinities

Salinity profiles from False Point Retreat (Figure 3) reflect much the same water structure and seasonal cycles as evidenced in the temperature profiles (Figure 2). Salinities generally increase from top to bottom, with greatest variation at the top, and least variation at the bottom. The minimum salinity was $17°/_{oo}$ in August, and the maximum was $31.9°/_{oo}$ in February 1971. Salinity changes were greatest in the upper 20 m, although the summer decrease was evident to about 50 m in July 1970. Below 50 m, the salinities generally remained above $31°/_{oo}$. Winter cooling and mixing produced nearly isohaline conditions in February 1970 and 1971. Between 75 and 300 m, the salinities varied between $31°/_{oo}$ and $33°/_{oo}$, with a winter minimum and a weak summer maximum. Below 300 m, the waters were almost isohaline, and varied little
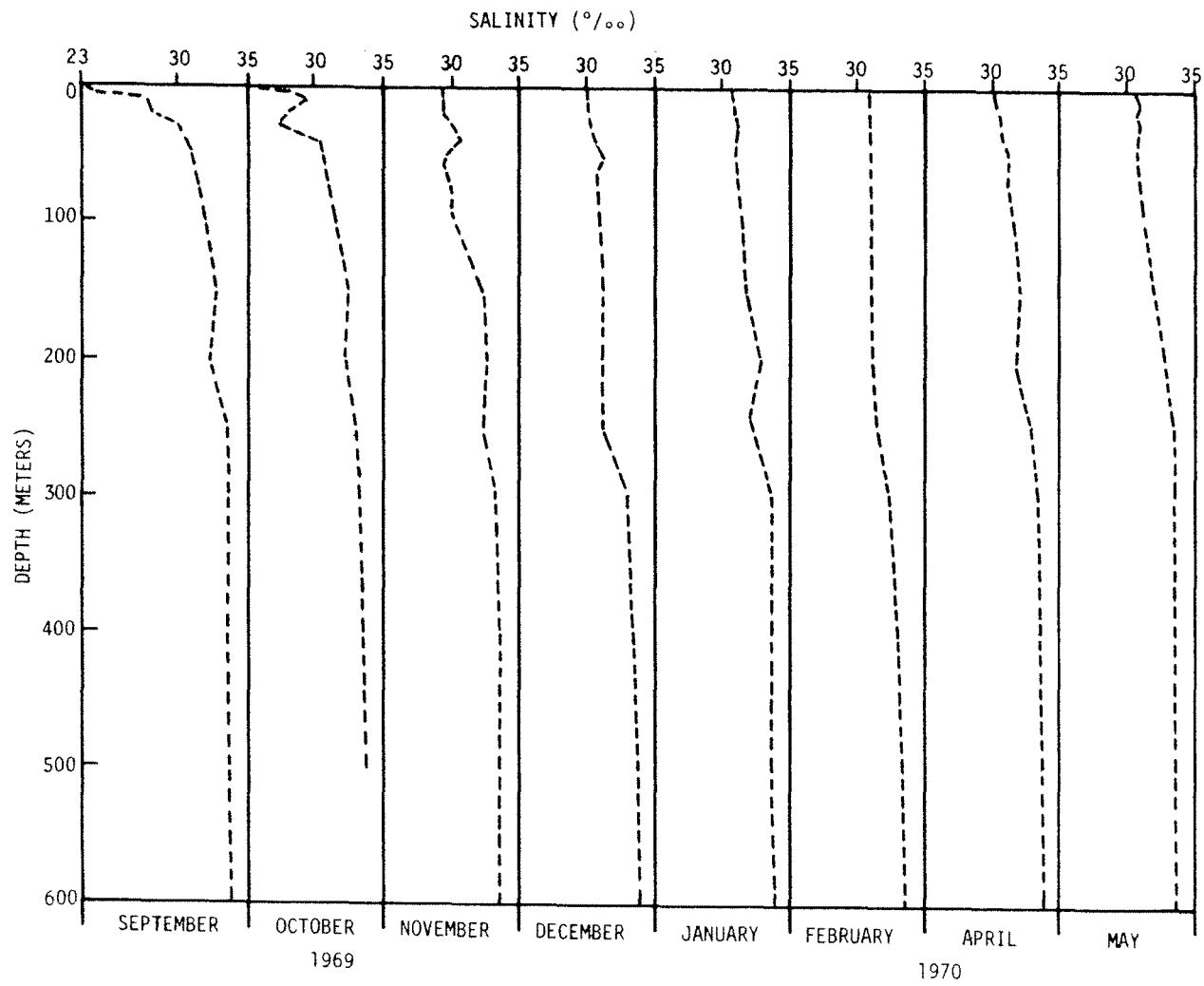
SALINITY (°/oo)

Fig. 3.--Monthly variation in vertical distribution of salinity at False
Point Retreat, Alaska, September 1969 to February 1971
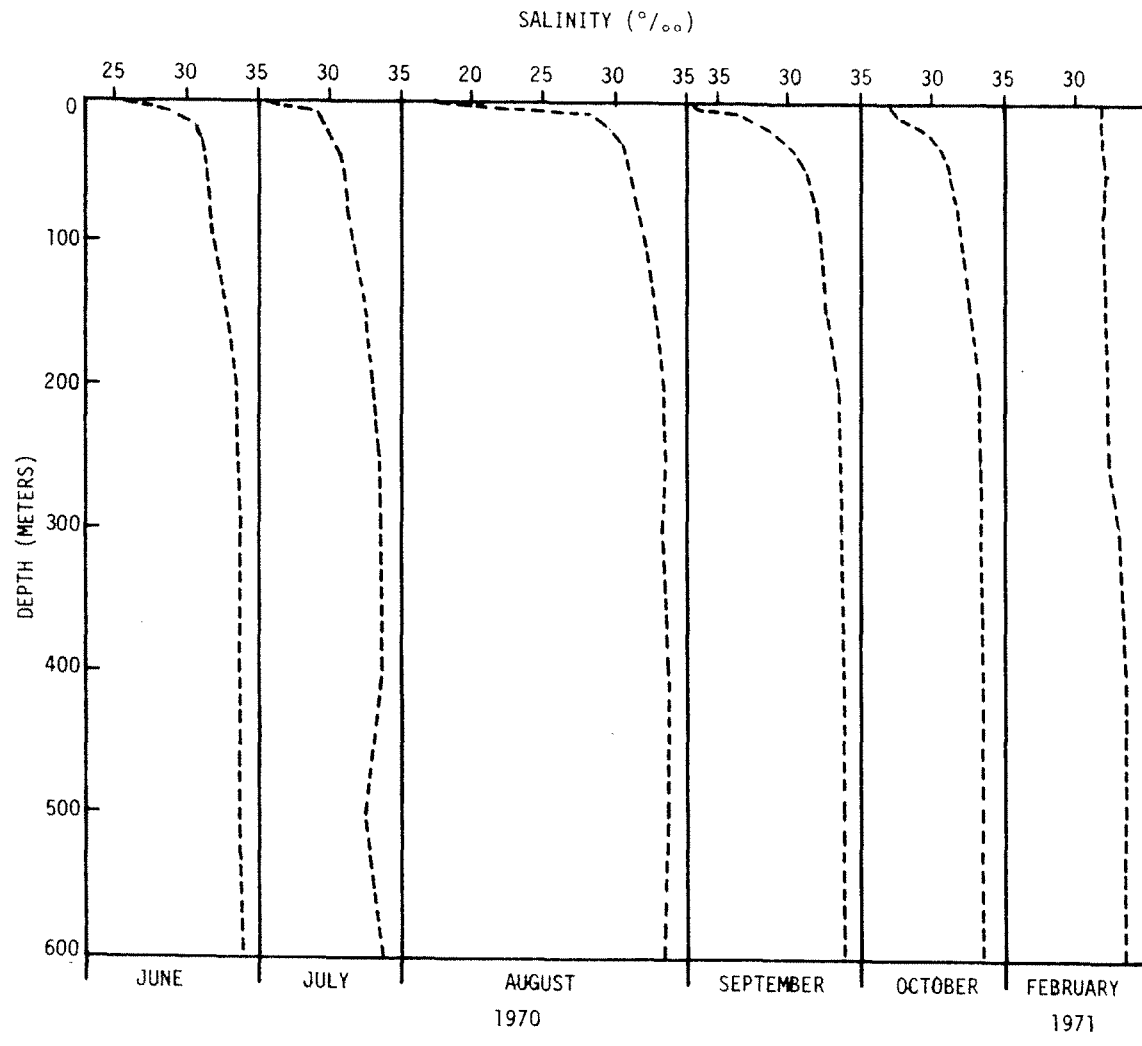
Fig. 3.--Continued

$(33-34°/_{oo})$.

A salinity minimum between 200 and 300 m was observed on five occasions. The actual depth and extent of this salinity minimum are not known. These data do not appear to have been caused by a faulty water sampler. This salinity minimum was recorded in May 1972 with a Plessy Salinity-Temperature-Depth recorder, and in October and November 1972, by bottle casts, but was not evident when searched for in September 1974 (data on file, 1972 MARMAP Cruises in southeastern Alaska, Auke Bay Fisheries Laboratory).

Densities

Sigma-t profiles and temperature-salinity plots of the False Point Retreat data support consideration of the division of the water column into three strata (Figures 4 and 5). The upper 50 m layer had strong seasonality in density associated with the temperature and salinity cycles, having lowest densities in midsummer and highest densities in midwinter. In the middle layer, the sigma-t increased with depth to between 200 and 300 m where the low salinity minimum was observed. On five and possibly six occasions, the low salinity reduced density enough to indicate an unstable water column. No ready explanation for this seemingly persistent instability has been found. Below 300 m, the bottom layer, the densities appear to vary little with depth or season.

Nutrient Cycles

Nitrate, phosphate, and silicate concentrations at False Point Retreat had very similar seasonal and depth distributions (Figures 6, 7, and 8). The highest variability occurred in the upper 50 m. From October to March, the mean concentrations are relatively high but the depth
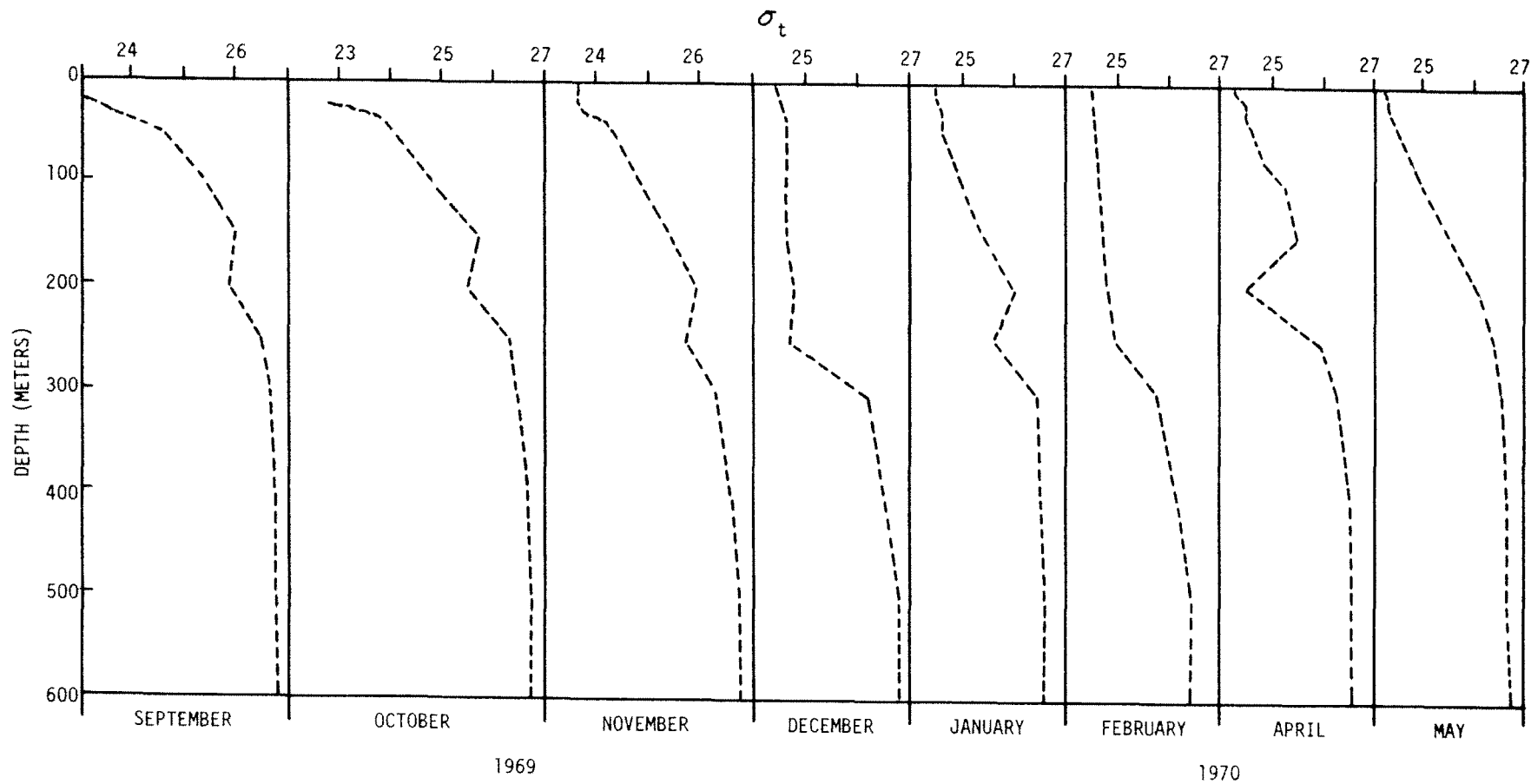
Fig. 4.--Monthly variation in vertical distribution of density expressed as σ_t at False Point Retreat, Alaska, September 1969 to February 1971.
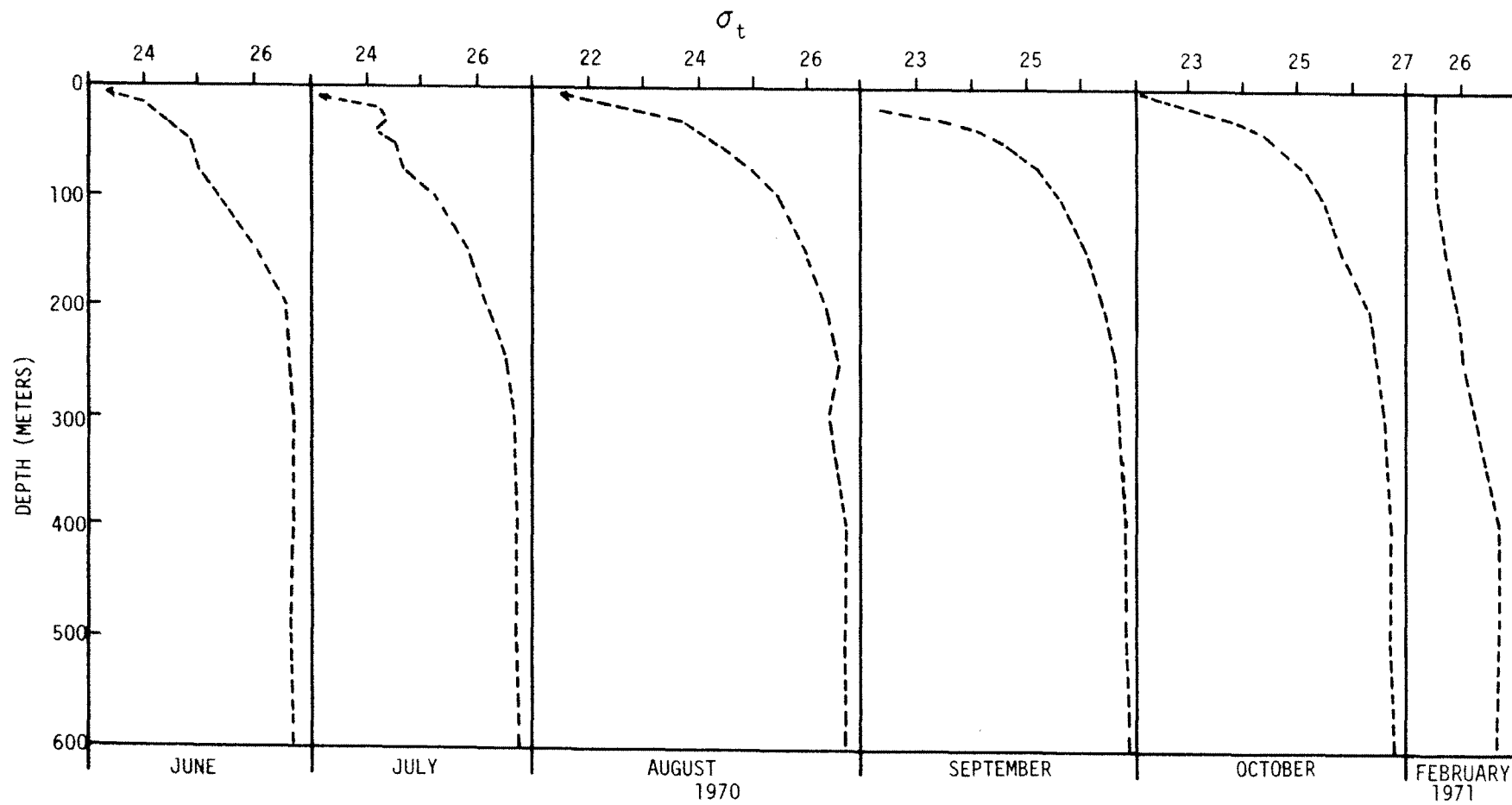
Fig. 4.--Continued
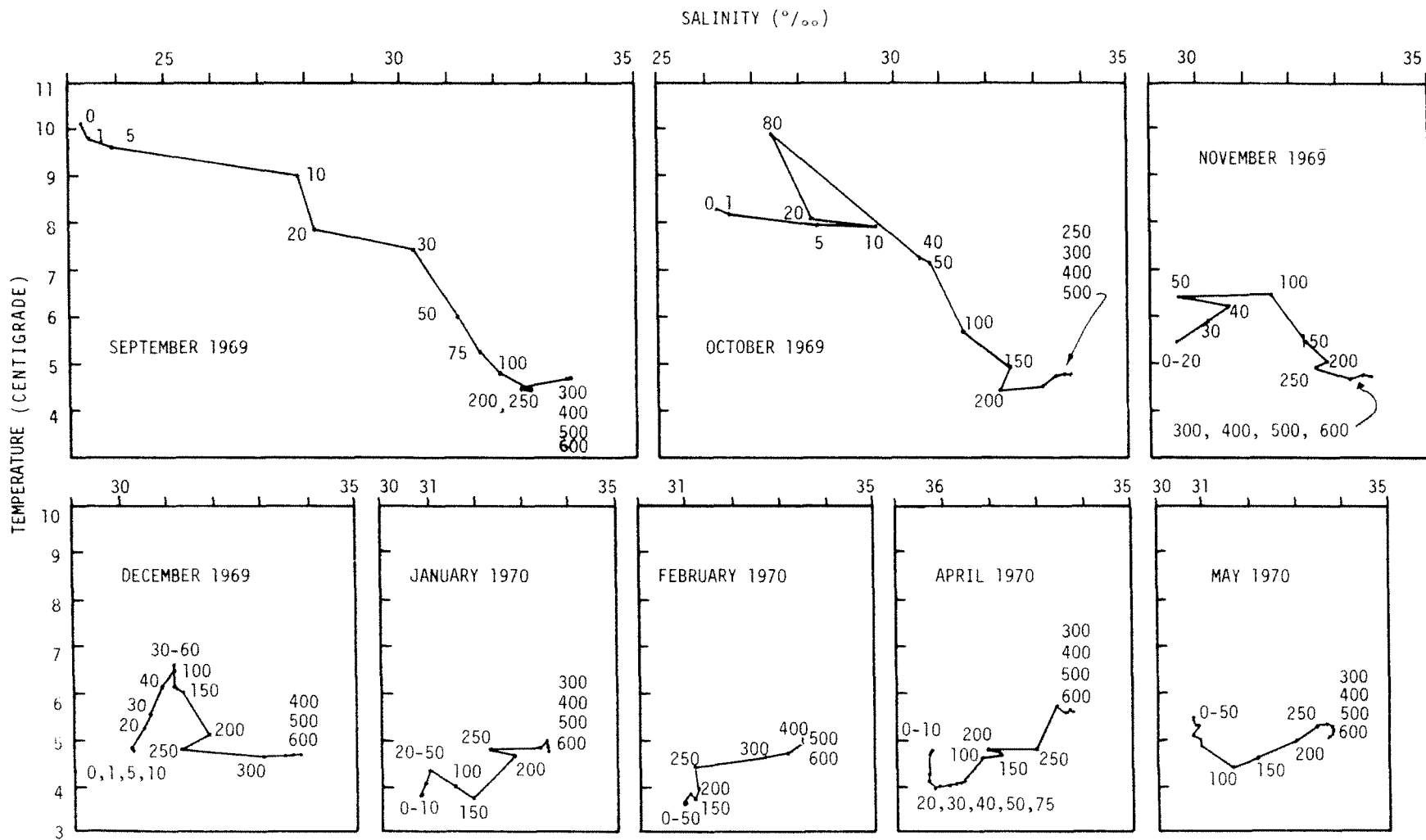
Fig. 5.--Monthly variation of temperature salinity curves at False Point Retreat, Alaska, September 1969 to September 1970.

SALINITY (°/₀₀)

TEMPERATURE (CENTIGRADE)

25   30   35   25   30   35

11
10 0 1
9   5   10
8
7   20
6   30
5   40 50
   JUNE 1970   75 150
4
      250, 300, 400, 500, 600

01   5   10
              20
              30
              40
   JULY 1970   50
              75
              100 150
      200, 250, 300, 400, 500, 600

20   25   30   35   25   30   35

13
12 0 1
11   5   10
10   20
9   30
8
7 AUGUST 1970   50
6   25
5   100, 150, 200, 250, 300, 400, 500, 600

01   5   10   20
                  30
                  40
   SEPTEMBER 1970   50   75
                    100
      150, 200, 250, 300,400, 600

Fig. 5.--Continued

41
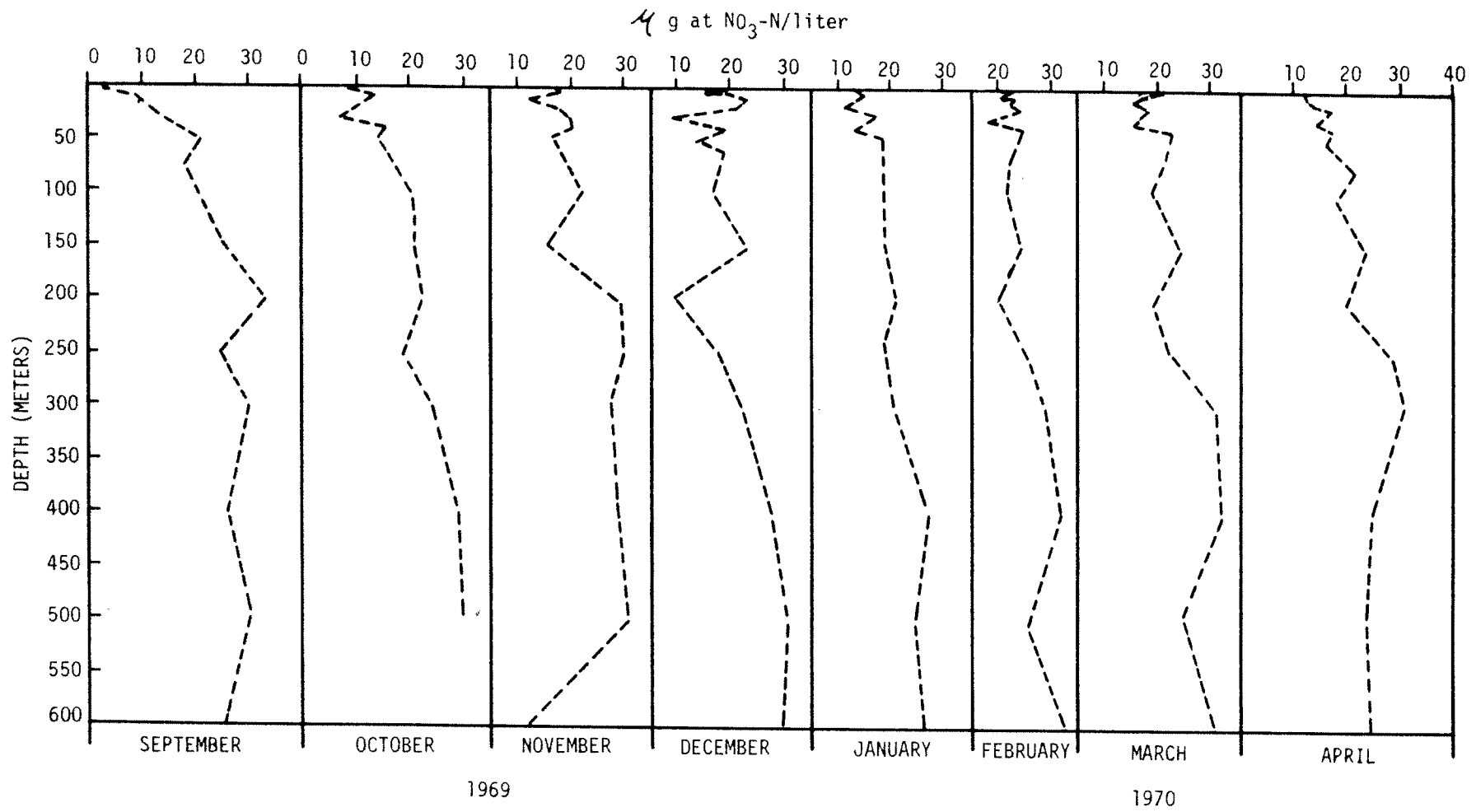
Fig. 6.--Monthly variation in vertical distribution of nitrates at False Point Retreat, Alaska, September 1969 to February 1971

Fig. 6.--Continued

43

Fig. 7.--Monthly variation in vertical distribution of phosphates at False Point Retreat, Alaska, September 1969 to February 1971

44

μg at PO$_4$-P/liter

0 1 2 3 0 1 2 0 1 2 0 1 2 3 0 1 2 0 1 2 3 0 1 2 3

0
50
100
150
200
250
300
350
400
450
500
550
600

DEPTH (METERS)

APRIL JUNE JULY AUGUST SEPTEMBER OCTOBER FEBRUARY

1970 1971

45

Fig. 7.--Continued

Fig. 8.--Monthly variation in vertical distribution of silicates at False Point Retreat, Alaska, December 1969 to October 1970

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distribution in the top 50 m is very irregular, possibly as the result of incomplete mixing or of instability in the water column. During the summer, there was a fairly uniform increase of nutrients with depth in the top 50 m, with concentrations at 50 m four to twenty times those at the surface. Lowest concentrations occur in June, followed by a small amount of replenishment from July through September. Convectional mixing in October 1970 returned near surface concentrations to the same levels as the previous fall.

Between 50 and 300 m, the nutrient concentrations averaged higher than in the top 50 m, although large variation occurred with depth and month. As in the top 50 m, the least variation occurred in the summer. Strong minima and maxima at 200 and 250 m may have been associated with the low-density water observed at the same depths.

Below 300 m, nutrient concentrations were relatively uniform. Variability in the 600-m samples may represent the result of turbulence and the possible disturbance of bottom sediments. Variability at 400 and 500 m may represent either variation of in situ regeneration of nutrients or the source of the bottom water.

Although long-term data for the nutrient concentrations of the major channels of southeastern Alaska are not available, it is noted that the nutrient concentrations observed in February 1971 are approximately two-thirds of those recorded in February 1972. A similar difference was observed in nutrient data for Auke Bay. Although localized differences may be great, the similar yearly differences in the two areas suggest that between-year variation of nutrient concentrations in 1971 and in 1972 was real and widespread in southeastern Alaska.

48

Dissolved Oxygen Concentrations

Dissolved oxygen concentration at False Point Retreat (Figure 9) is dependent on levels of primary productivity and physical oceanographic conditions. Although primary productivity was low in the winter, low temperatures, high winds, and strong mixing of the water column resulted in O_2 concentrations of 11-12 mg/l in the upper 50 m in January. A slight decline to 9-10 mg/l was evident in February and March, but with the initiation of the spring phytoplankton blooms, O_2 levels rose again to nearly 12 mg/l in June, to be followed by a decline throughout the summer to an October minimum of 8 mg/l.

Below 50 m, the oxygen concentrations followed a cycle dependent upon the annual winter mixing down to 250 m. The late fall 1969 O_2 concentrations of 4-5 mg/l rose to 9-10 mg/l in February, followed by a decline to 3-4 mg/l in the fall of 1970. If the February 1971 data are valid, mixing and oxygenation of the water column were strong, and O_2 levels of 10-12 mg/l existed throughout the water column down to 250 m.

Below 300 m, oxygen concentrations were usually uniform with depth and varied from lows of 2.7 mg/l in September 1969, and 1.2 mg/l in October 1970, to a maximum of 7 mg/l in May 1970.

Deep oxygen maxima were observed on seven cruises at 200 and 250 m, twice at 100 m, and possibly once each at 300 and 400 m. Although they may be related to the low density and the nutrient minima and maxima observed in the 200- to 300-m range, the presence or absence of these oxygen maxima do not appear to be directly correlated with the presence or absence of the sigma-t minima or the nutrient peaks.

MILLIGRAMS O_2 /LITER
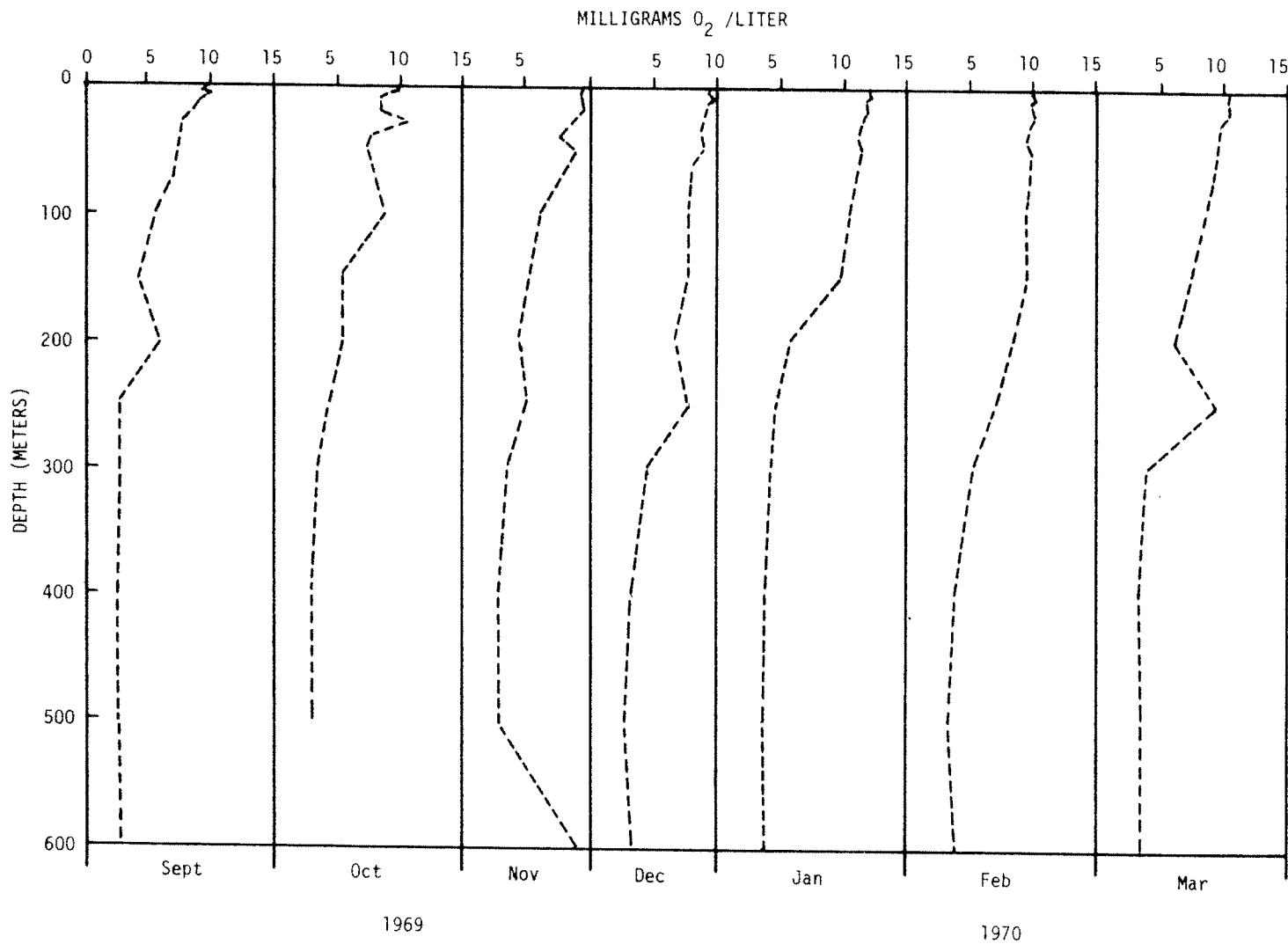
Fig. 9.--Monthly variation in vertical distribution of dissolved oxygen at False Point Retreat, Alaska, September 1969 to February 1971.

MILLIGRAMS O$_2$ /LITER

Fig. 9.--Continued

50
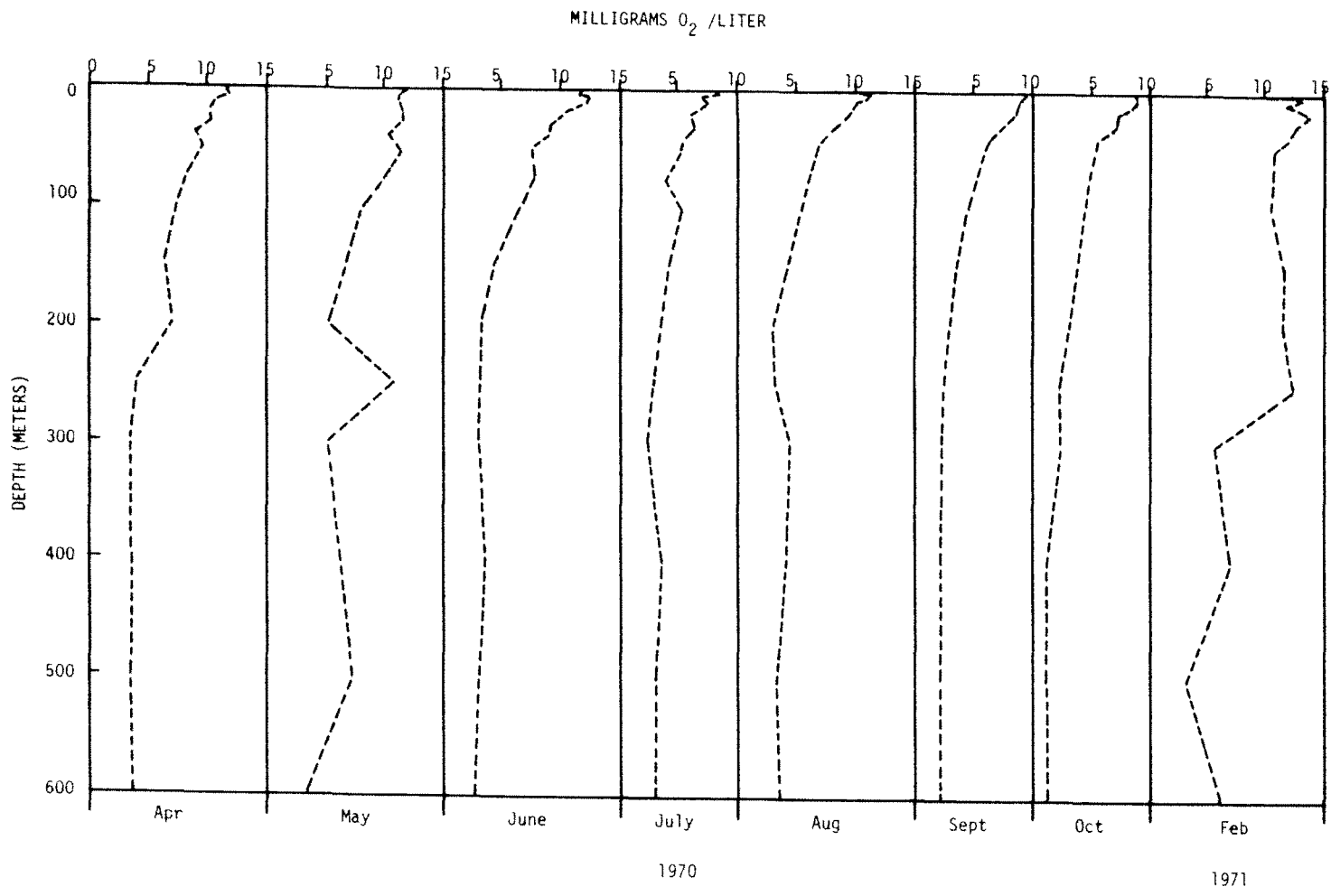
Primary Productivity

Although rates of primary production were not measured, primary productivity is reflected in the chlorophyll a concentrations, which were measured in the top 50 m (Figure 10). The annual cycle of primary productivity exhibited a low through the early winter (November-February), with chlorophyll a concentrations of 0.1-0.3 μg/l. In March, increased sunlight and day length may have initiated a small increase in phytoplankton reproduction. This increase reached bloom proportions in April with the first indications of a seasonal warming and stratification. The depth profiles of chlorophyll a characteristically had a maximum at 5 m (highest in May at 7.5 μg chlorophyll a/l) and a minimum at 40 m. Most of the primary productivity occurred in the top 10 m. Corresponding to the nutrient depletion in the summer, chlorophyll a concentration declined through the summer although some nutrient regeneration was observed. No fall bloom was recorded, and in October 1970, chlorophyll a concentration was comparable to that of the previous November.

The phytoplankton species composition at False Point Retreat (Table 5) is less diverse than in Auke Bay, but follows a similar seasonal pattern. Diversity is lowest in the early spring (March and April), and highest in the summer. During most months, diatoms predominate in both abundance and variety. The first indication of the annual spring increase in productivity was in March when Coscinodiscus spp. became very abundant. This was followed by a Thalassiosira aestivalis bloom in April, and a T. nordenskioldii bloom in May. Microflagellates were predominant during the June minimum nutrient period. Skeletonema costatum predominated through most of the summer. Ceratium spp. were the most abundant forms in September 1970, and through the winter months of January and February
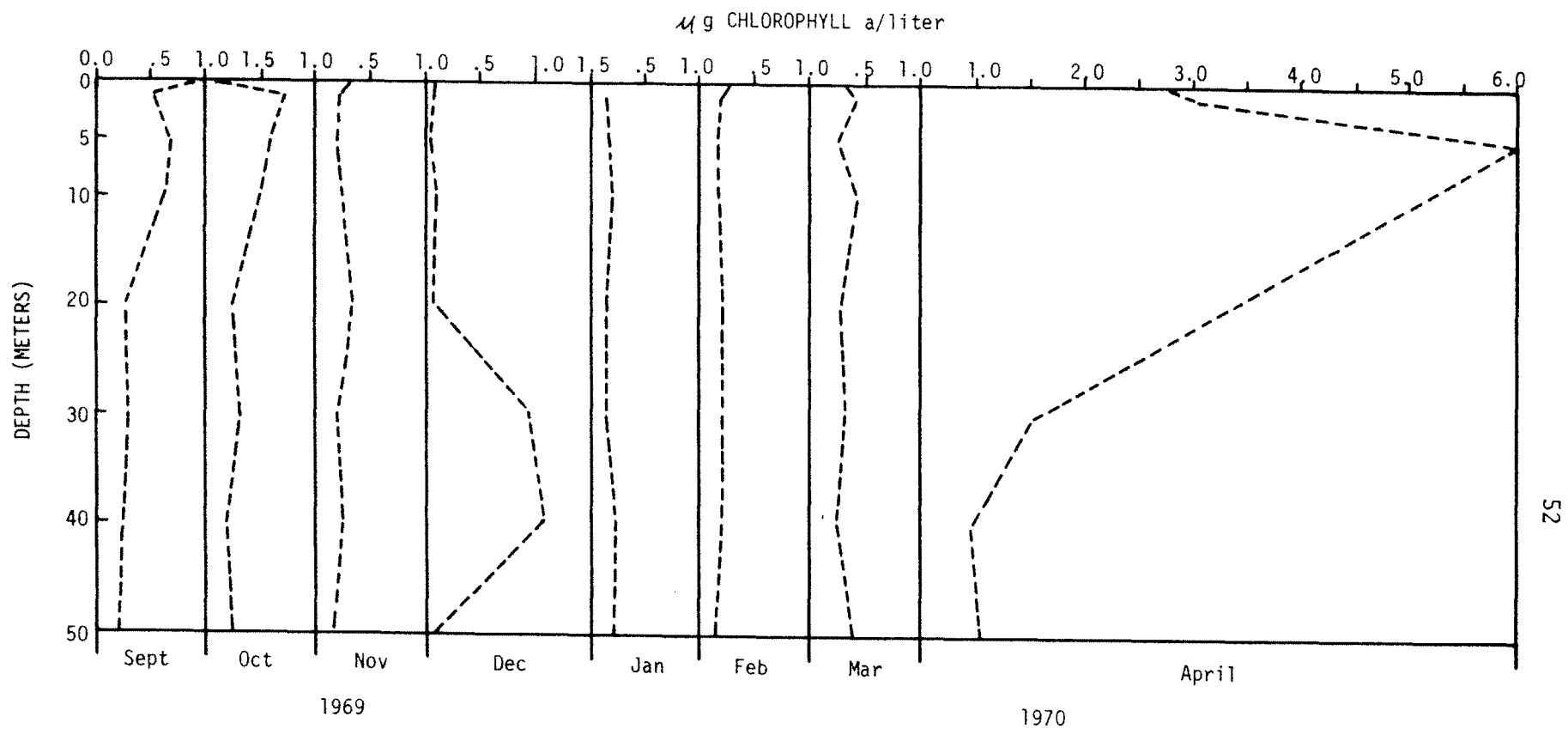
μg CHLOROPHYLL a/liter

0.0 .5 1.0 1.5 1.0 .5 1.0 .5 1.0 1.5 .5 1.0 .5 1.0 .5 1.0 1.0 2.0 3.0 4.0 5.0 6.0

DEPTH (METERS)

0

5

10

20

30

40

50

Sept   Oct   Nov   Dec   Jan   Feb   Mar   April

1969   1970

52

Fig. 10.--Monthly variation in vertical distribution of Chlorophyll a at False Point Retreat, Alaska, September 1969 to February 1971

μg CHLOROPHYLL a/liter

Fig. 10.--Continued

53
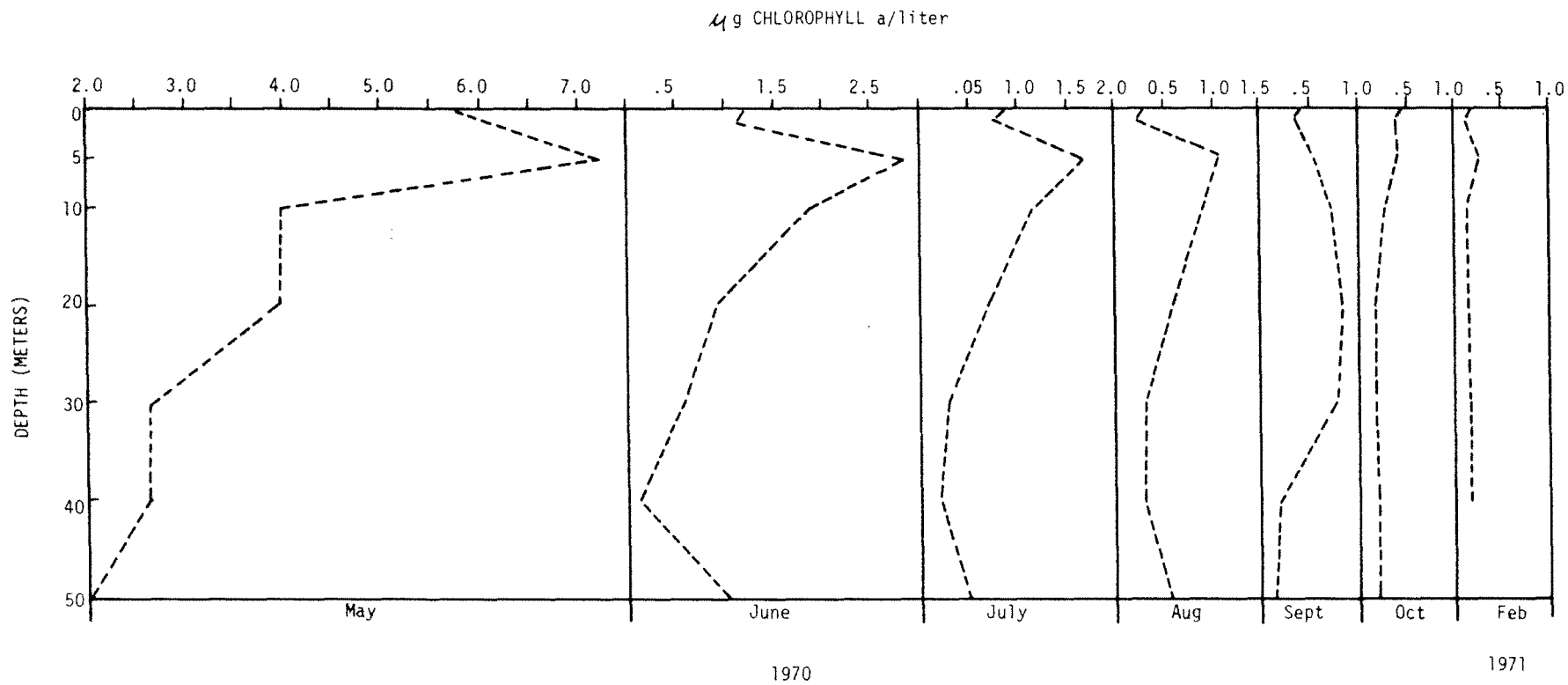
TABLE 5.--Phytoplankton species composition at False Point Retreat, September 1969 to February 1971 (1 indicates most numerous; 2, numerous; 3, many; 4, few; 5, very few; 6, rare)

Genera/species	1969						1970								1971
	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	March	April	May	June	July	Aug.	Sept.	Oct.	Feb.
Skeletonema															
costatum	4	1	4	..	..	..	6	..	4	5	1	1	..	..	..
Chaetoceros															
decipiens	..	5	1	..	4	4	..	..	6	6	5	5	6	1	6
didymus	..	..	..	..	..	..	..	..	..	..	..	1	..	..	..
debilis	5	..	..	..	..	..	..	..	..	..	5	5	6	..	..
compressus	..	..	..	..	..	..	..	..	5	6	6	6	..	..	..
constrictus	5	..	..	..	..	..	..	..	..	4	..	..	..	..	..
lacinosus	..	5	..	..	..	..	..	..	..	..	..	..	..	..	..
radicans	..	..	..	..	..	..	..	..	..	3	..	4	..	..	..
concavicornis	5	5	..	..	5	4	5	5	6	..	6	..	..	2	..
subsecundus	..	..	..	..	5	5	..	..	..	6	6	..	..	..	..
atlanticus	..	..	..	..	5	..	..	..	..	..	..	..	..	..	..
similis	..	..	..	..	..	..	..	..	..	..	..	6	..	..	..
convolutus	..	..	4	..	..	..	6	..	..	..	..	..	..	..	..
sp.	..	..	..	..	..	..	..	..	..	..	..	..	..	..	6
Thalassiosira															
aestivalis	..	..	..	..	..	..	..	1	2	..	..	..	..	..	..
nordenskjoldii	..	..	..	..	..	..	..	..	1	5	..	..	..	..	..
rotula	..	..	6	..	..	..	..	..	..	..	..	..	..	..	..
decipiens	..	..	..	..	..	..	..	..	5	5	5	4	..	..	..
Thalassionema															
nitzschoides	5	..	..	..	6	..	..	..	..	..	4	5	..	6	..
Nitzschia															
spp.	..	5	5	..	..	..	..	..	..	4	4	..	6	6	..
Coscinodiscus															
spp.	3	5	3	..	3	3	1	5	6	..	..	..	6	3	6
Ditylum															
brightwelli	..	..	..	..	6	6	..	..	6	..	..	..	..	..	..

54

TABLE 5.--Continued

Genera/species	1969				1970										1971
	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	March	April	May	June	July	Aug.	Sept.	Oct.	Feb.
Biddulphia															
aurita	..	5	..	..	6	..	..	..	..	..	..	..	..	..	..
Eucampia sp.	..	..	..	..	..	..	..	..	6	..	..	..	..	..	..
Pleurosigma sp.	..	..	..	..	6	..	..	..	..	..	..	..	..	..	..
Dinophysis sp.	..	..	..	..	..	..	..	..	..	..	6	..	..	..	..
Ceratium															
horridum	1	6	..	..	1	1	6	..	..	..	..	..	1	..	1
lineatum	..	..	..	..	5	5	..	..	..	..	..	..	..	..	..
tripos	..	..	..	..	6	5	..	..	..	..	..	..	..	..	..
sp.	..	..	5	..	6	..	..	..	..	6	6	6	..	6	..
Peridinium															
depressum	..	..	..	..	..	..	..	..	..	..	..	..	..	..	6
sp.	6	..	..	..	..	..	..	..	6	6	..	..	..	..	..
Unidentified															
dinoflagellates	..	..	..	..	..	..	..	..	..	..	6	..	..	..	..
Microflagellates	..	..	..	..	..	..	..	..	..	1	..	..	..	..	..

in contrast to Auke Bay, where Chaetoceros spp. are the major winter component of the phytoplankton.

Oceanographic Conditions in Auke Bay
September 1969-February 1971

The general oceanographic environment and seasonal cycles of Auke Bay were summarized earlier. This section presents the results of monthly observations made between September 1969 and February 1971.

Temperatures

In September 1969, temperatures of Auke Bay (Figure 11) were $10°$ C at the surface, $7.2°$ C at 20 m (the base of the summer pycnocline), and $5.5°$ C at 50 m. By mid October 1969, the surface had cooled to $6.8°$ C, although temperatures at 1-20 m were nearly uniform $(7.5-7.8°$ C) and at 50 m (the bottom) they had warmed to $6.2°$ C. The seasonal thermocline disappeared in November when the whole water column was between $5.7°$ and $6.1°$ C except for the chilled surface of $4.8°$ C. Cooling continued into December when an inverse thermal profile was observed with $2.6°$ C water in the top 10 m over $4.7-5.0°$ C in the bottom waters. By March, an isothermal water column of $3.7°$ C resulted from the combined cooling at the surface and downward mixing into the warmer bottom waters. With the increased spring insolation, the waters began to warm in April but strong stratification was not evident until June when surface temperatures reached $11°$ C and the thermocline extended to 10 m, with the lower layers at $5.6°-4.6°$ C at the bottom. The surface thermocline gradually descended, and the whole water column continued to warm through August. Cooling began again in September 1970, and by October, the waters were approximately $1°$ C cooler than in the previous year; in February 1971, the water column was $1.5°$ C colder than the previous year.
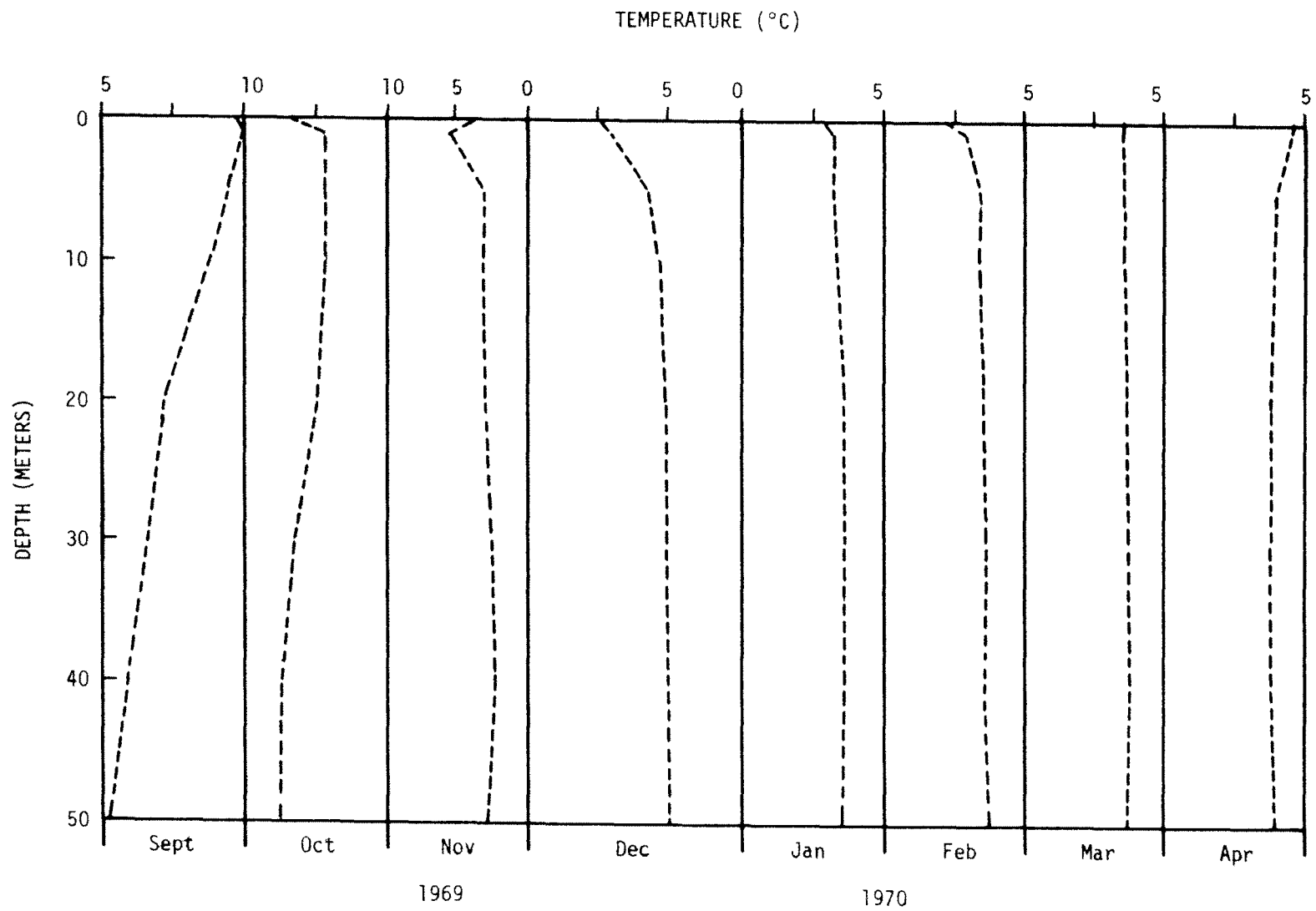
TEMPERATURE (°C)

Fig. 11.--Monthly variation in vertical distribution of temperatures in Auke Bay, Alaska, September 1971 to February 1971
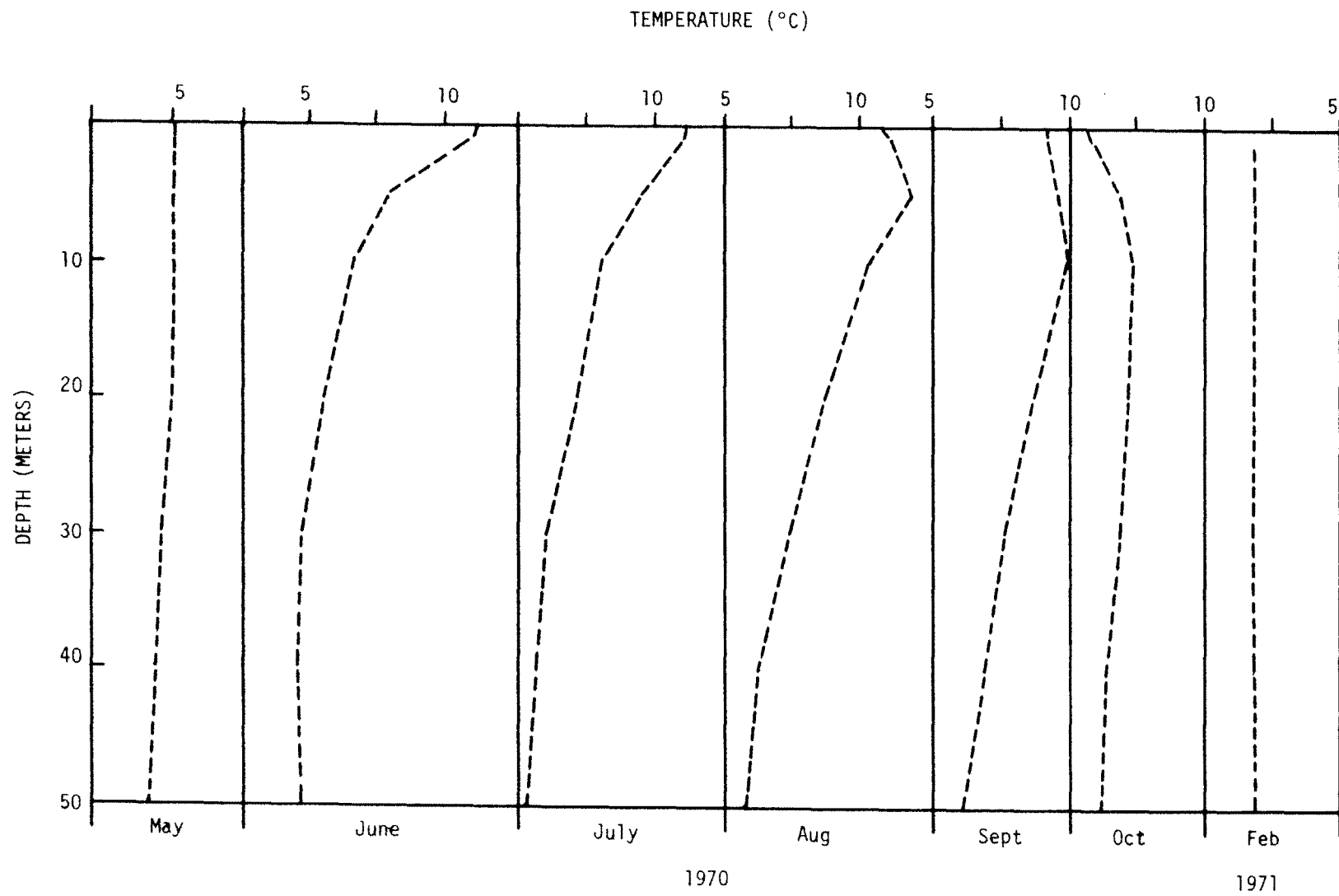
TEMPERATURE (°C)

Fig. 11.--Continued

The overall temperature cycle for September 1969 through October 1970 did not differ significantly from that previously described by Bruce (1969), Wing and Reid (1972) or Bruce and McLain (in prep.). The temperatures were within the range of the reported averages for most of the study period. However, the winter seemed to come a little early and the February water temperatures of 1.8° C were below the reported 2-3° C average for February.

Salinities

The seasonal variation of salinities in 1969-70 closely followed and approximated the trends reported by Bruce and McLain (in prep.) for the 6-year period of 1961-66 (Figure 12). Surface salinities were highest in January and February (31.00-31.46°/oo), and lowest during the peak runoff period of the Mendenhall River in August (13.32°/oo). A strong seasonal halocline was present from June through September, during which time the bottom of the halocline was from 5-20 m. At 20 m, salinities varied from a late summer low of 28.76°/oo to a winter high of 31.92°/oo. At 30-50 m, the salinities were relatively constant, although they increased slightly with depth. Lowest salinities (29.74-30.47°/oo) occurred in November as a result of the fall mixing, and highest salinities (30.42-31.46°/oo) were observed in the summer months of September 1969, June 1970, and July 1970. Isohaline or nearly isohaline conditions existed from November through May.

February 1971 was preceded by a long period of exceptionally cold clear weather, which may have resulted in higher than normal winter evaporation and consequently increased salinities. Salinities in February 1971 were roughly 1°/oo higher than in the previous year, being in the range of 31.46-32.04°/oo compared to the norm of 30.00-31.00°/oo for midwinter.
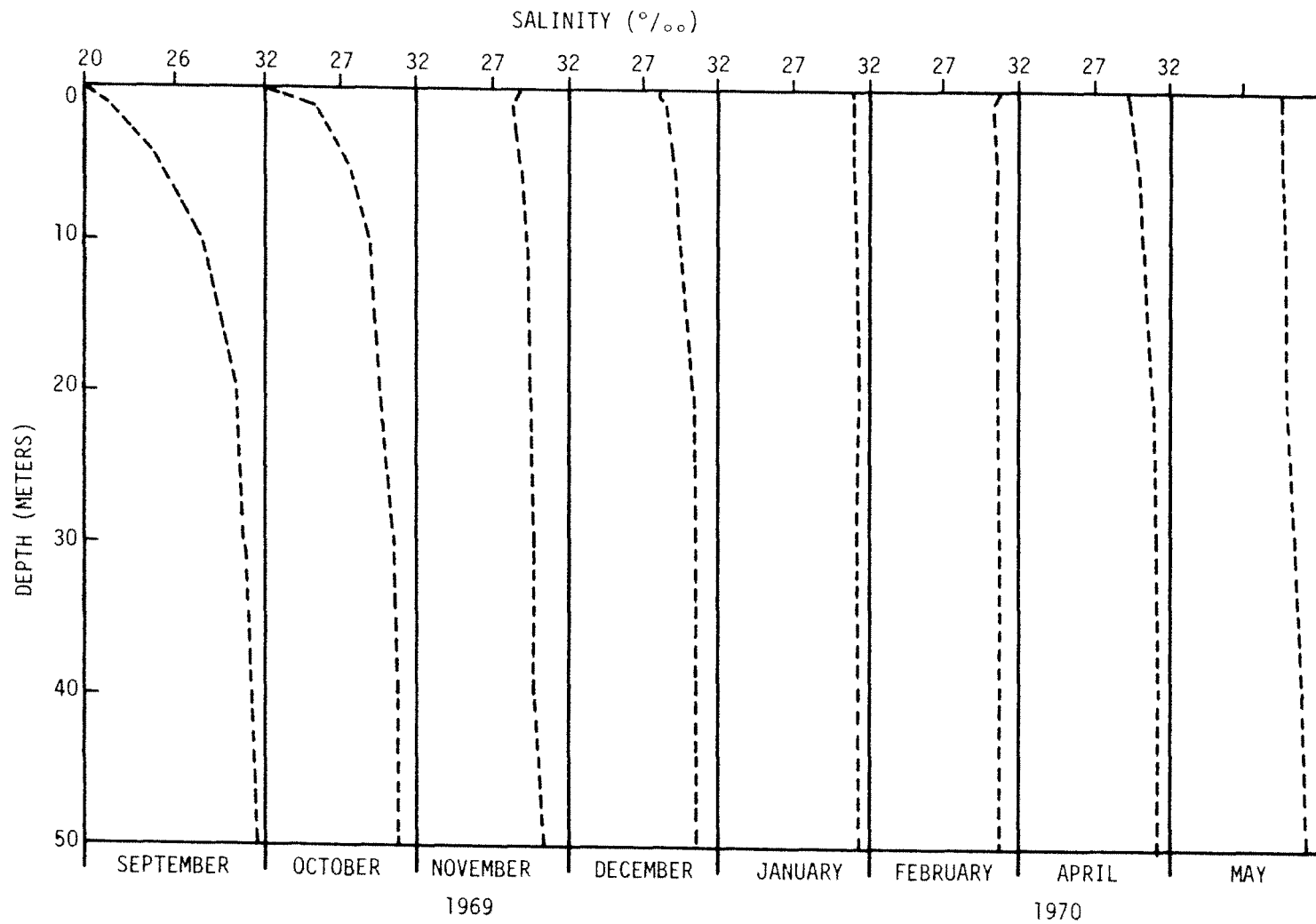
Fig. 12.--Monthly variation in vertical distribution of salinity in Auke Bay, Alaska, September 1969 to February 1971

SALINITY (°/oo)

Fig. 12.--Continued

JUNE · JULY · AUGUST · SEPTEMBER · OCTOBER · FEBRUARY

1970 · 1971

61
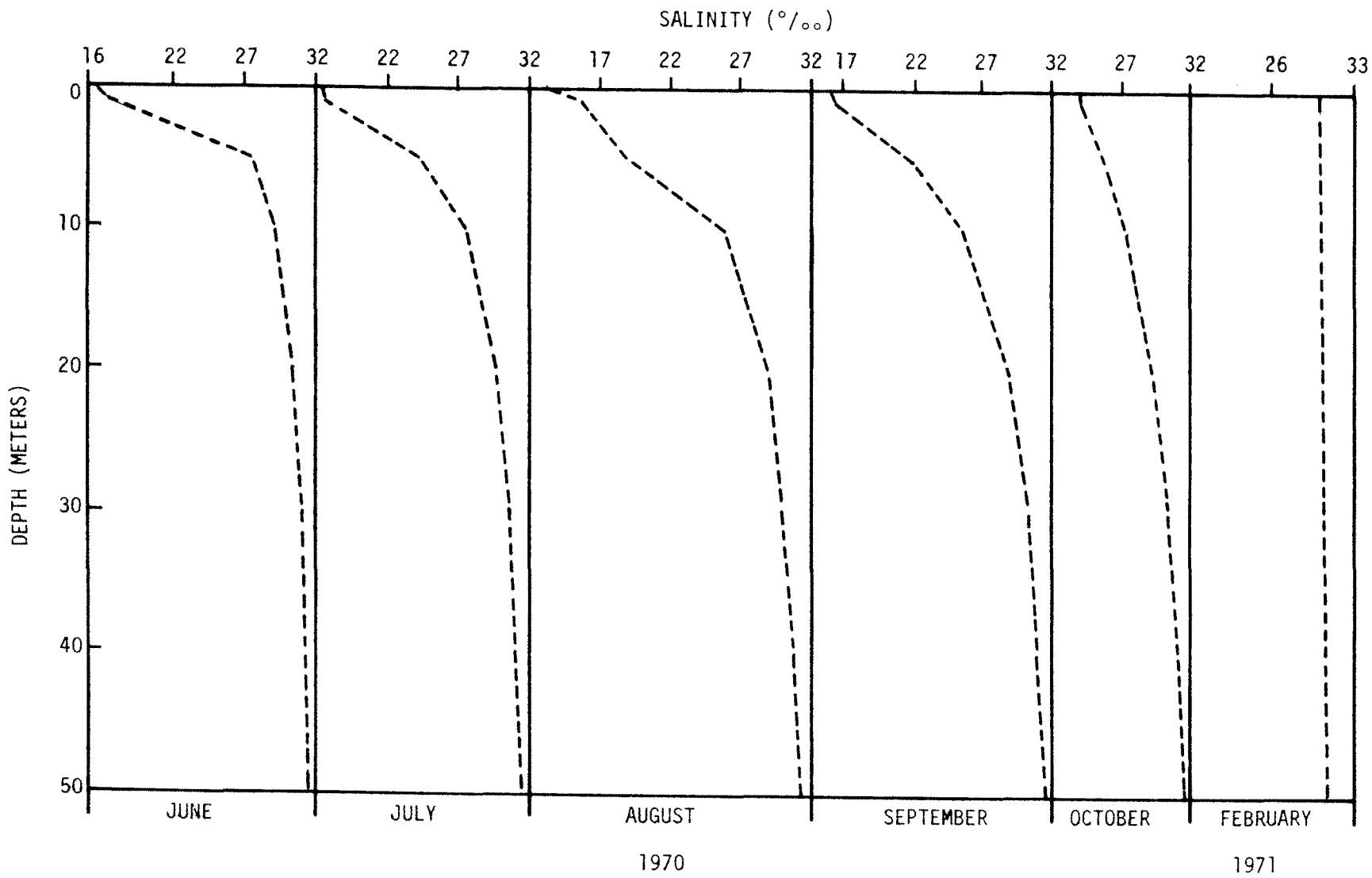
Densities

Sigma-t profiles and temperature-salinity diagrams for Auke Bay were drawn primarily to compare the potential for mixing of Auke Bay water and that of the outer channels as represented by the station at False Point Retreat (Figures 13 and 14). They also served to provide additional insight concerning the stability of the Auke Bay water column and the form of the seasonal pycnocline. When present from April to October, the pycnocline extended from the surface to 10-30 m, with the strongest gradient in the top 5 m. The stratification of the water column was absent in the midwinter, with nearly uniform density from top to bottom. Initial stratification in April was weak, and was destroyed by late storms as shown by the May profile where the upper 20 m were isopycnal but of lower density than the bottom.

Nutrient Cycles

Nutrient cycles for September 1969-February 1971 (Figures 15, 16, and 17), although following the expected estuarine cycle, differed in timing from the cycles reported by Bruce and McLain (in prep.). Normally, the maximum nutrient concentrations are reached by late November or early December; however, during the present study they were not attained until February. An early April, phytoplankton bloom lowered near-surface nutrient concentrations by 50% or more, but remixing by a storm appears to have brought deep silicate-rich water to the surface. Nitrates and phosphates remained low, however. Minimum nutrient concentrations occurred in July 1970.

The nutrient profiles show considerable variation with depth but have a general trend of low values at the surface and high values at the bottom. The differences between top and bottom concentrations are
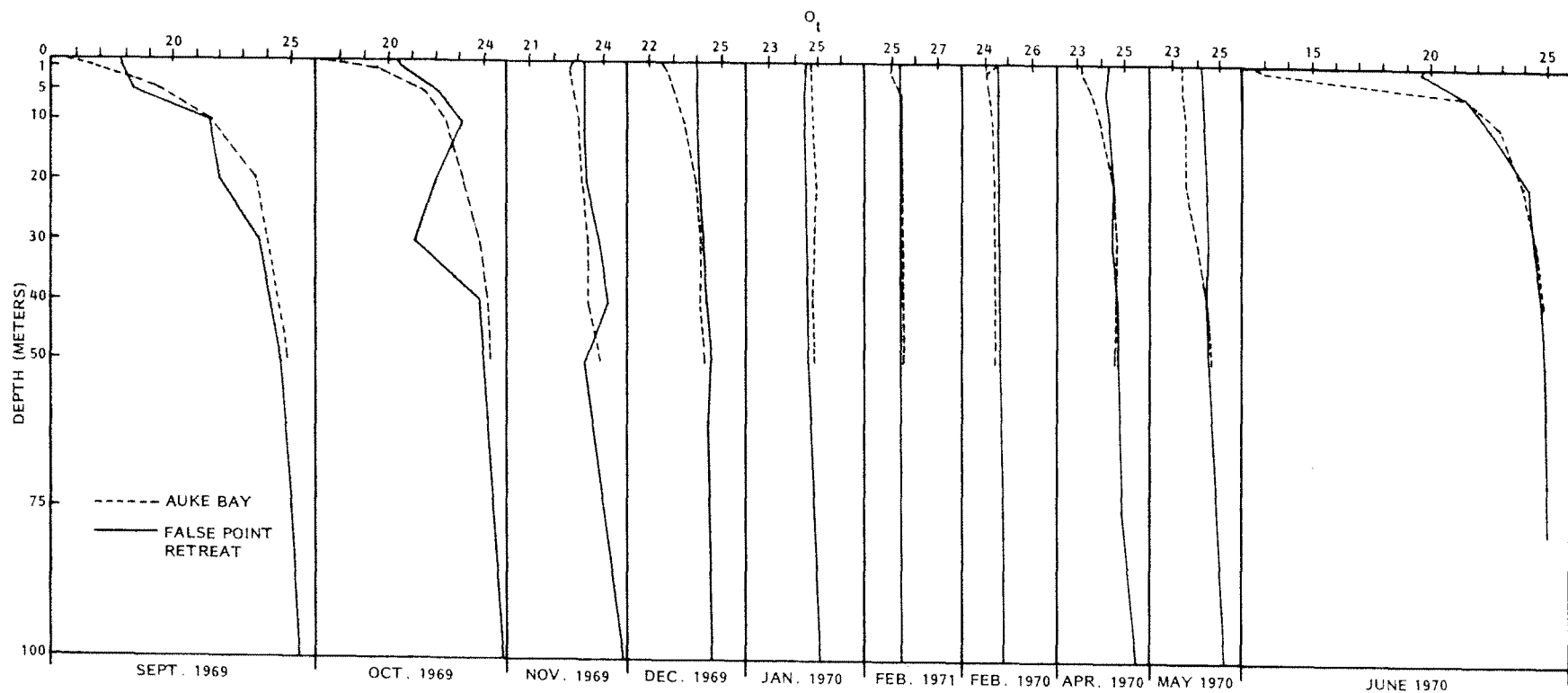
Figure 13.--Monthly variation in vertical distribution of density expressed as σ_t in Auke Bay and the surface 75 m at False Point Retreat, Alaska, September 1969 to October 1970
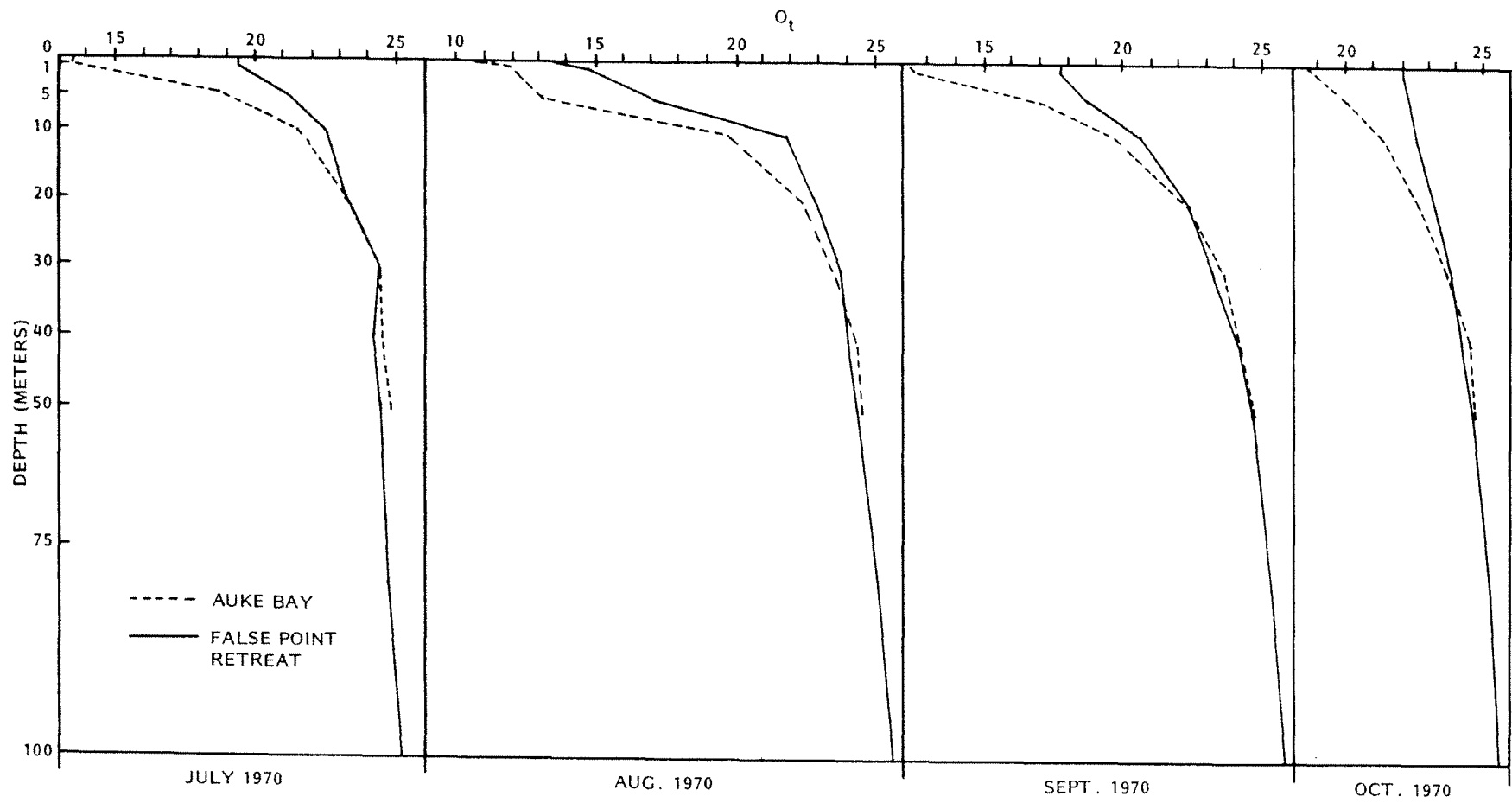
Fig. 13.--Continued
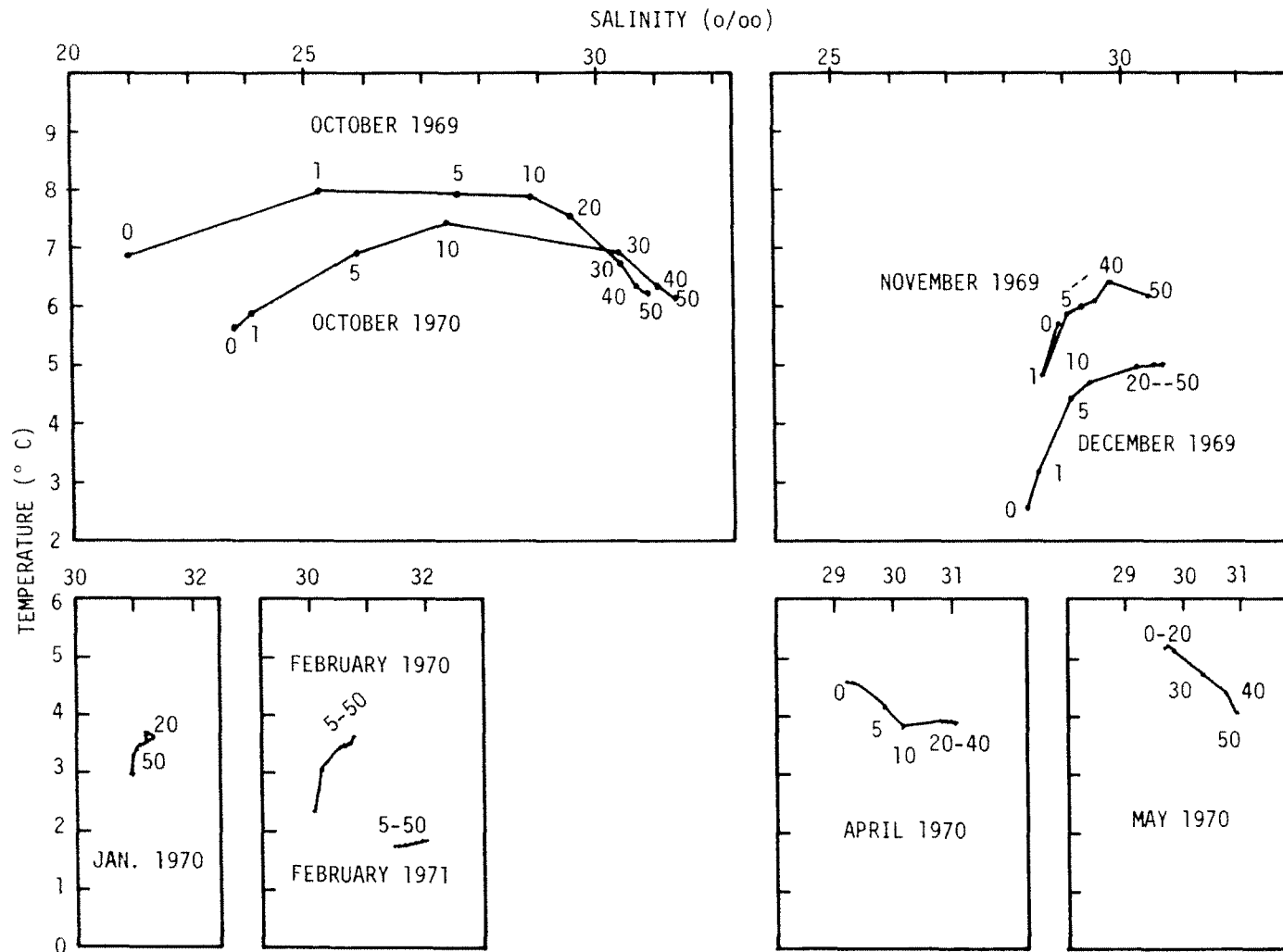
Fig. 14.--Monthly variation of temperature salinity curves from Auke Bay, Alaska, September 1969 to February 1971

SALINITY (o/oo)

TEMPERATURE (° C)

JUNE 1970

Fig. 14.--Continued

JULY 1970

SALINITY (o/oo)

TEMPERATURE (° C)
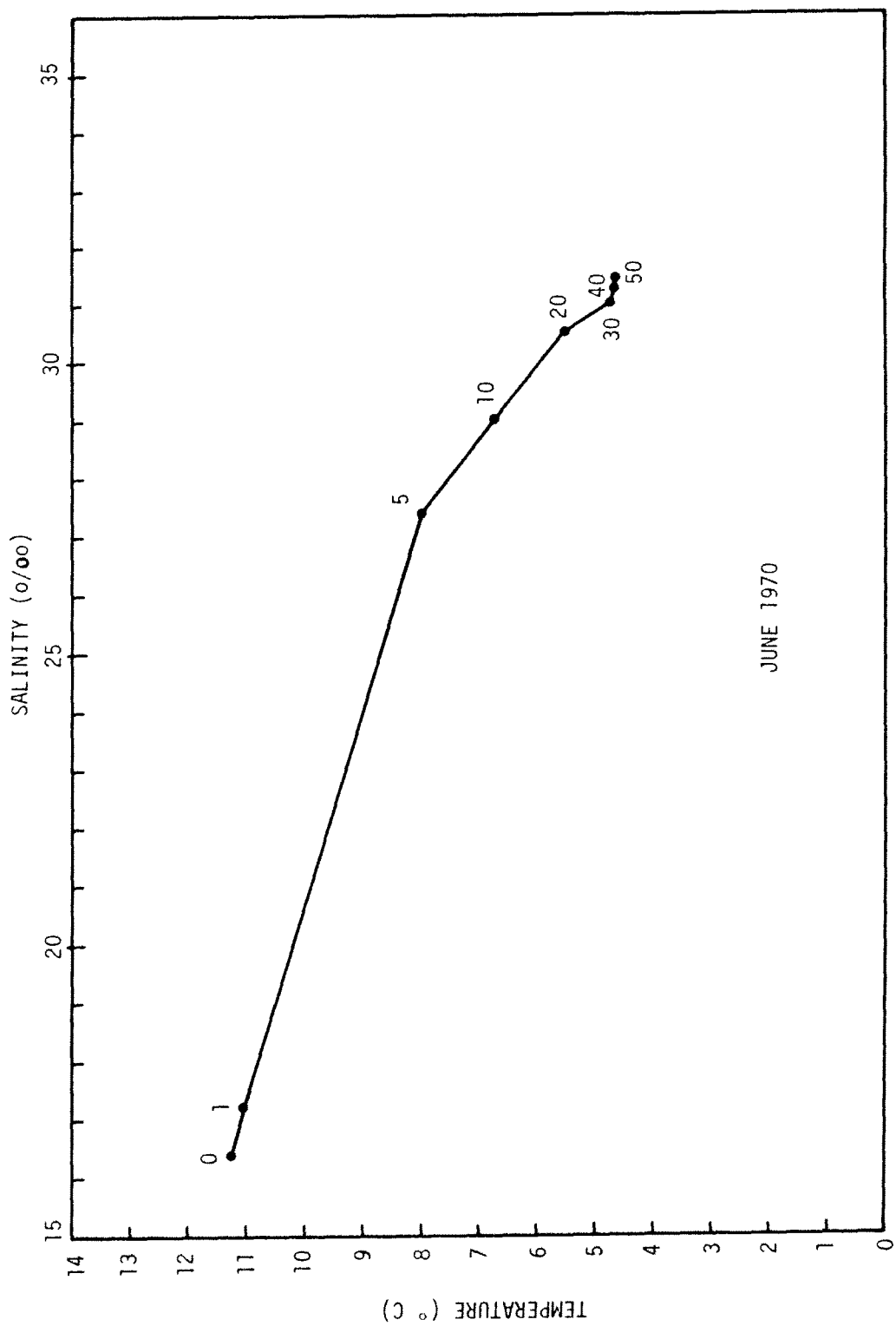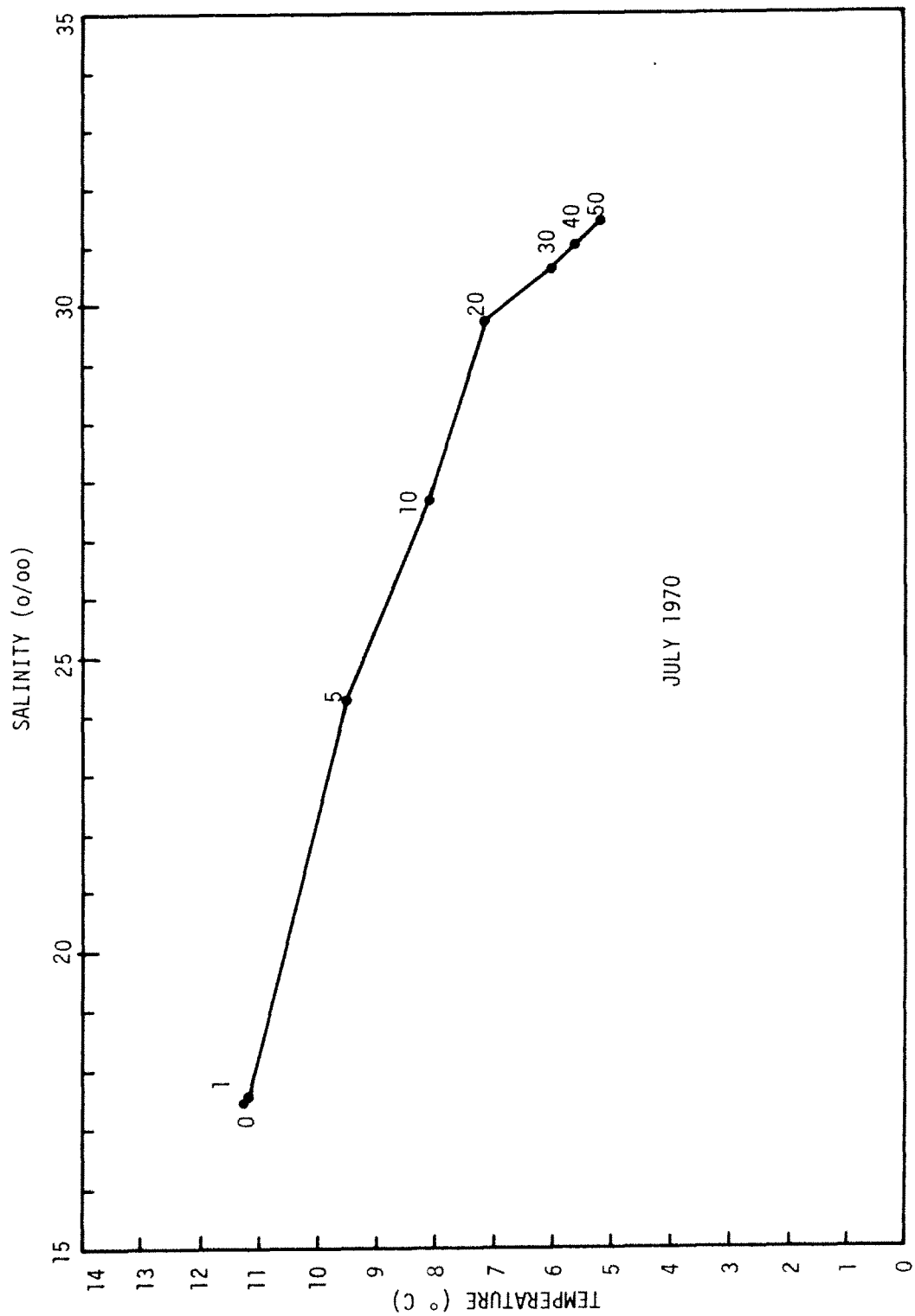
Fig. 14.--Continued

Fig. 14.--Continued

Fig. 14.--Continued

μg at NO_3-N/liter
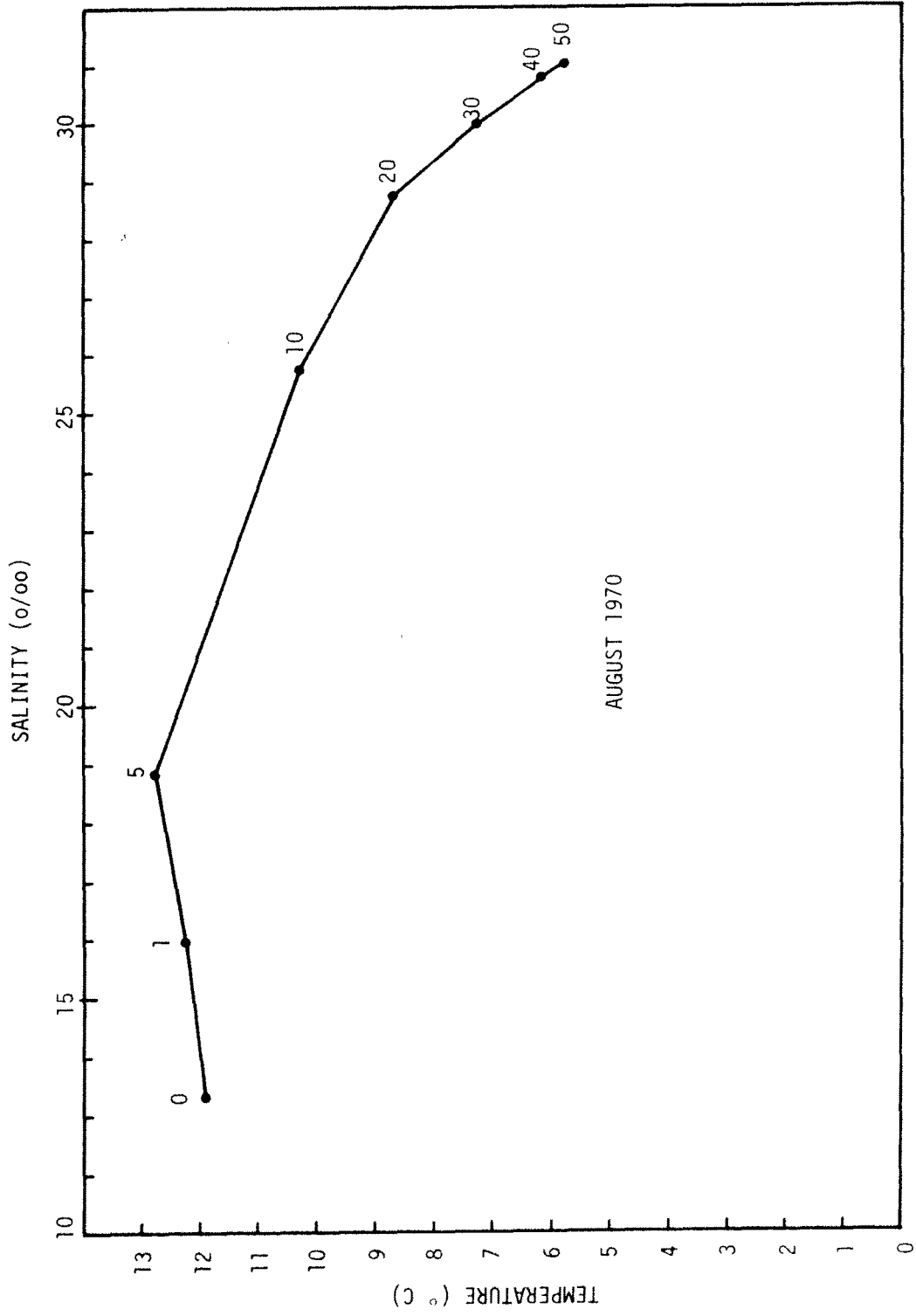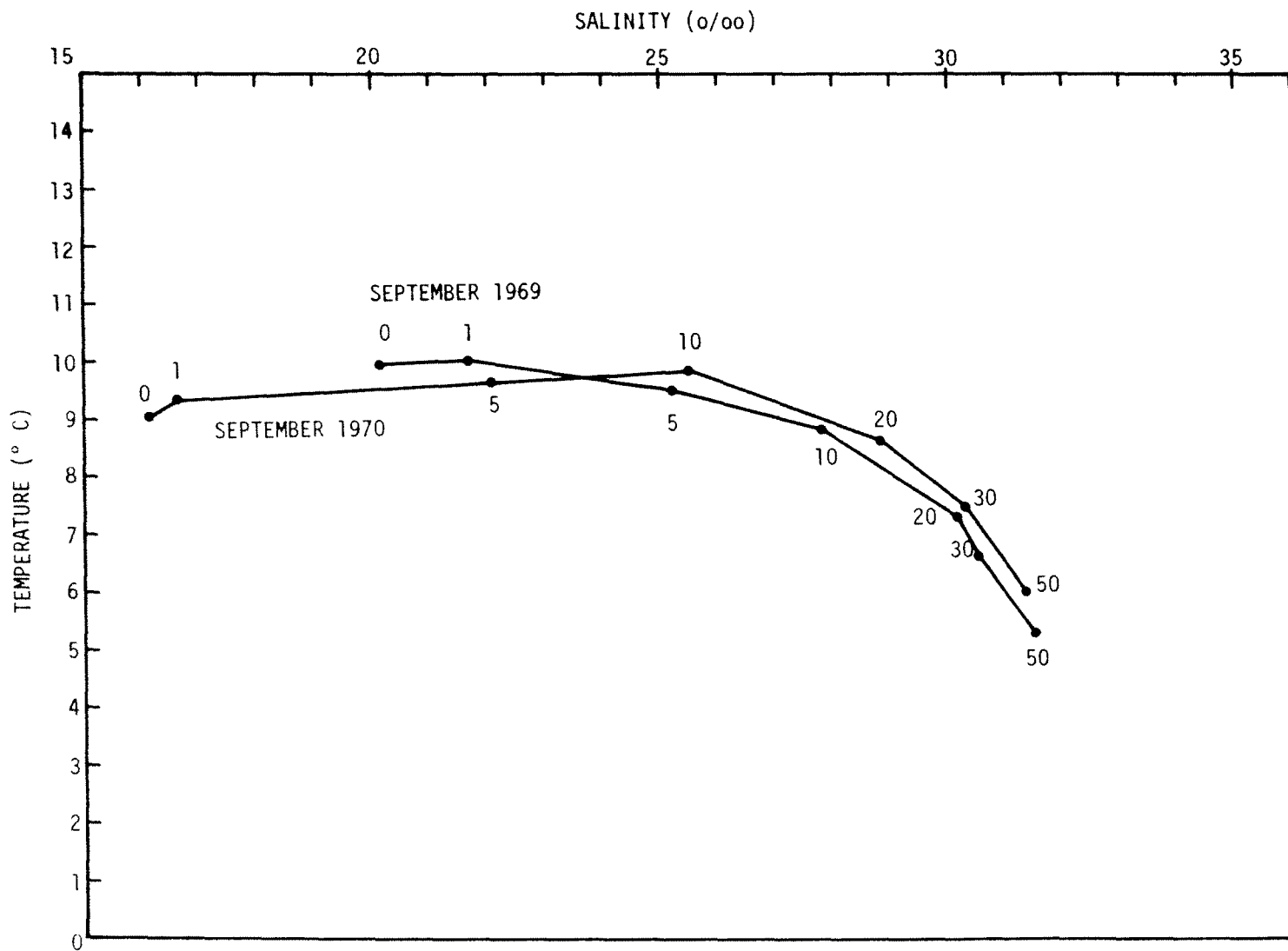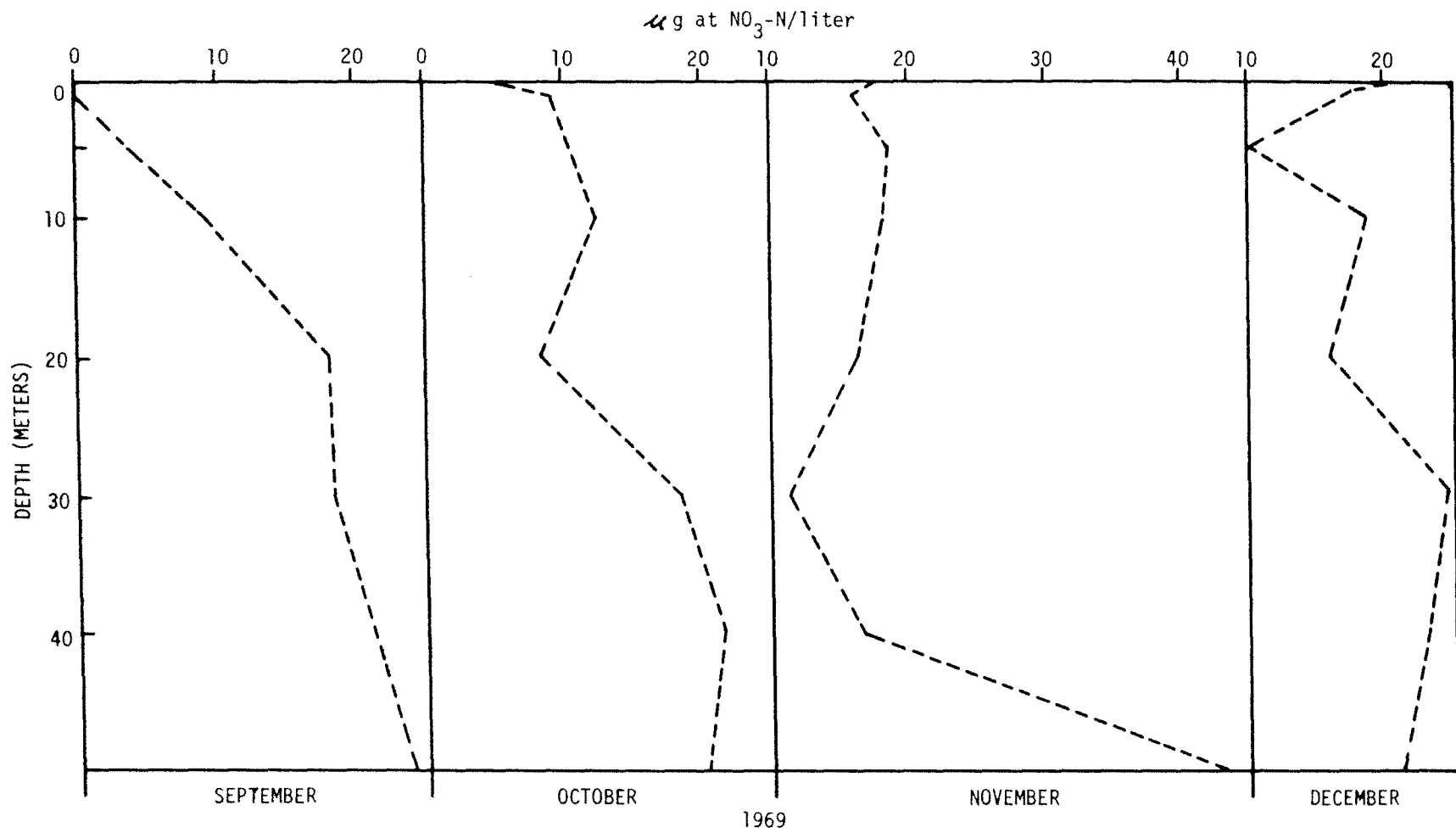
Fig. 15.--Monthly variation in vertical distribution of nitrates in Auke Bay, Alaska, September 1969 to February 1971
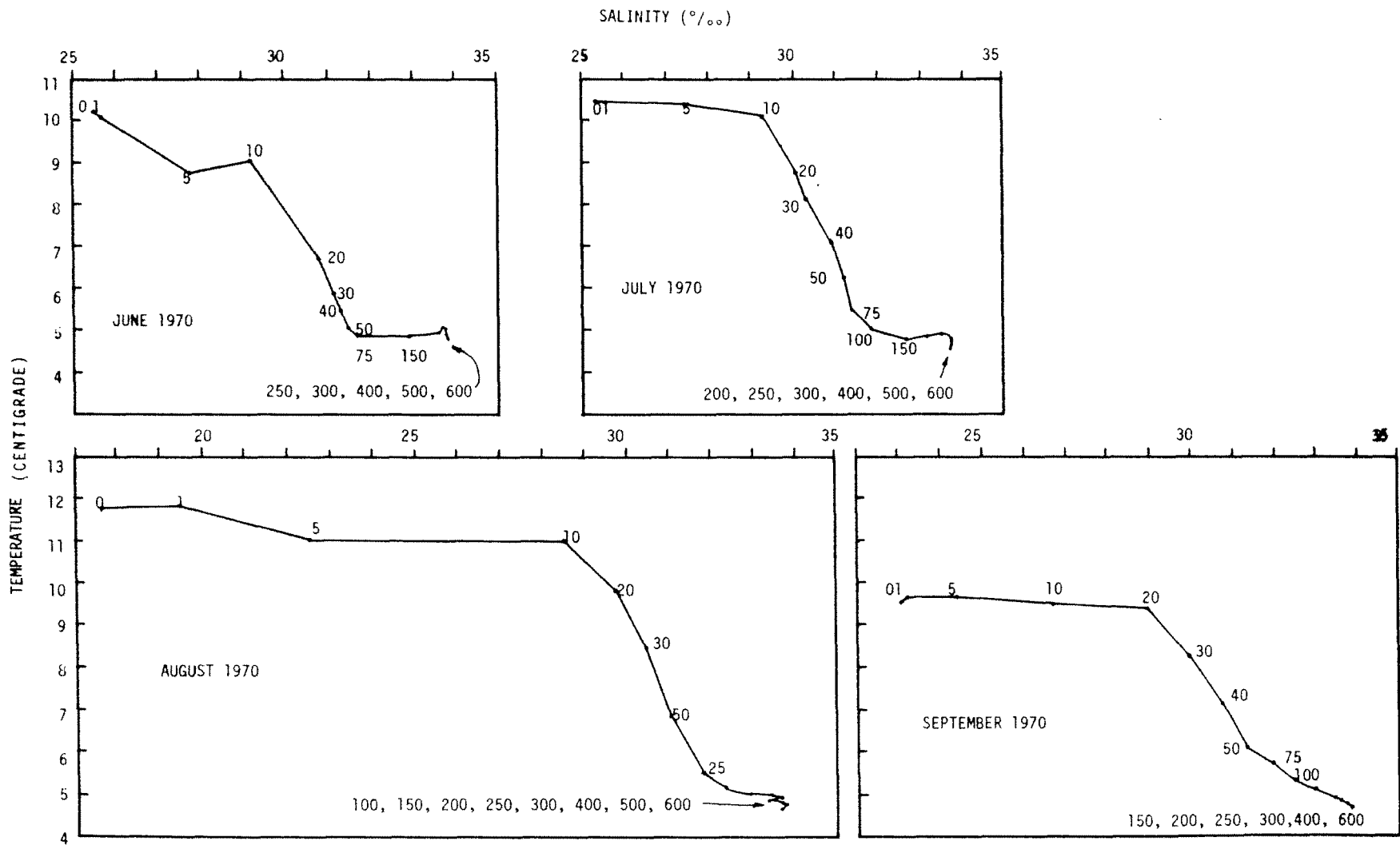
Fig. 15.--Continued

$\mathcal{U}$ g at NO_3-N/liter

Fig. 15.--Continued

72
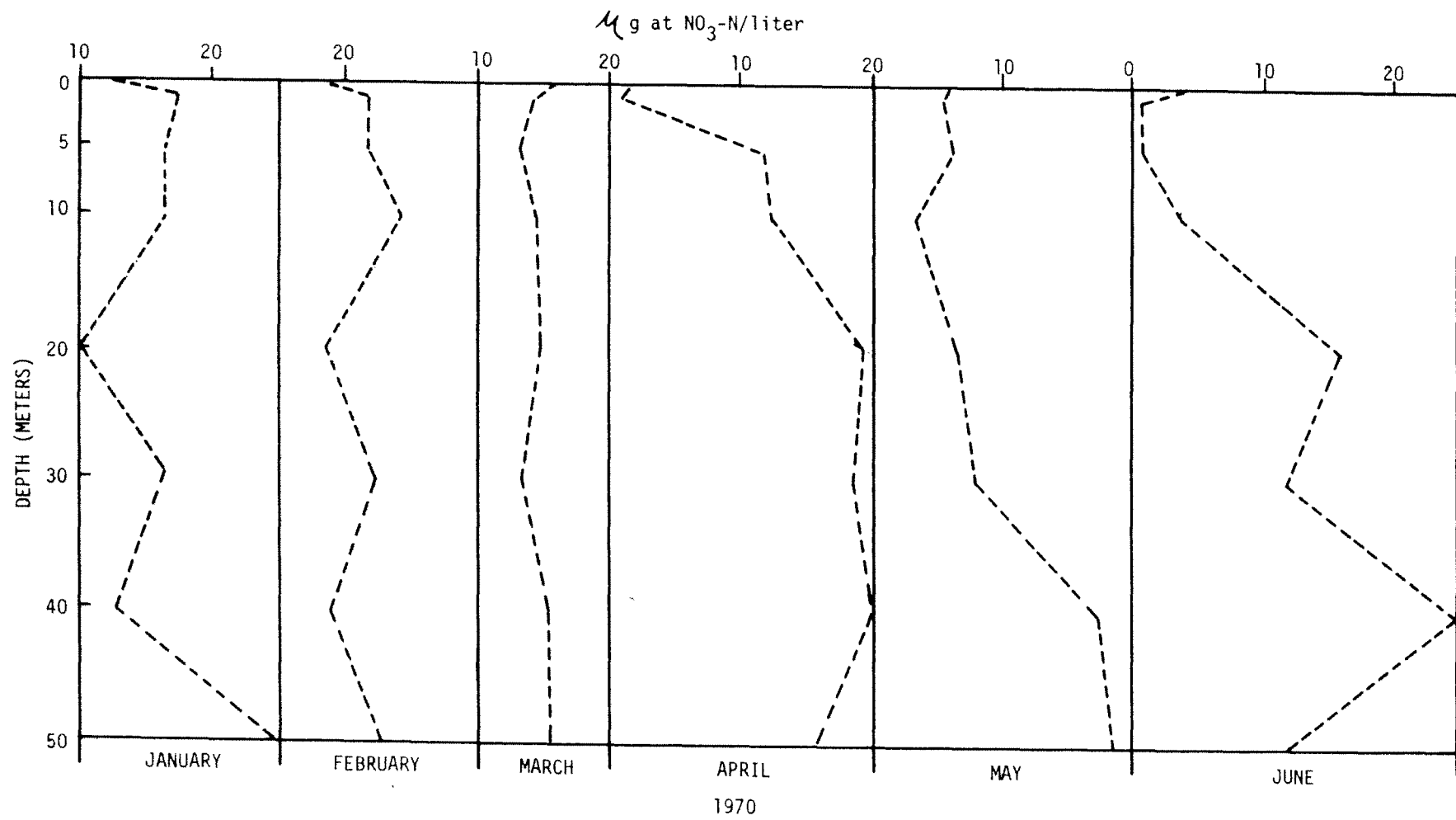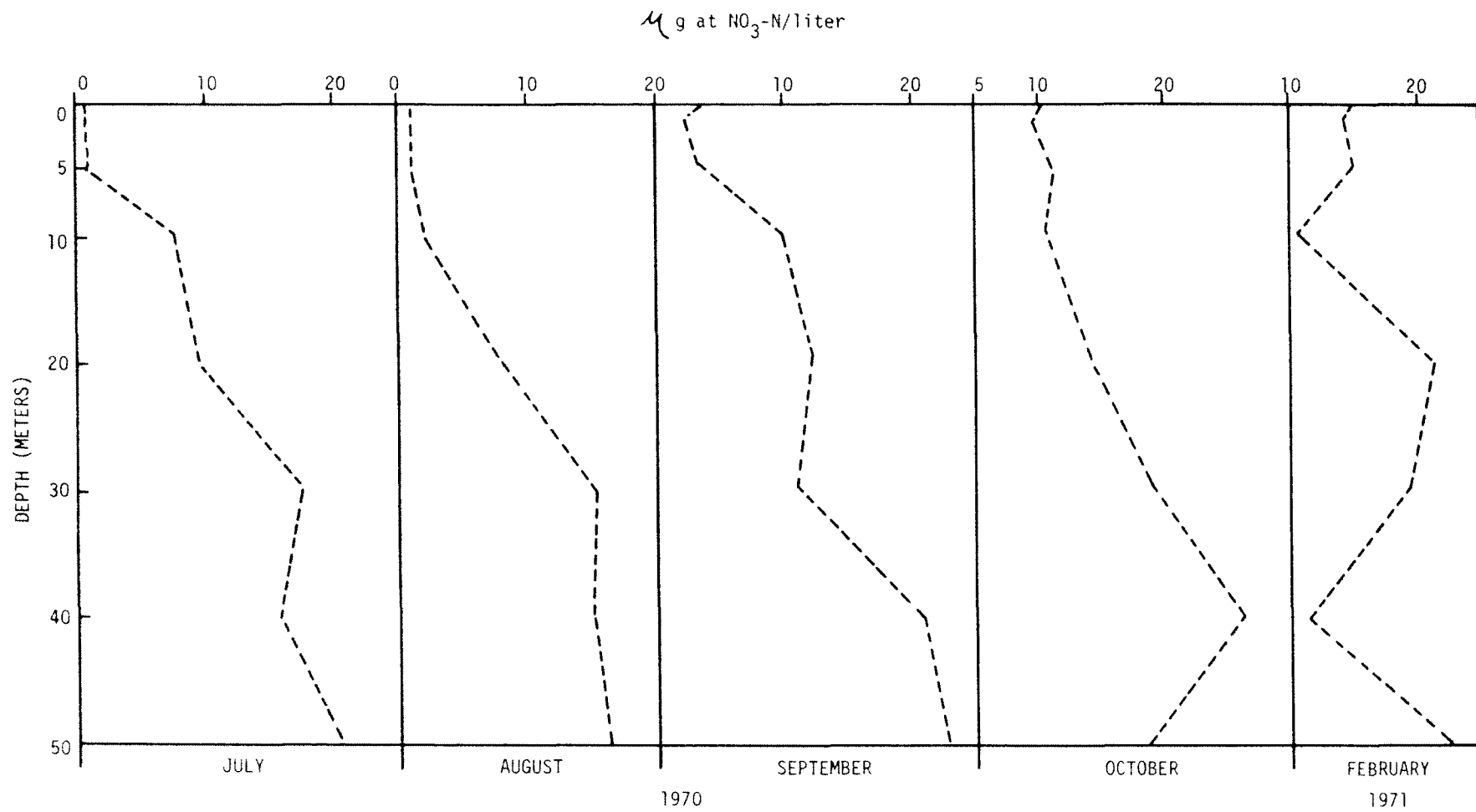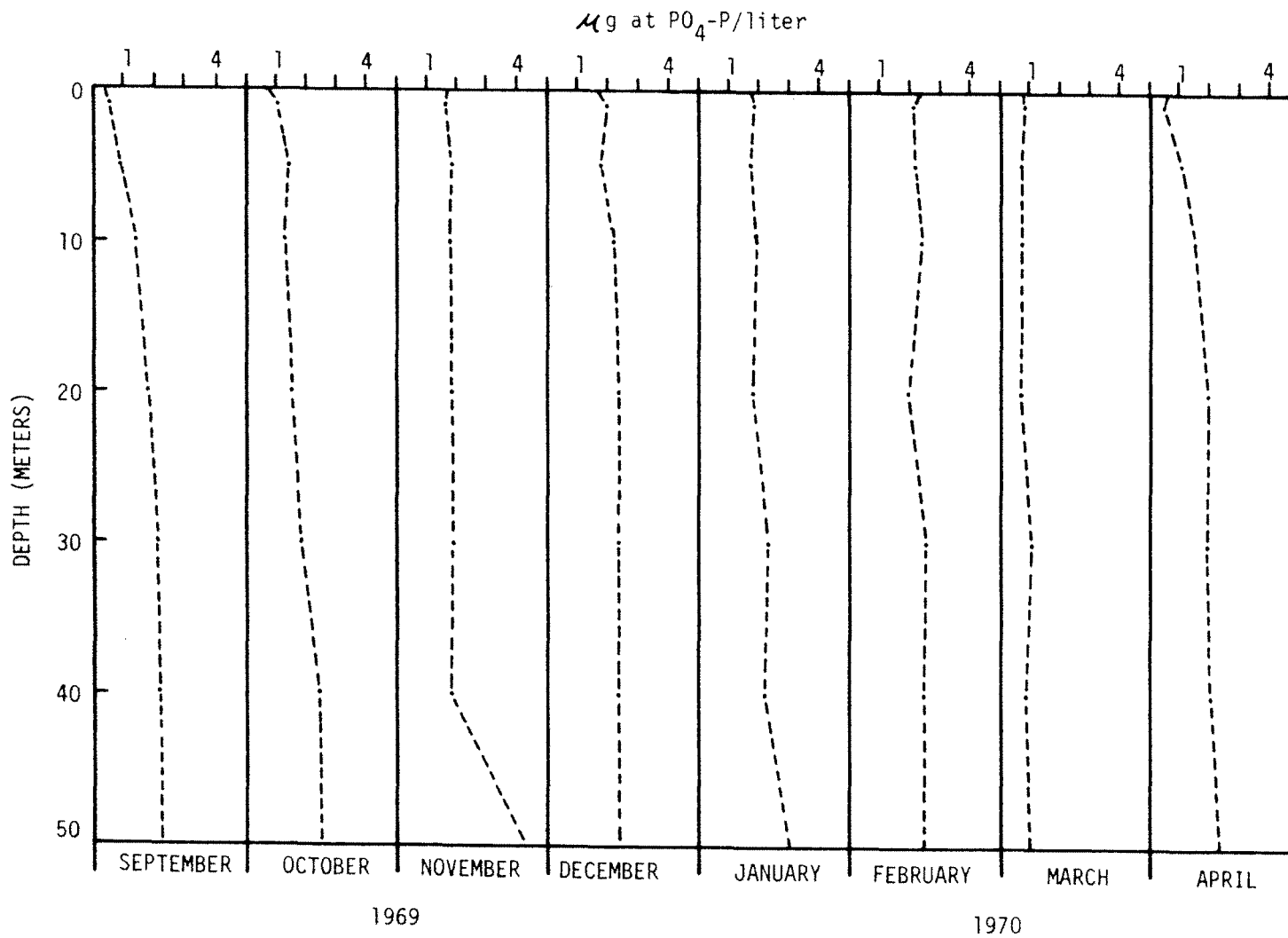
Fig. 16.--Monthly variation in vertical distribution of phosphates in Auke Bay, Alaska, September 1969 to February 1971.

μg at PO$_4$-P/liter

DEPTH (METERS)

0

10

20

30

40

50

1   4   1   4   1   4   1   4   1   4   1   4   1   4

MAY   JUNE   JULY   AUGUST   SEPTEMBER   OCTOBER   FEBRUARY

1970

1971

74
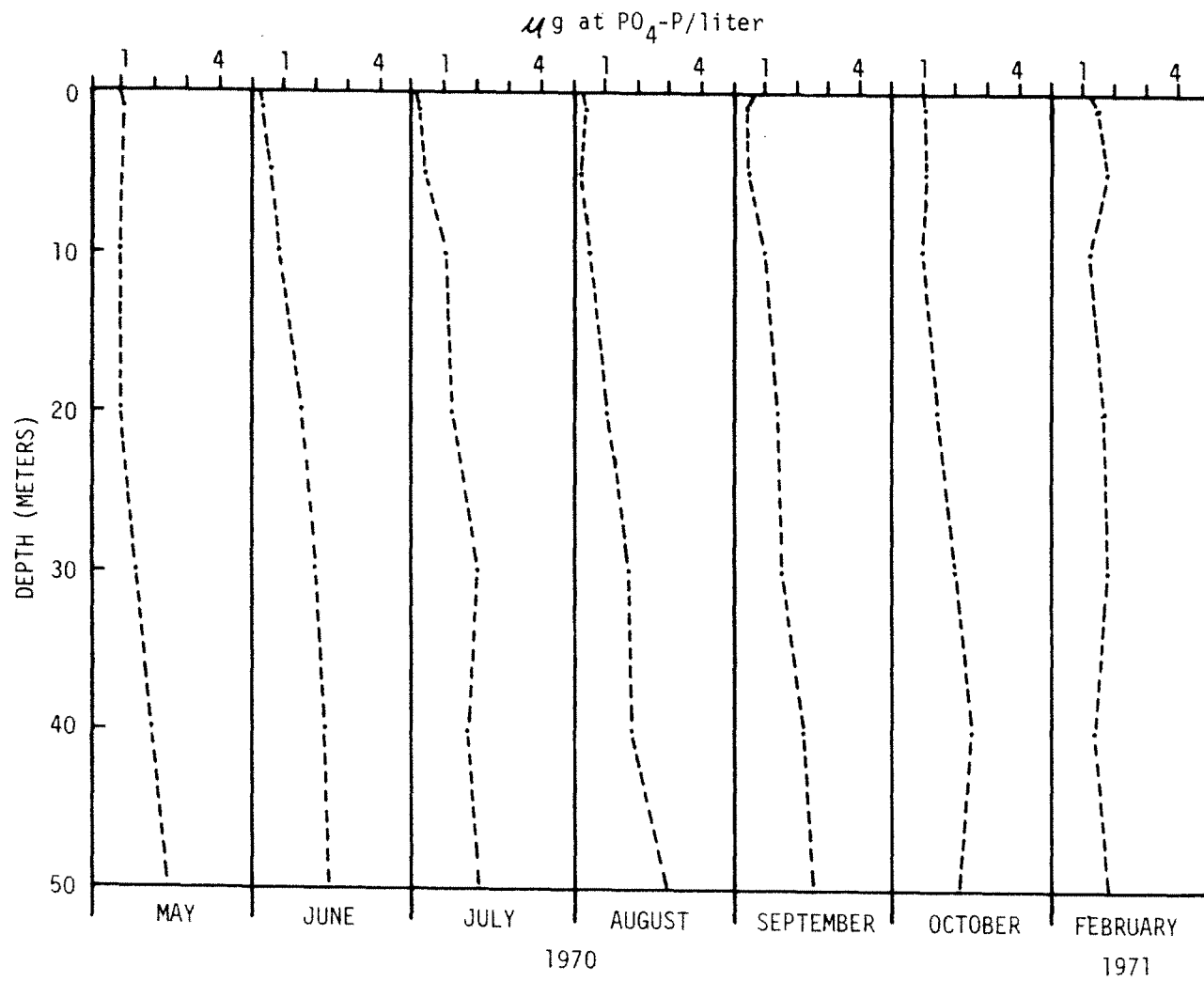
Fig. 16.--Continued
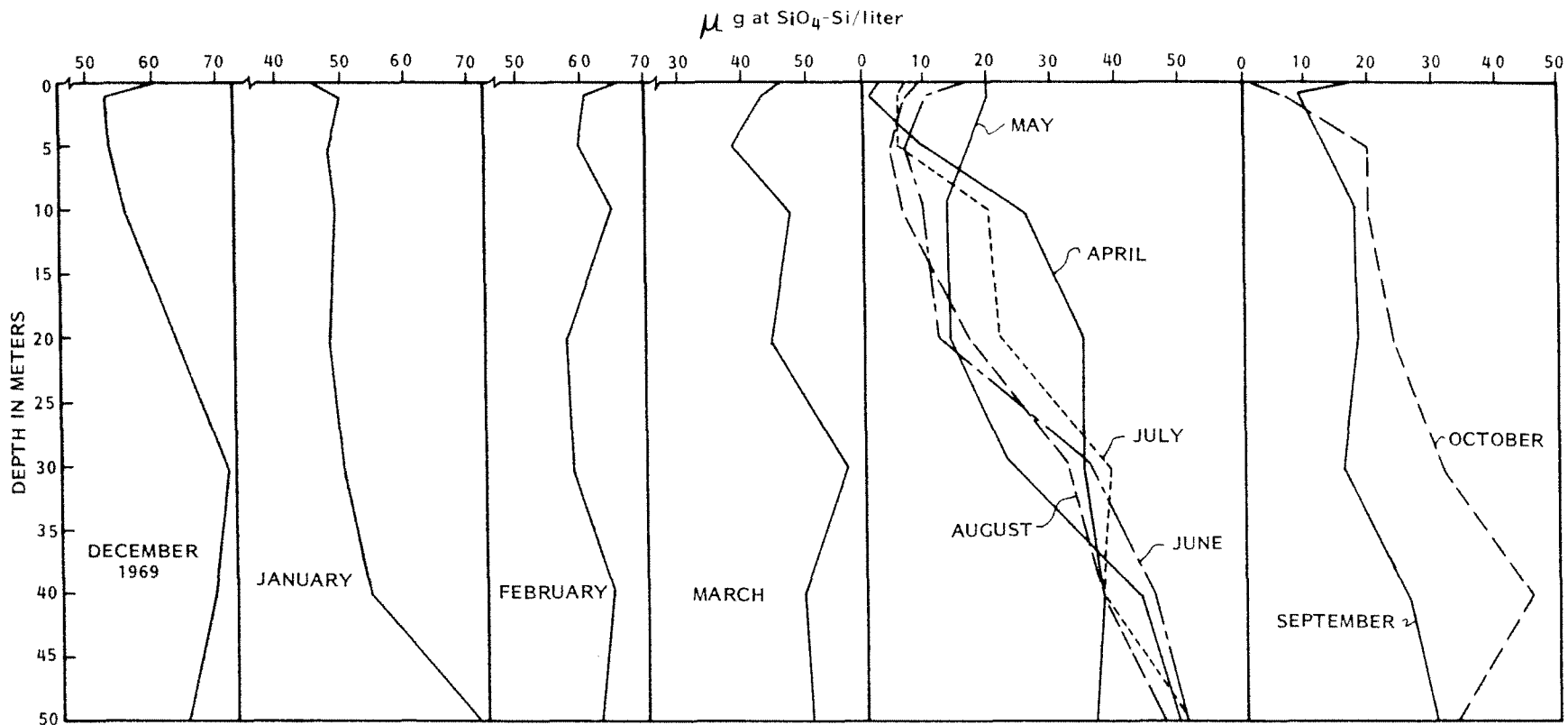
Fig. 17.--Monthly variation in the vertical distribution of silicates in Auke Bay, Alaska, December 1969 to October 1970

least in February 1970, and greatest during the months of April, June, and July. Strongest gradients occurred above the pycnocline. The concentrations of nutrients observed during the summer of 1970 were approximately the same as observed by Bruce and McLain (in prep.) for 1961-66. The minimum July values in my data are slightly higher than Bruce and McLain's averages, probably as a result of sampling between blooms rather than during blooms. My winter concentrations of nitrate and phosphate for February 1971 are about 60 percent of the winter concentrations of February 1970, and both years are below the average February values for 1961-66 reported by Bruce and McLain (in prep.).

Dissolved Oxygen Concentrations

Dissolved oxygen concentrations during the summer of 1970 did not deviate much from the expected values, ranging from 6.5-12.0 mg/1 above to 5 mg/1 below the pycnocline base (Figure 18). Winter concentrations of 10-11 mg/1 were well above the expected 8-9 mg/1, possibly because of the introduction of oxygen into the water by strong wind and wave action.

Primary Productivity

Primary productivity, as estimated from chlorophyll a measurements, was lowest in the winter (Figure 19). Chlorophyll a values averaged 0.25 µg chlorophyll a/1 from November 1969 through March 1970. In April, increased sunlight and temporary stratification coincided with the first bloom when a high value of 19.32 µg chlorophyll a/1 was observed at 5 m. From April through September, productivity remained high in the upper 20 m. Below 20 m, chlorophyll a values were low throughout the year; they exceeded the winter mean only in May.
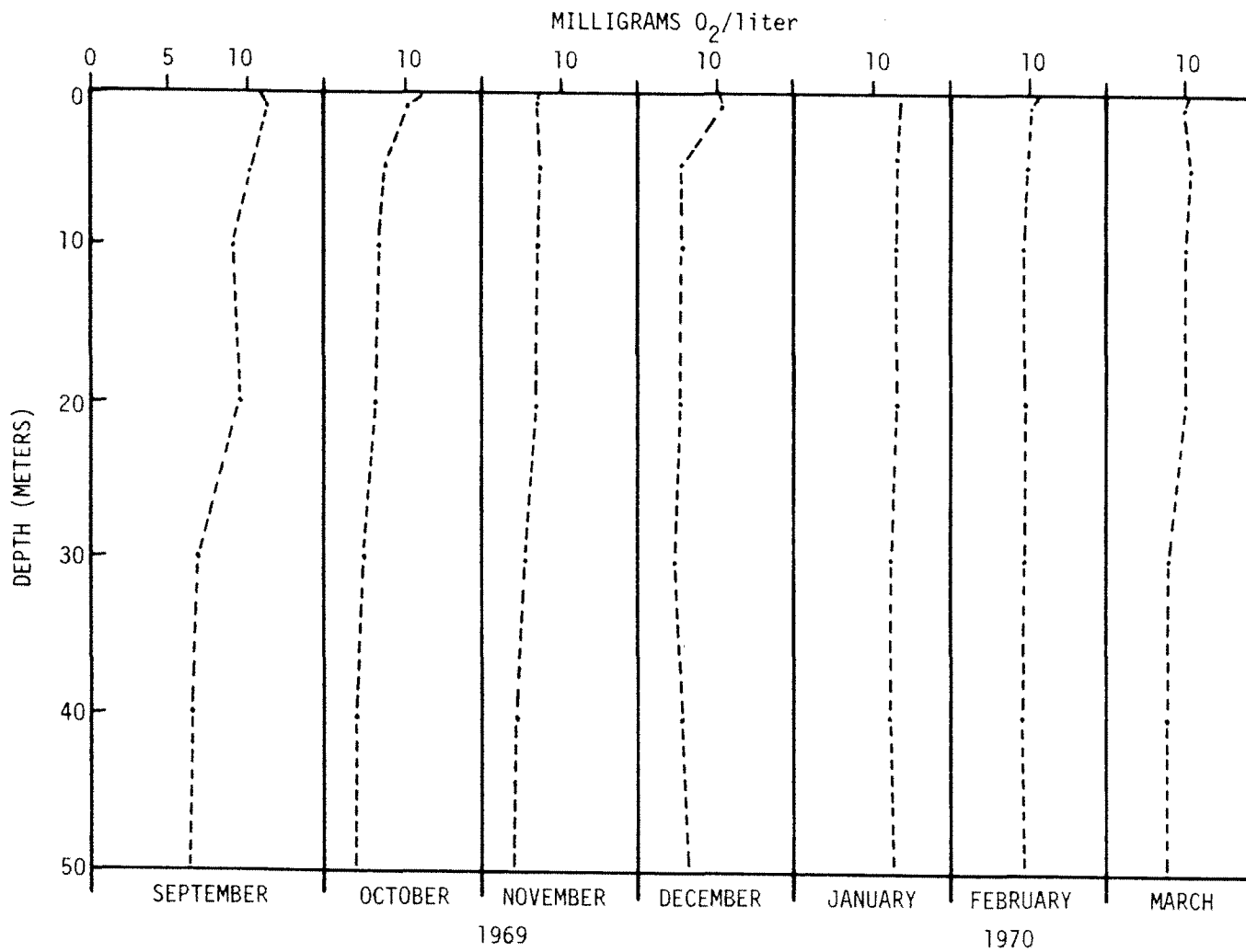
Fig. 18.--Monthly variation in vertical distribution of dissolved oxygen in Auke Bay, Alaska, September 1969 to February 1971.
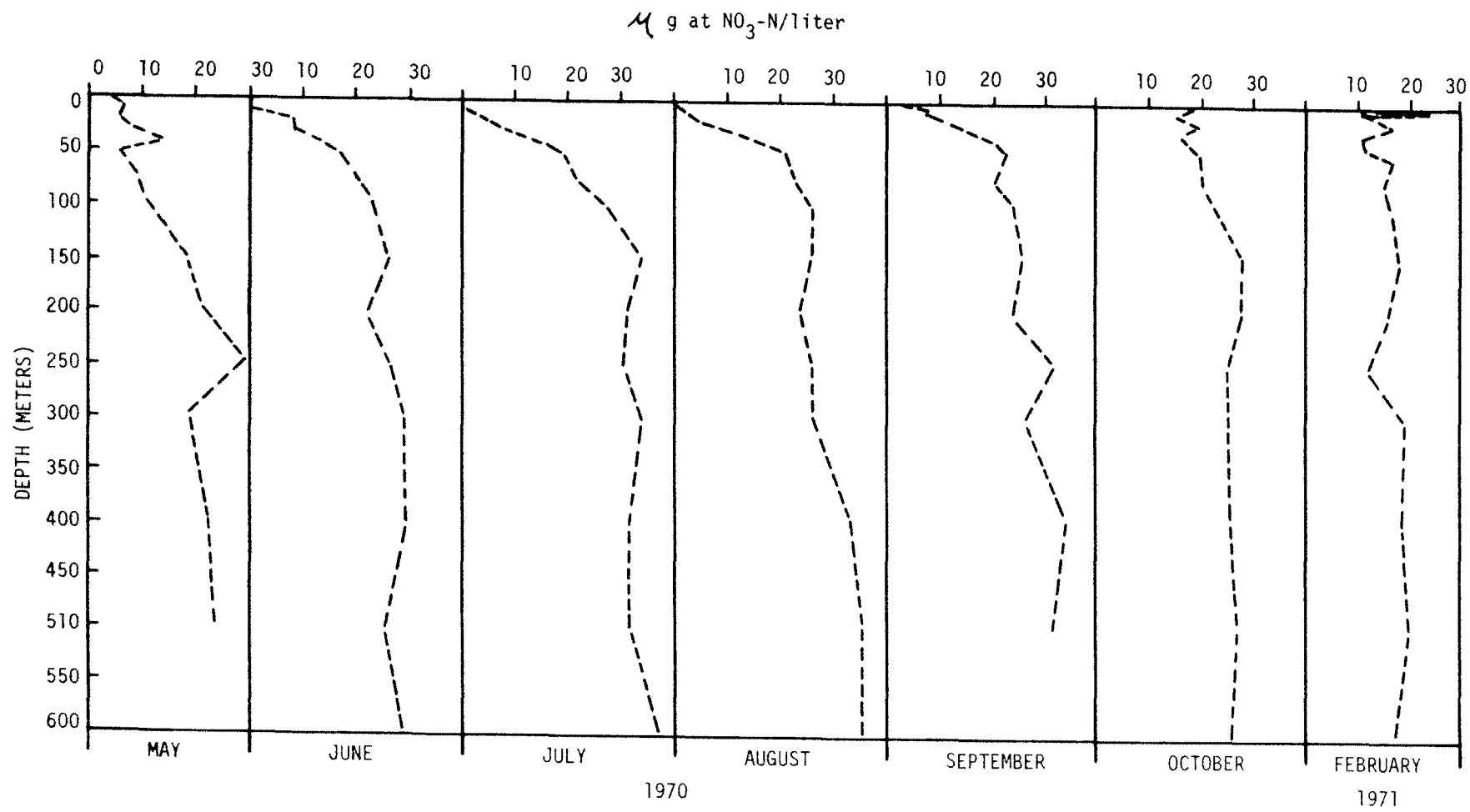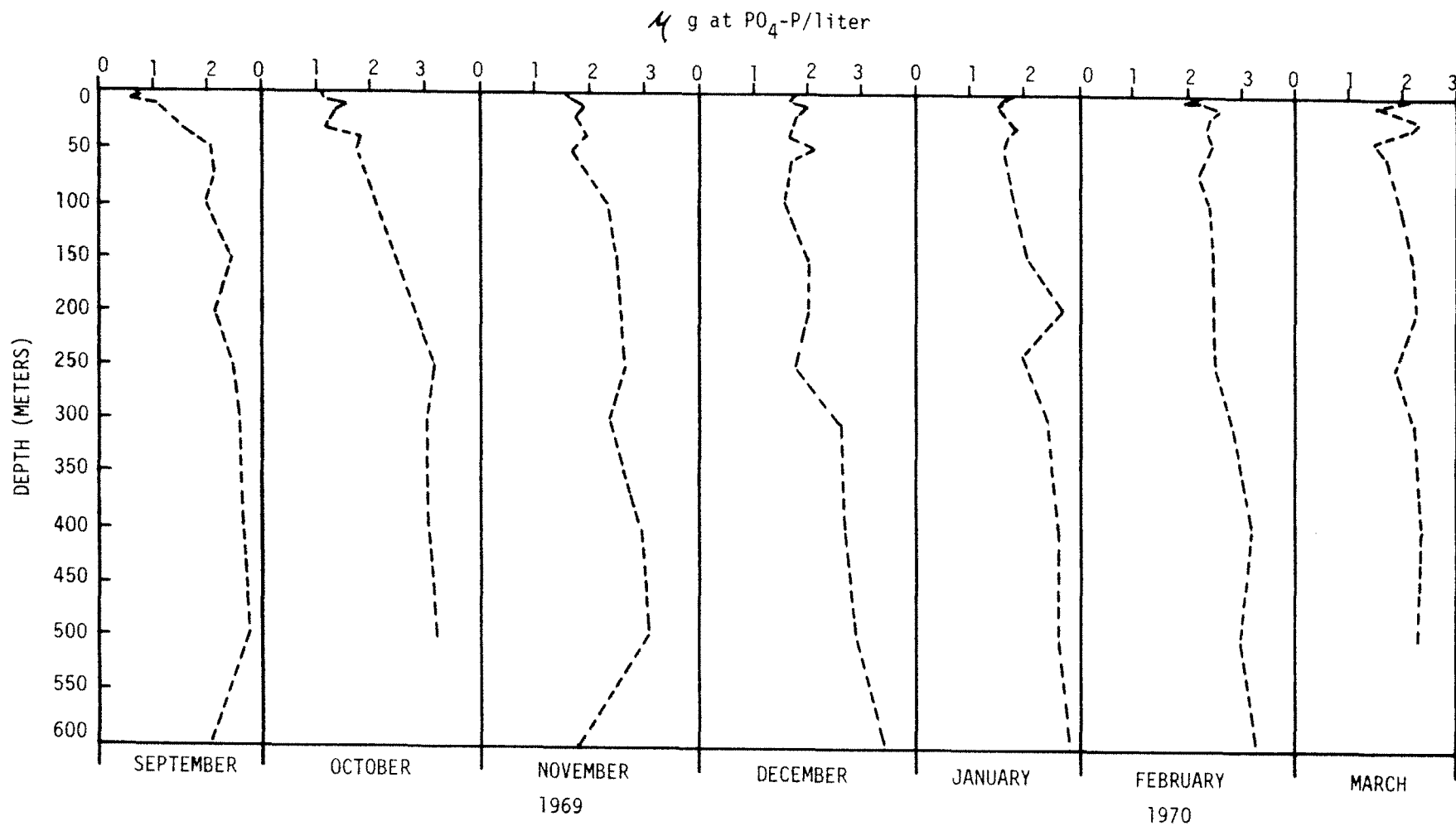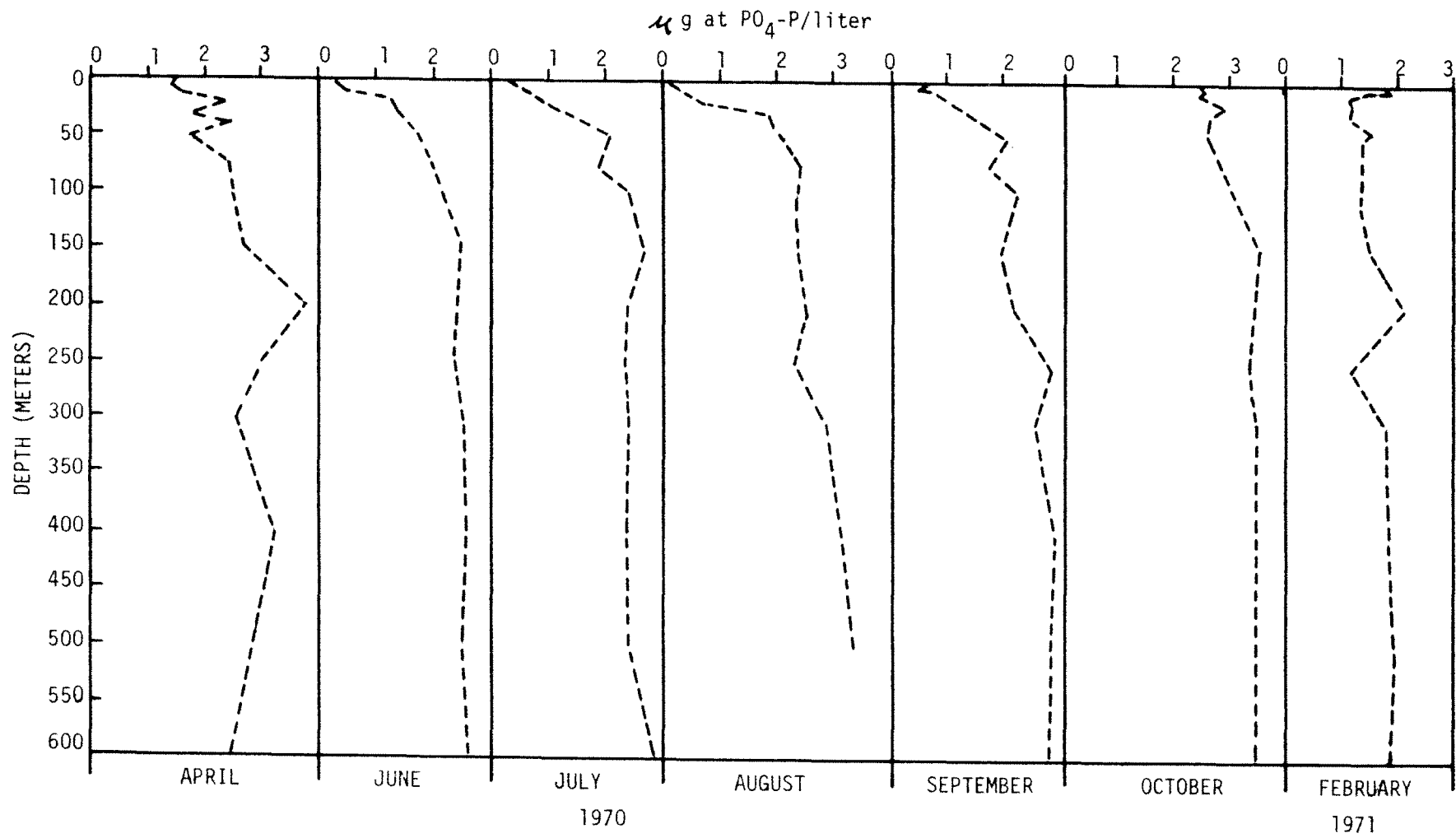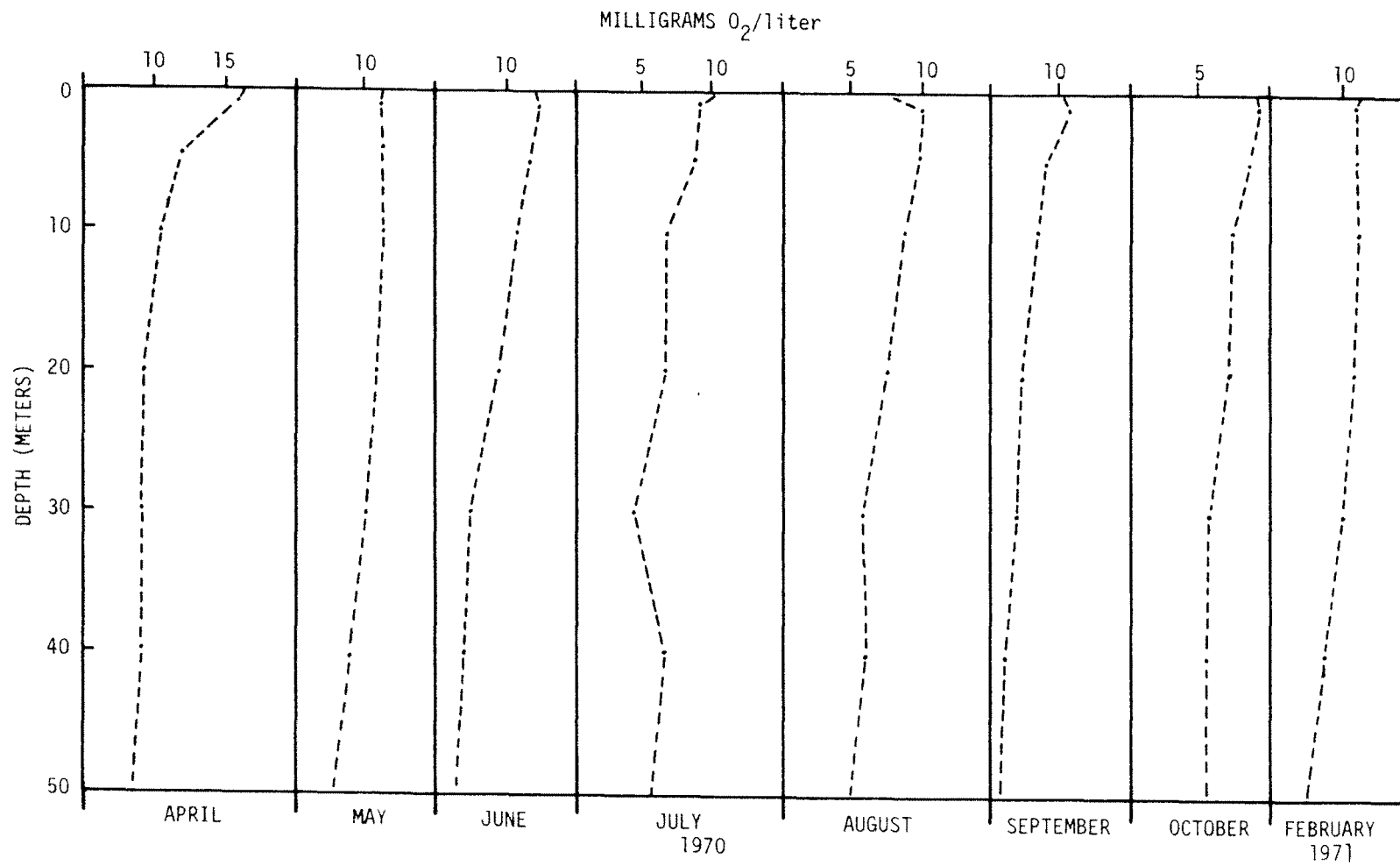
Fig. 18.--Continued
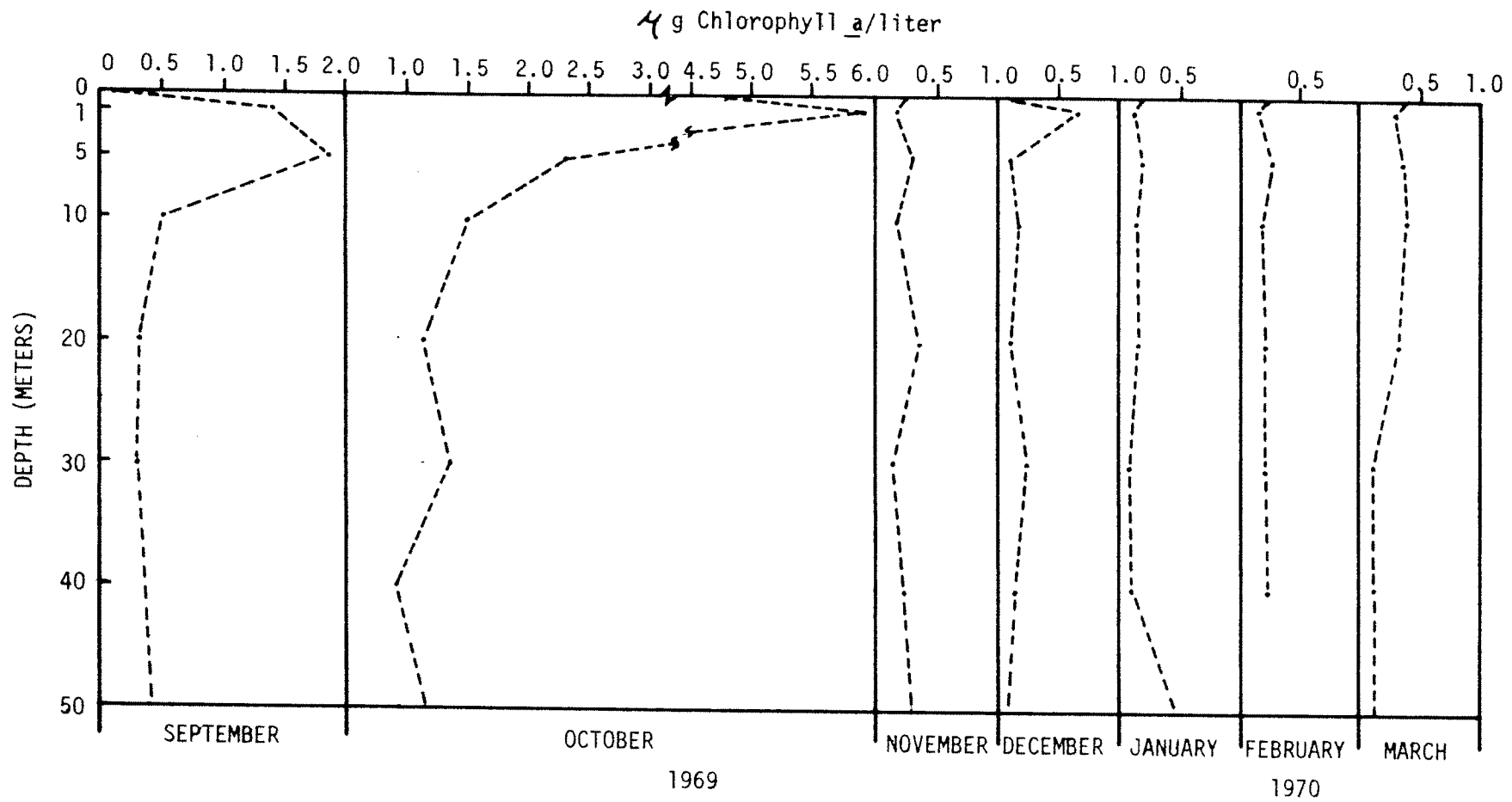
Fig. 19.--Monthly variation in vertical distribution of chlorophyll a in Auke Bay, Alaska, September 1969 to February 1971
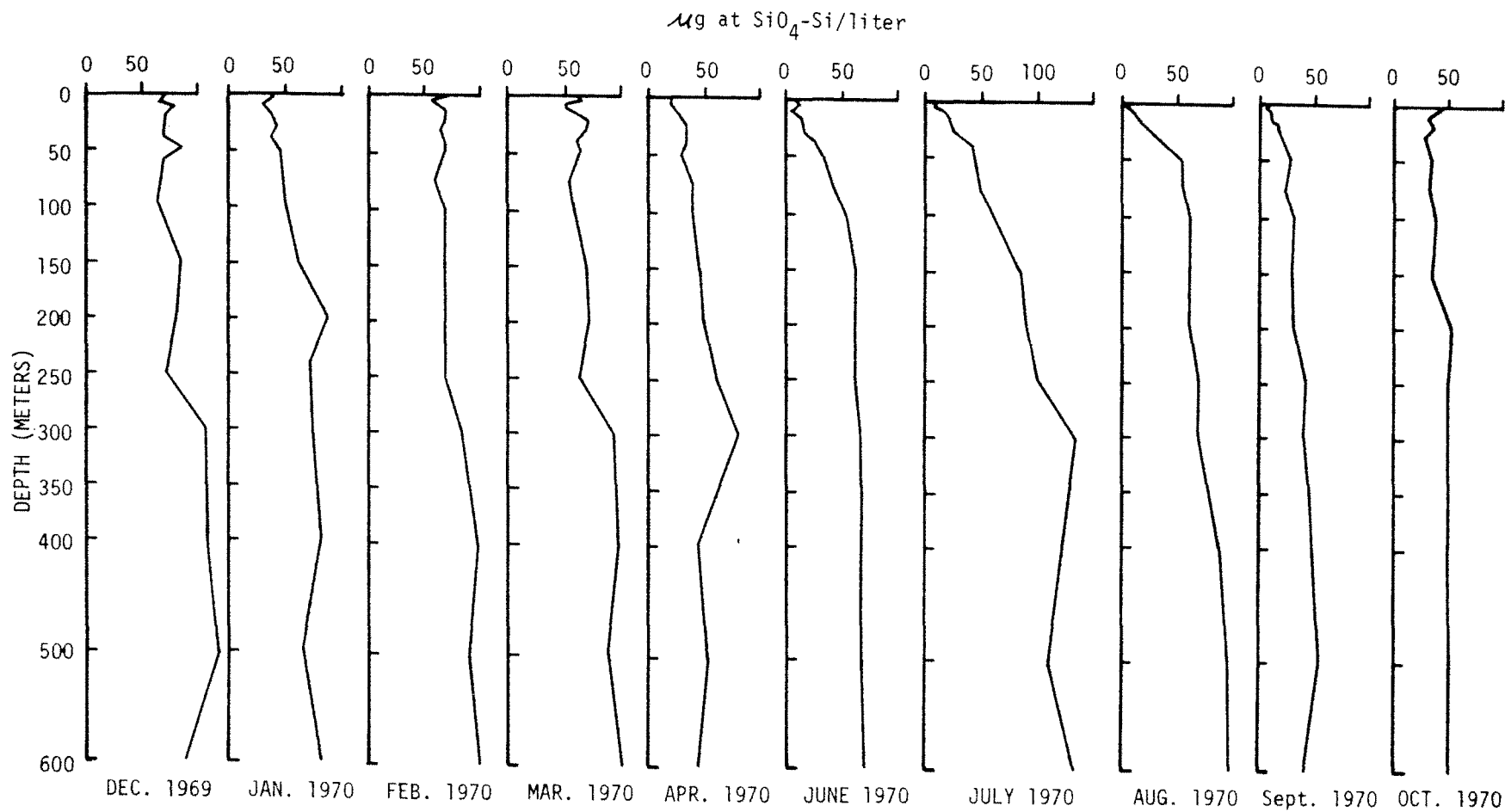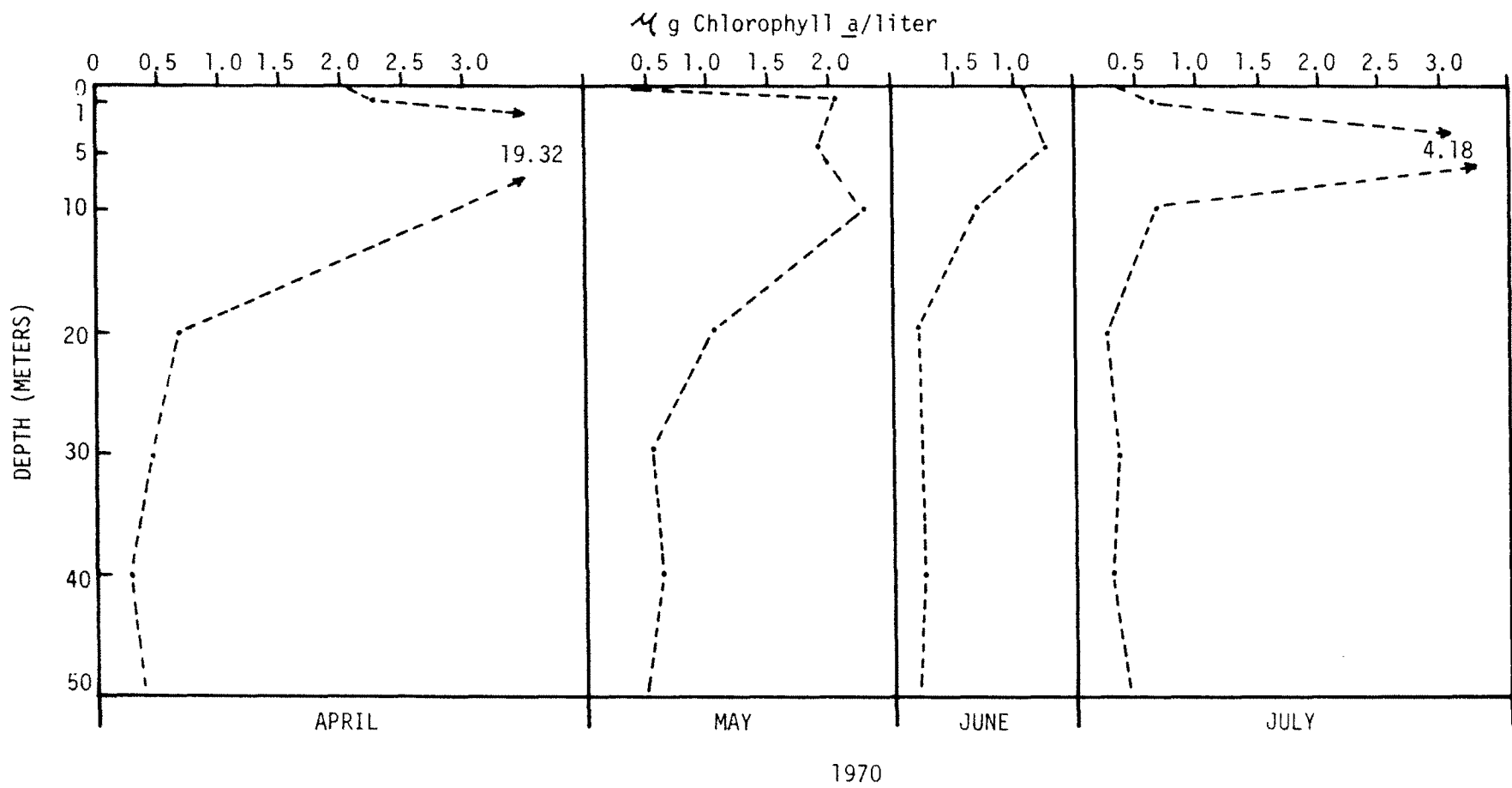
Fig. 19.--Continued
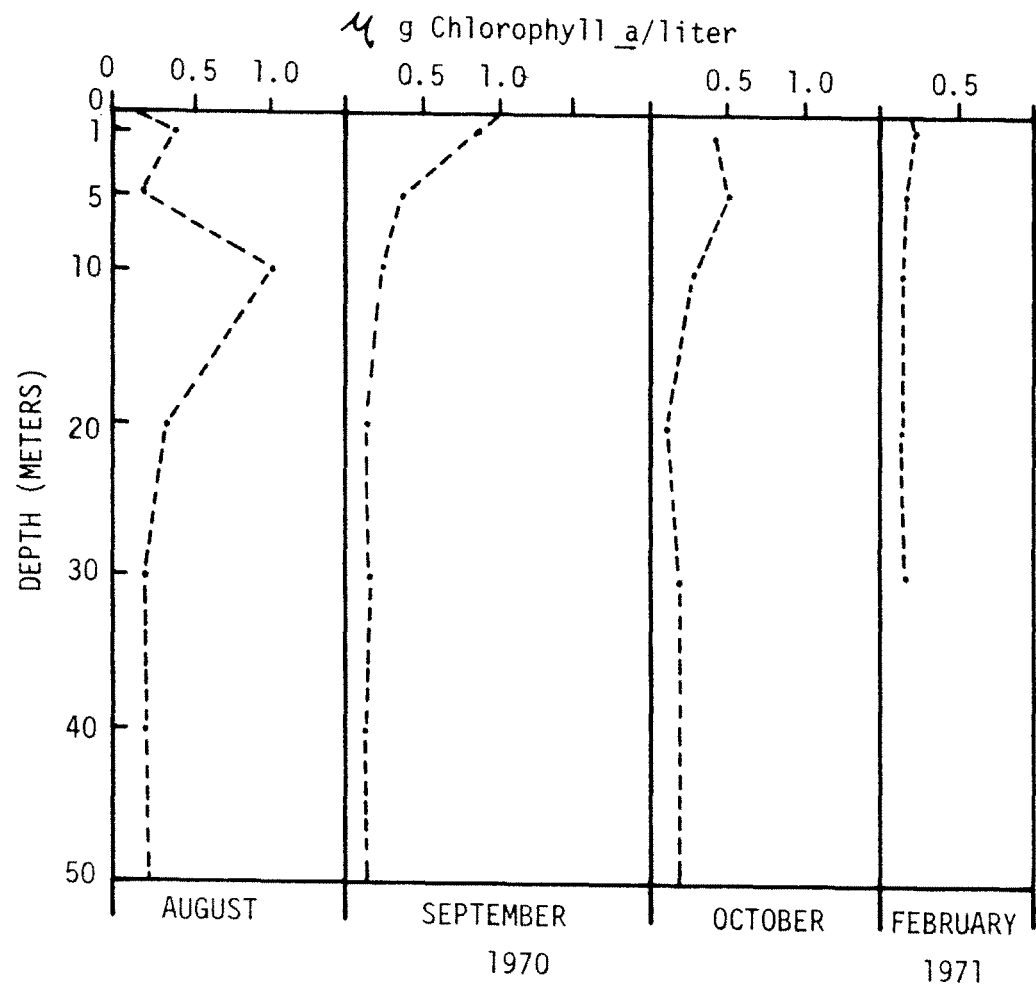
Fig. 19.--Continued

Photosynthetic compensation depth, as determined by the 1% incident sunlight level (Figure 20), was deepest in February 1971 when the 1% light level occurred at 20-30 m. During the 1969-70 winter (October to March) compensation depth was between 20 and 25 m. With the advent of spring phytoplankton blooms, the compensation depth diminished and generally remained above 15 m, with April and June minima of 11 and 9 m respectively.

The Auke Bay phytoplankton species composition (Table 6) and cyclic pattern did not follow the previously reported patterns as closely as was expected. Skeletonema costatum was the predominant form in September and October 1969, while Chaetoceros decipiens predominated from November through January, and Coscinodiscus spp. predominated in February and March. Expected winter populations of Biddulphia, Melosira, and Ceratium were very low in contrast to previous data. Thalassiosira aestivalis dominated the spring blooms instead of the usual T. nordenskioldii. The summer blooms were composed primarily of microflagellates in late June. Skeletonema costatum in July and August, and Chaetoceros spp. in September and October. Maximum species diversity (17 species) was observed in September 1969, and minimum diversity (5 species) was observed in April of the same year.

Comparison of Oceanographic Conditions At False Point Retreat and in Auke Bay

Although only 38 km apart, the oceanographic conditions at Auke Bay Monitor station and False Point Retreat station reflect several differences in temperature, salinity, and productivity cycles which may influence the occurrence of Parathemisto spp., as well as other zooplankton, at these
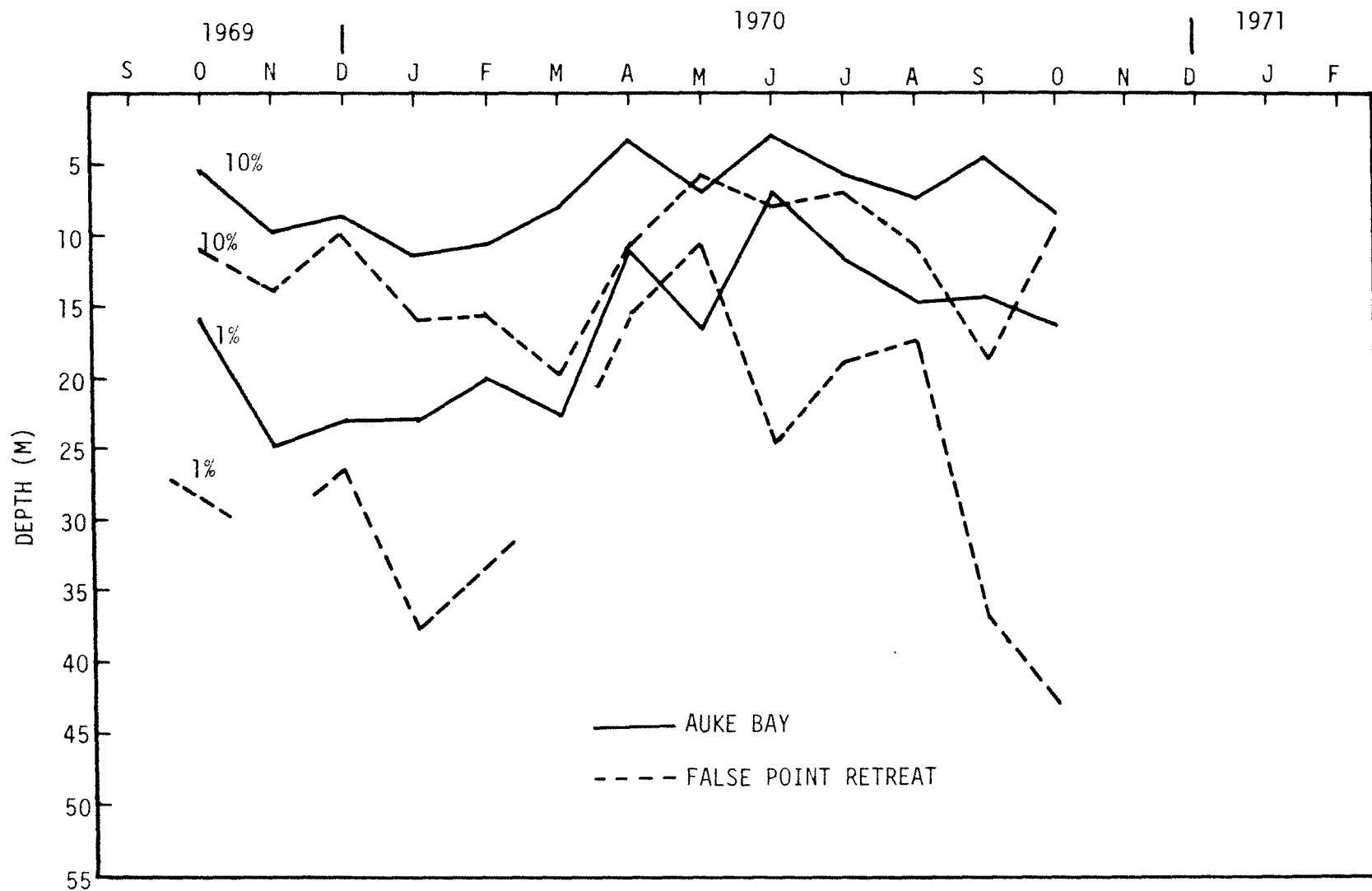
Fig. 20.--Monthly variation in the depth of penetration of 10% and 1% incident sunlight in Auke Bay and at False Point Retreat Alaska, October 1969 to October 1970

TABLE 6. --Phytoplankton species composition in Auke Bay, September 1969 to February 1971
(1 indicates most numerous; 2, numerous; 3, many; 4, few; 5, very few; 6, rare)

Genera/ species	1969 Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	March	April	May	June	July	Aug.	Sept.	Oct.	1971 Feb.
Skeletonema															
costatum	1	1	4	..	3	..	4	5	..	6	1	1	6	..	..
Chaetoceros															
decipiens	..	5	1	..	1	5	4	..	..	6	4	4	2	1	4
didymus	3	5	..	..	..	..	..	..	..	..	5	6	..	..	..
danicus	5	..	..	..	..	..	..	..	..	..	..	..	1	..	..
debilis	5	5	..	..	..	..	..	..	3	5	..	5	4	..	..
compressus	6	..	..	..	..	..	..	..	..	4	5	6	..	..	..
constrictus	4	..	5	..	6	..	..	..	..	5	5	..	4	..	..
lacinosus	2	5	6	..	..	..	..	..	..	6	..	..	5	..	..
radicans	4	..	..	..	..	..	..	..	..	..	..	..	..	..	..
concavicornis	..	..	5	..	2	6	4	..	5	5	..	..	..	6	6
subsecundus	..	..	..	..	6	..	..	..	..	..	..	..	..	..	..
atlanticus	..	..	..	..	6	..	..	..	..	..	..	..	..	..	..
similis	..	..	..	..	..	..	..	..	..	..	..	6	..	..	..
sp.	..	..	..	..	..	..	..	..	..	5	..	..	..	..	6
Thalassiosira															
aestivalis	5	5	..	..	..	..	6	1	1	2	..	..	..	..	..
nordensk	..	..	..	..	..	..	..	..	4	6	..	..	..	..	..
rotula	5	5	6	..	..	..	..	..	..	..	..	..	..	..	..
decipiens	..	..	..	..	5	..	..	..	..	4	4	5	6	..	..
gravida ?	..	..	..	..	..	..	..	..	4	..	..	..	..	..	..
sp.	..	..	..	..	..	6	..	..	..	..	..	..	..	..	6
Thalassionema															
nitzschoides	4	5	..	..	..	..	..	..	..	..	..	5	..	6	..
Cerataulina															
bergonii	6	..	..	..	..	..	..	..	..	..	..	..	..	..	..

TABLE 6.--Continued

Genera/species	1969				1970										1971
	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	March	April	May	June	July	Aug.	Sept.	Oct.	Feb.
Nitzschia spp.	3	4	..	..	6	5	5	6	6	5	5	5	5	6	..
Coscinodiscus spp.	5	..	3	..	4	1	1	5	2	5	..	..	6	2	3
Stephanopyxis niponica	5	..	..	..	..	..	..	..	6	..	6	..	..	..	..
Melosira moniliformis	..	..	6	..	..	..	4	..	..	..	..	..	..	..	..
Ditylum brightwelli	..	..	..	..	5	..	..	..	..	..	..	..	..	..	6
Biddulphia aurita	..	..	..	..	..	..	4	..	..	..	..	..	..	..	6
Coscinosira polychorda	..	..	..	..	..	..	..	..	6	5	..	..	..	..	..
Fragilaria	..	..	..	..	..	..	..	..	..	6	..	..	..	..	..
Leptocylindricus danicus	..	..	..	..	..	..	..	..	..	3	..	..	..	..	..
Rhizosolena delicatula	..	..	..	..	..	..	..	..	..	6	..	..	..	..	..
Distaphanus speculum	4	6	..	..	..	..	..	..	..	..	..	..	..	..	..
Ceratium horridum	4	..	5	..	5	5	6	..	..	..	..	..	..	..	1
lineatum	..	..	6	..	1	..	..	..	..	..	..	..	..	..	..
tripos	..	..	..	..	5	6	..	..	..	..	..	..	..	..	..
sp.	..	..	..	..	..	..	..	..	..	6	..	6	6	6	..

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two stations. False Point Retreat, with a water column over 620 m deep, has a much more varied choice of environments than Auke Bay with a depth of only 50 m. This is reflected in the greater diversity of zooplankton and nekton in the channel than in the small bays, although the two areas have many species in common.

Within the upper 50 m, the temperatures of Auke Bay and False Point Retreat had a similar seasonal cycle (Figure 21). Temperatures were about the same from February to April 1970. During the summer, water temperatures of the top 10 m were warmer in Auke Bay than at False Point Retreat, while during much of the fall and early winter, near-surface temperatures were lower in Auke Bay. With the exception of November 1969, water temperatures below 10 m were 0.5-2.0° C colder in Auke Bay than at False Point Retreat. Apparently, the shallower waters and greater degree of protection from winds allows Auke Bay to cool and warm more rapidly than the open channel areas.

Salinity changes in the upper 10 m are greater in Auke Bay than at False Point Retreat (Figure 22) because of the nearness of freshwater source streams. Below 10 m, the differences are generally less than $0.3°/oo$ although at the time of fall mixing, salinities in Auke Bay were $1°/oo$ less than at False Point Retreat to a depth of 50 m.

Whether there is a direct exchange of waters between Auke Bay and False Point Retreat area and/or Lynn Canal is unknown. A comparison of the sigma-t profiles in the top 50 m (Figure 13) suggests that through most of the year surface waters of the upper 5-20 m from Auke Bay would layer on top of Lynn Canal waters. Below 20 m, the sigma-t's are almost equal most of the year, suggesting that mixing would occur if the two areas were brought together. In spite of having different temperatures
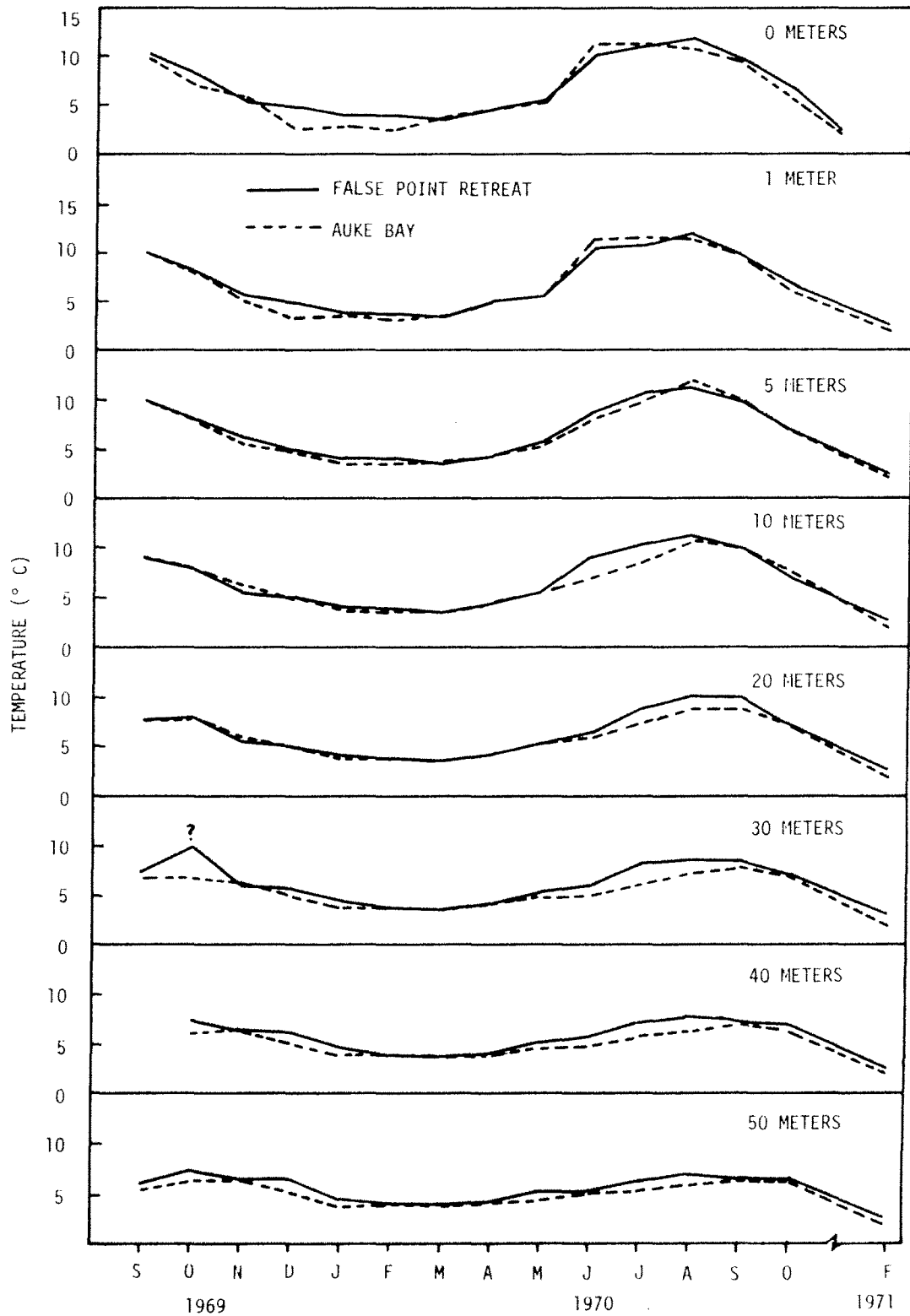
Fig. 21.--Seasonal cycle of temperature at selected depths in Auke Bay and at False Point Retreat, Alaska, September 1969 to February 1971.
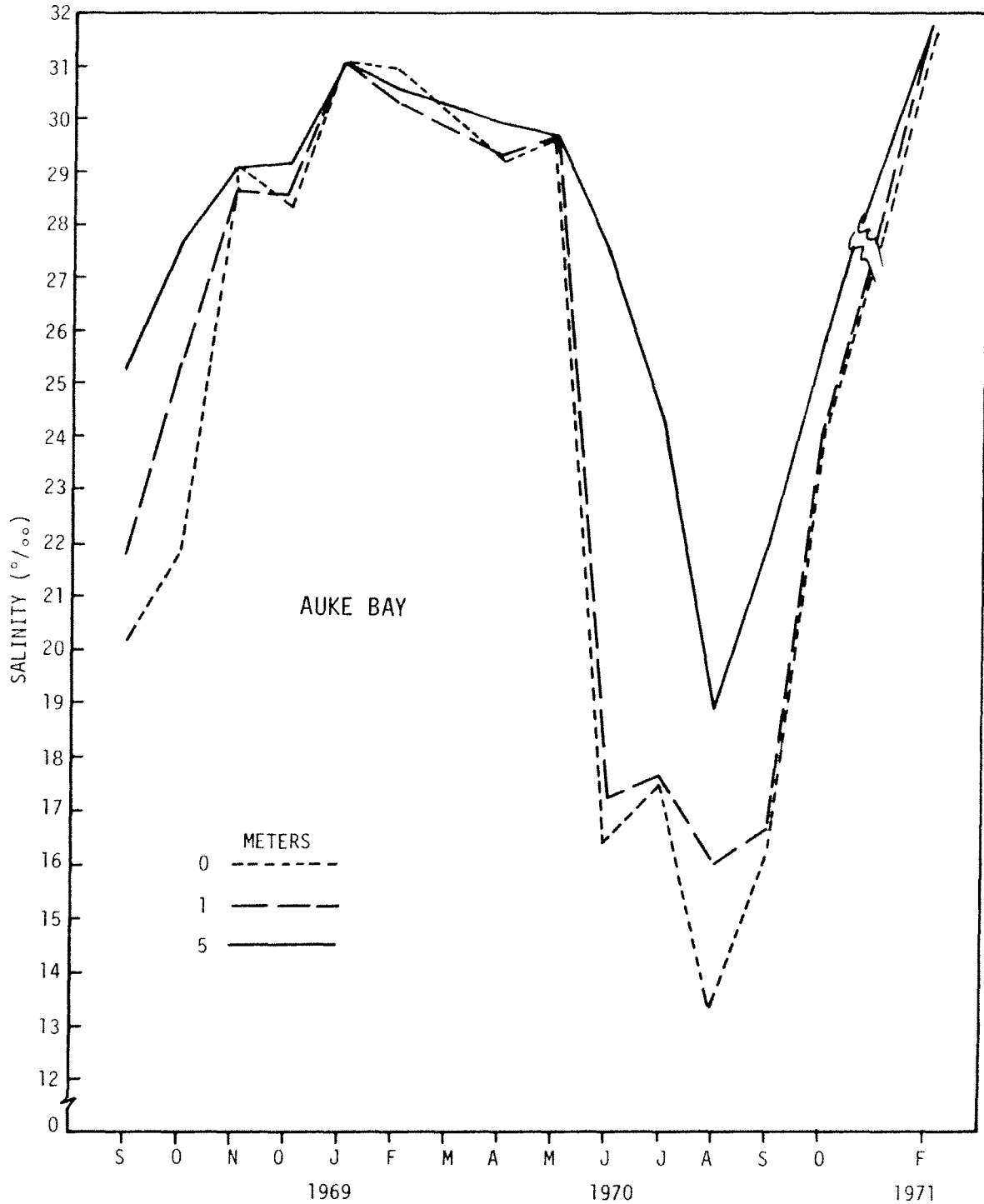
Fig. 22.--Seasonal cycle of salinity at selected depths in Auke Bay and at False Point Retreat, Alaska, September 1969 to February 1970. (a) Auke Bay salinities at 0, 1, and 5 m. (b) False Point Retreat salinities at 0, 1, and 5 m. (c) Auke Bay and False Point Retreat salinities at 10, 20, 30, 40, and 50 m
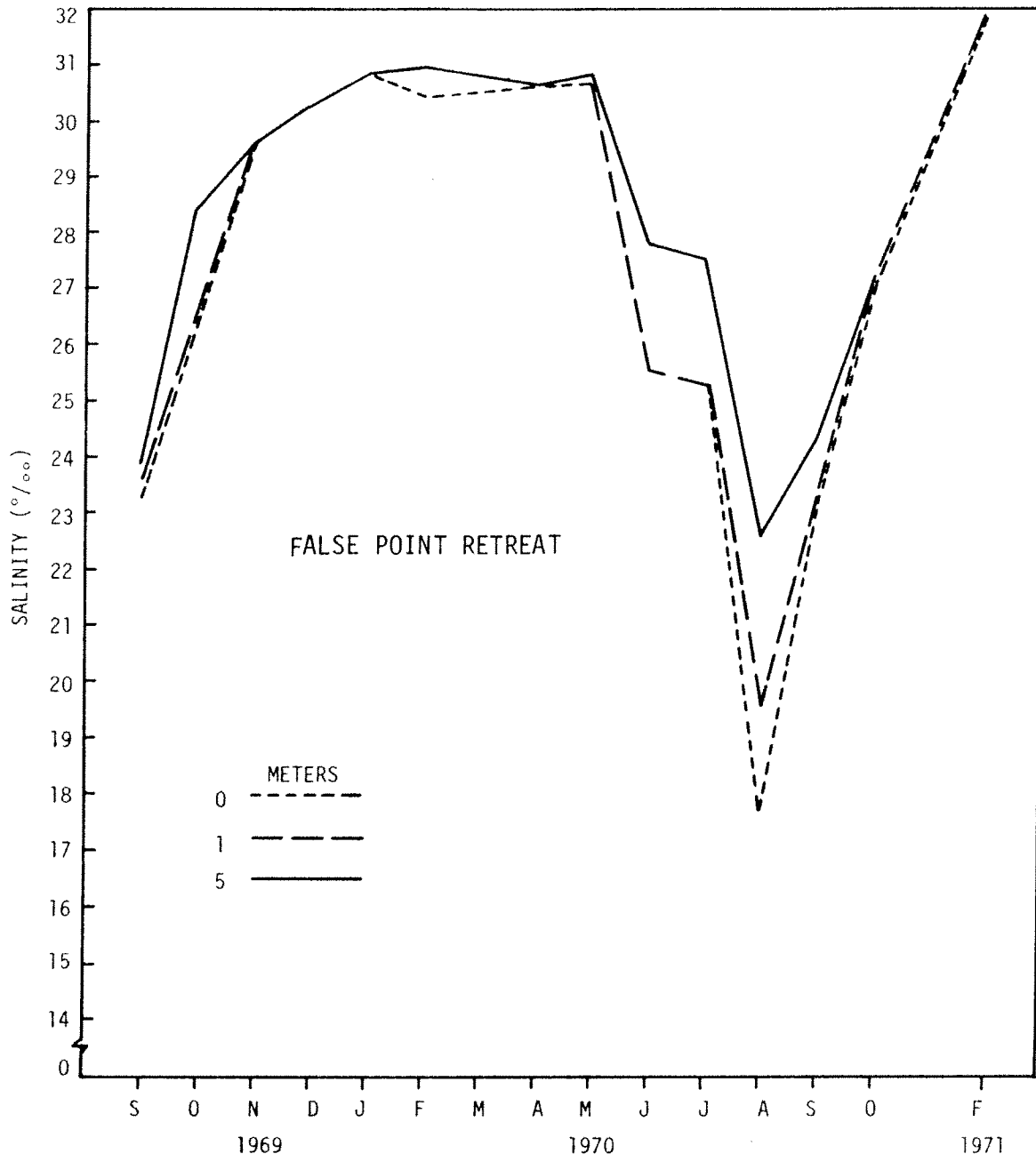
Fig. 22.--Continued
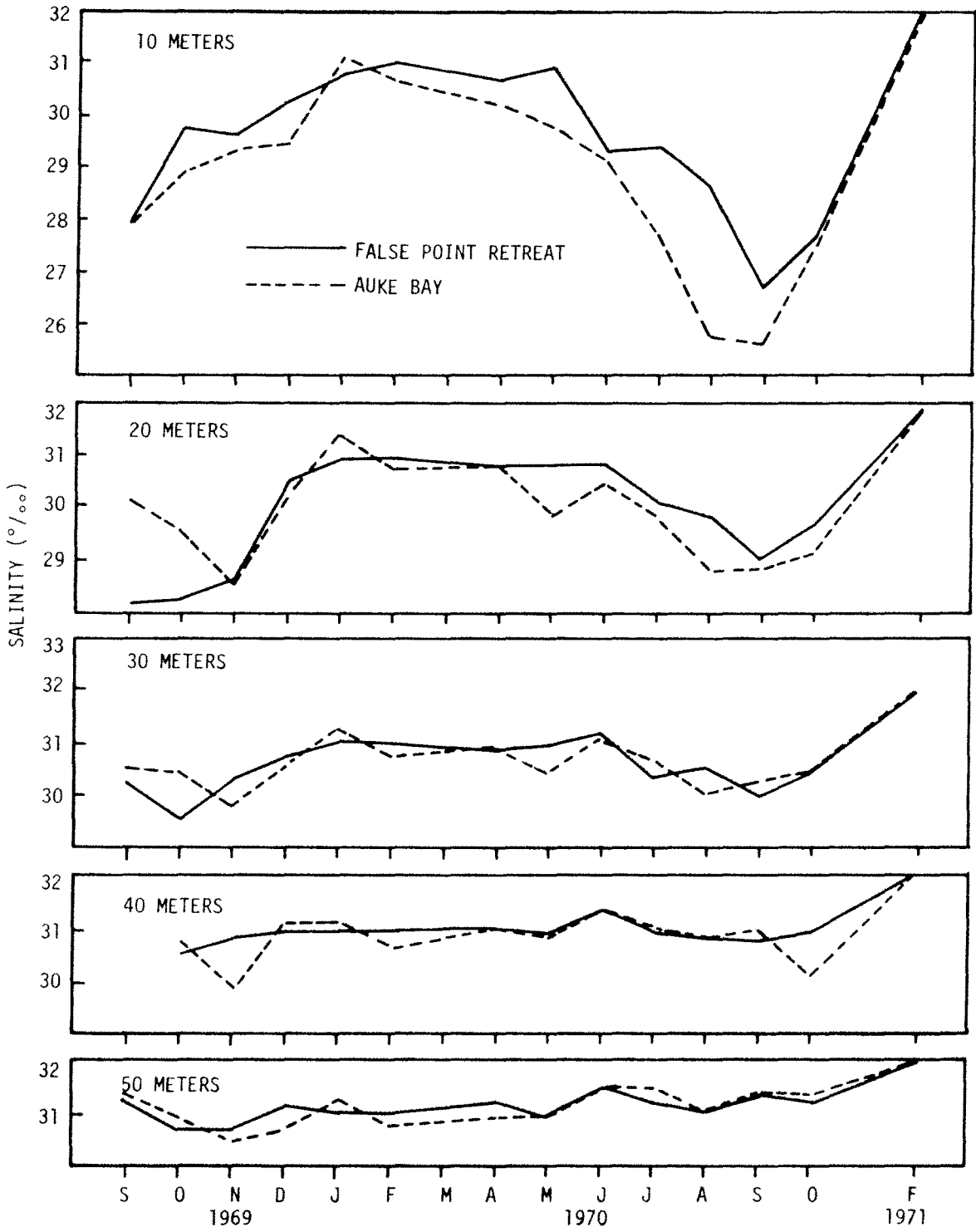
Fig. 22.--Continued

and salinities, the two areas have similar densities, which in itself could be expected to increase the probability of exchange. If Lynn Canal water enters Auke Bay, possibly it comes in below the pycnocline and is then modified by local mixing with Auke Bay surface water. The potential for exchange of Auke Bay and Lynn Canal water appears to be greatest in the winter, when frequent north winds could drive Lynn Canal water south through Favorite and Saginaw channels--past Auke Bay as well as False Point Retreat.

Nutrient cycles at False Point Retreat and in Auke Bay differed, in that the cycle appeared more regular at False Point Retreat (Figures 23, 24, and 25). Concentrations of nutrients were slightly higher in the spring and fall, and slightly lower in the midsummer at False Point Retreat than in Auke Bay. These small differences could be due to differences in the timing of phytoplankton blooms. Chlorophyll a concentrations were not as stratified at False Point Retreat as in Auke Bay, but the mean concentrations of chlorophyll a at False Point Retreat were higher from March through September than in Auke Bay (Figure 26). In 1969, a strong fall phytoplankton bloom occurred in Auke Bay but not at False Point Retreat. Peak productivity appeared to occur later at False Point Retreat in the summer of 1970 than in Auke Bay, possibly because of later stratification in the upper water column.
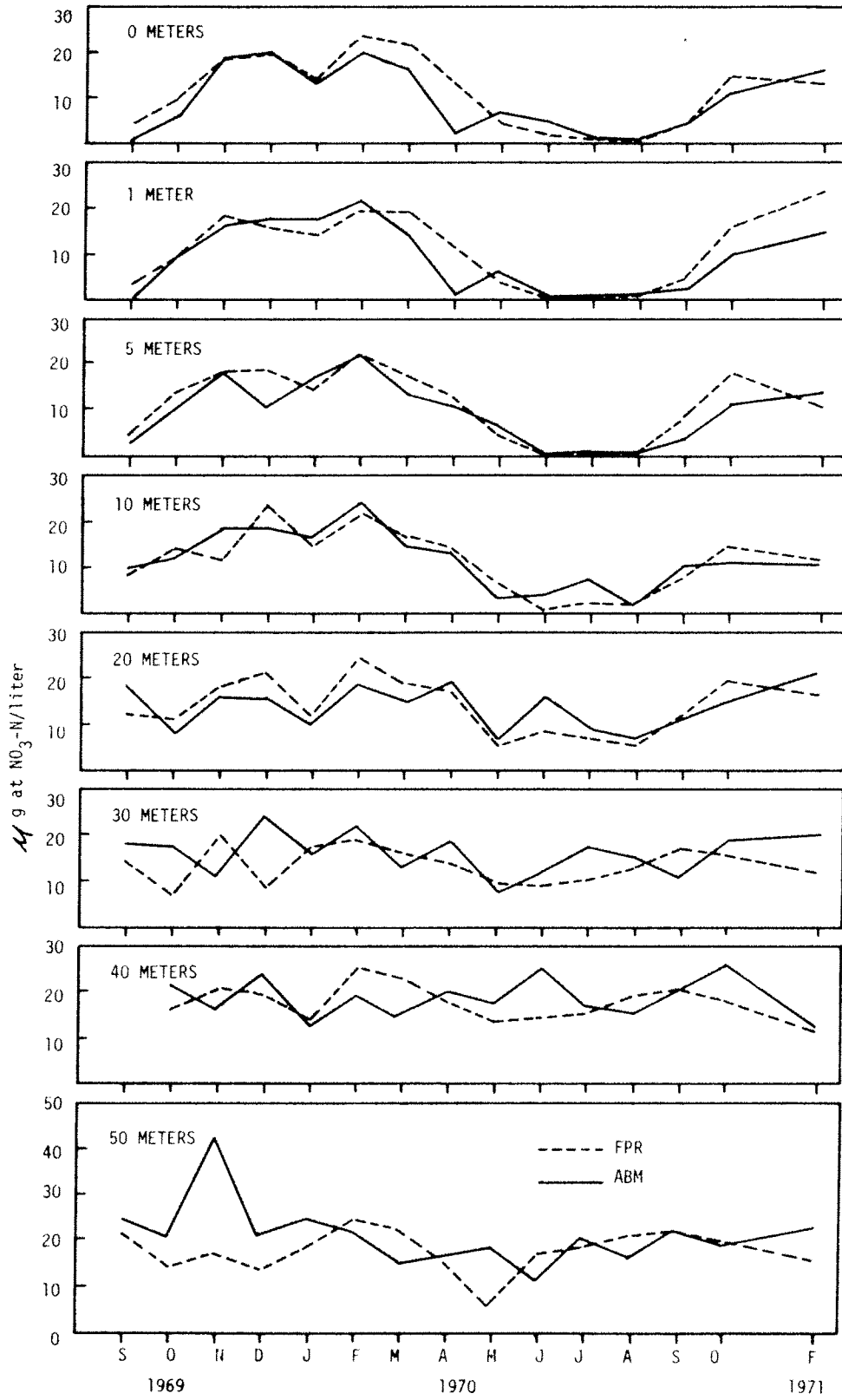
Fig. 23.--Seasonal cycle of nitrates at selected depths in Auke Bay and at False Point Retreat, Alaska, September 1969 to February 1971.
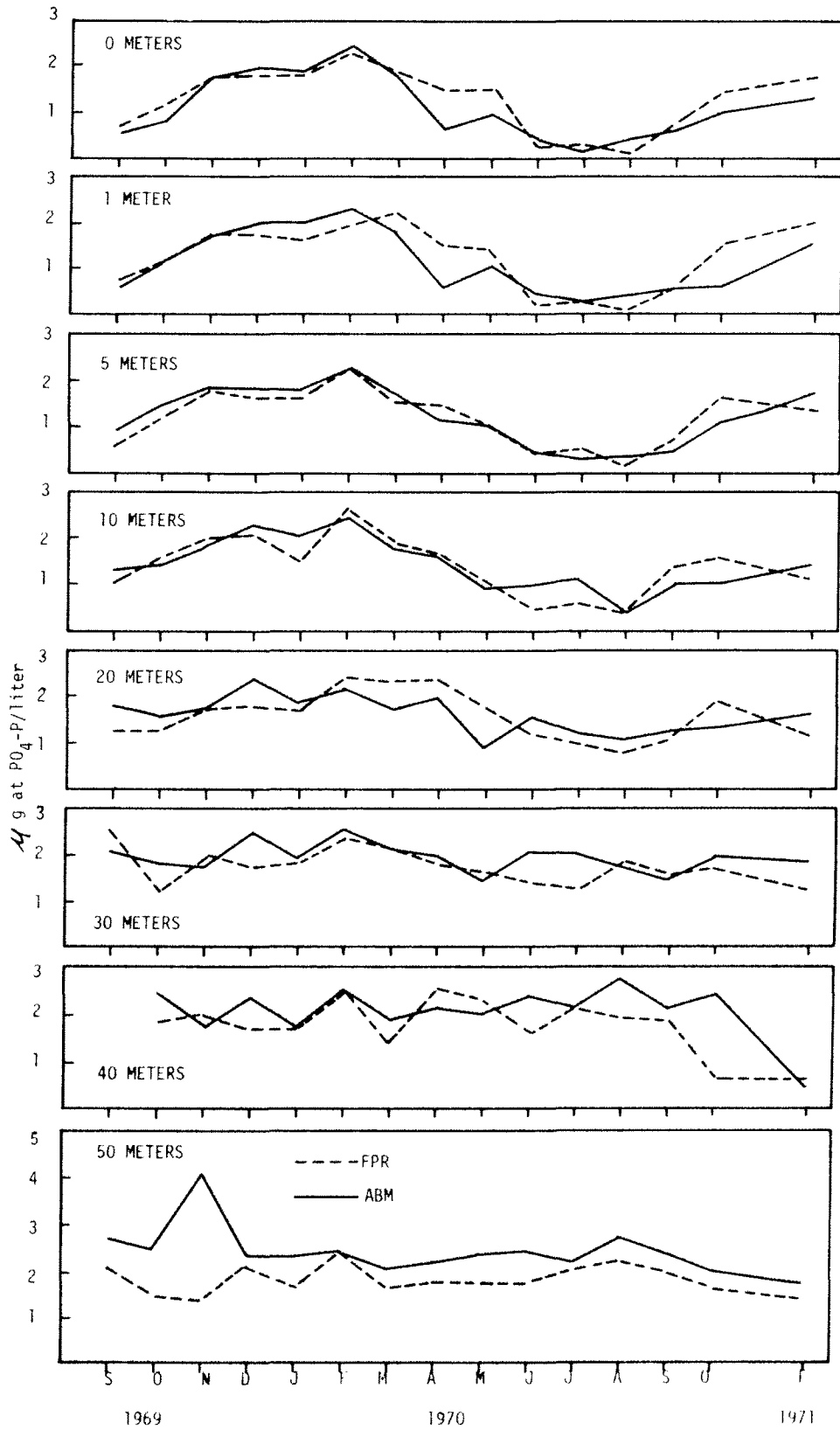
Fig. 24.--Seasonal cycle of phosphates at selected depths in Auke Bay and at False Point Retreat, Alaska, September 1969 to February 1971

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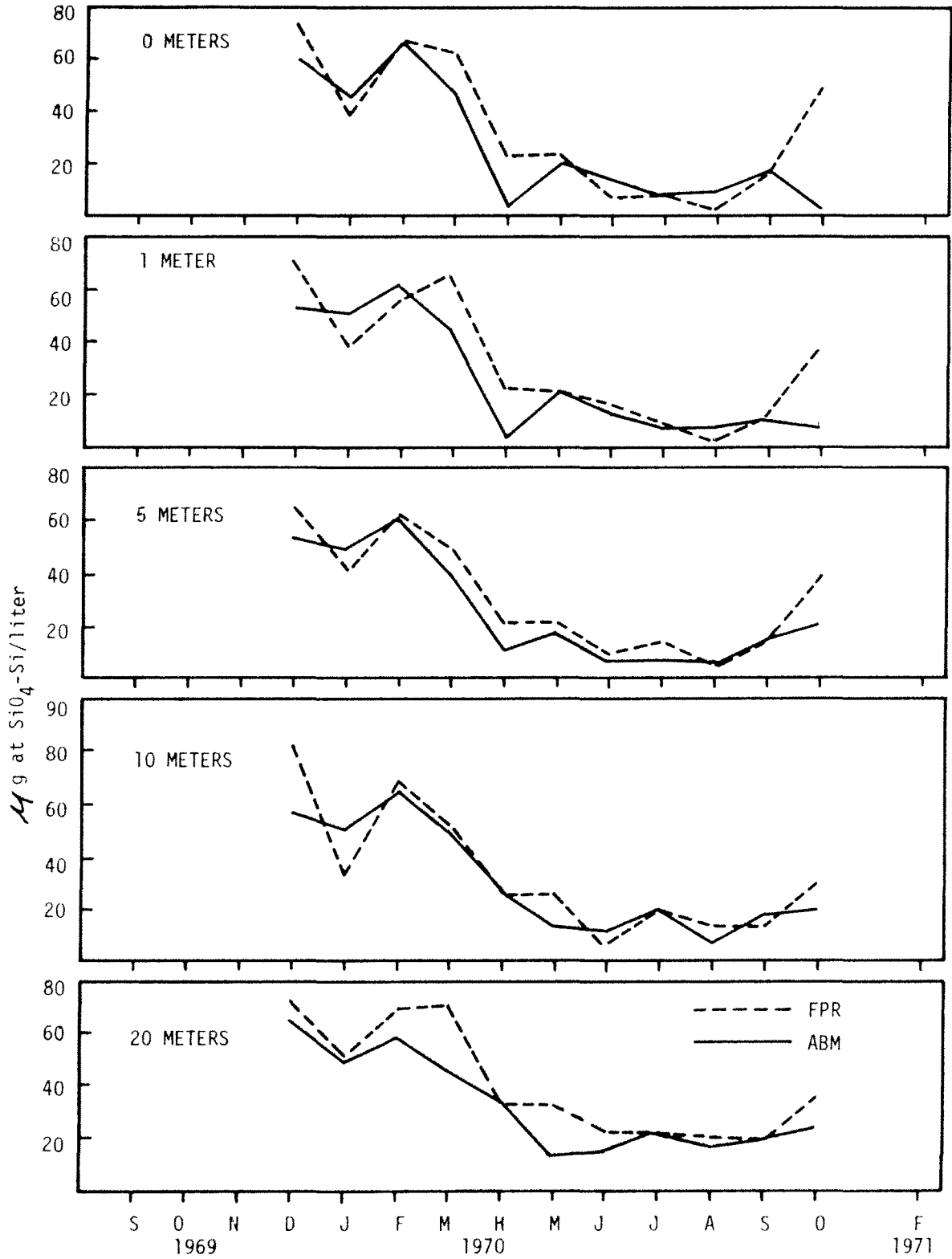
Fig. 25.--Seasonal cycle of silicates at selected depths in Auke Bay and at False Point Retreat, Alaska, December 1969 to October 1970
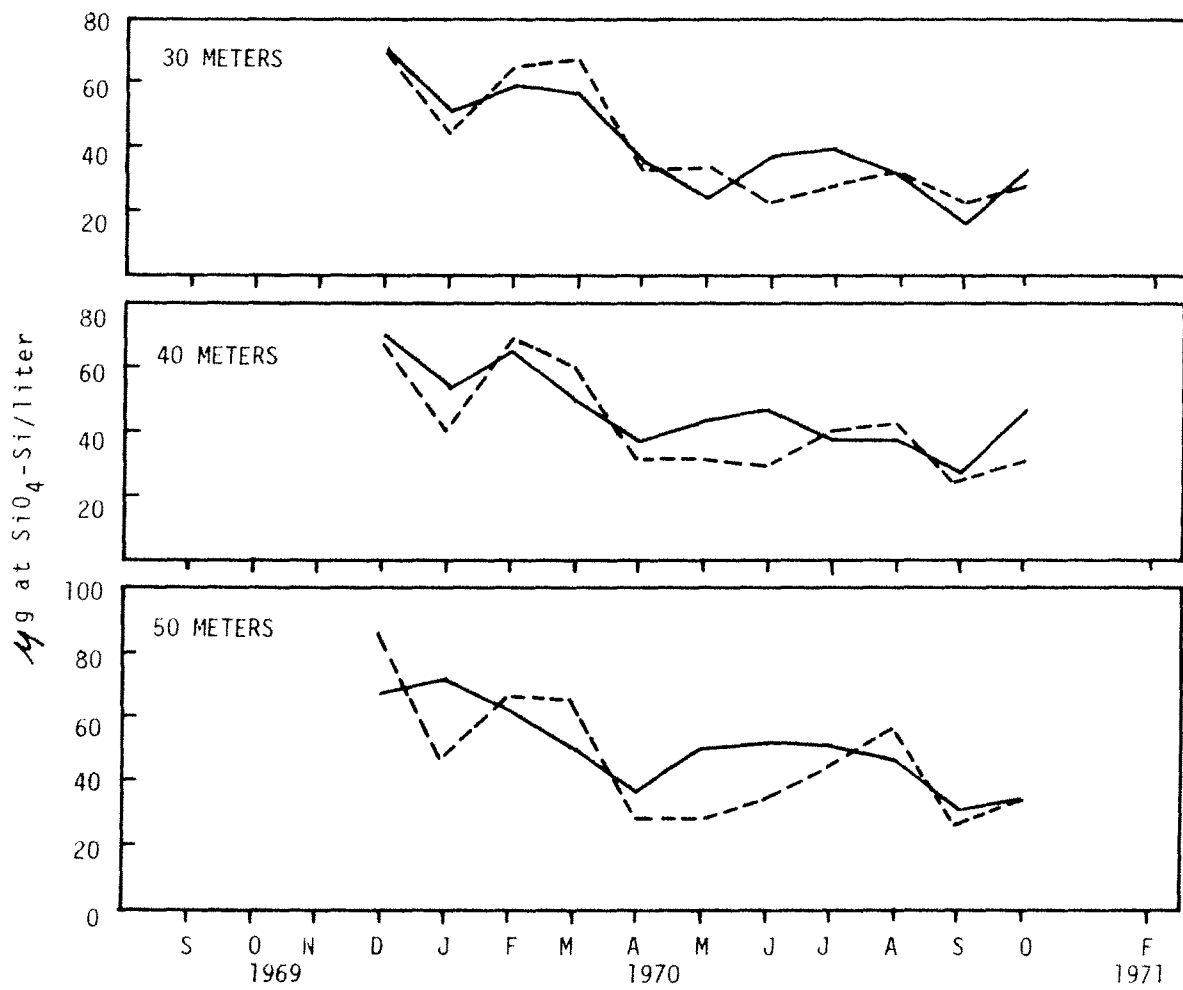
Fig. 25.--Continued
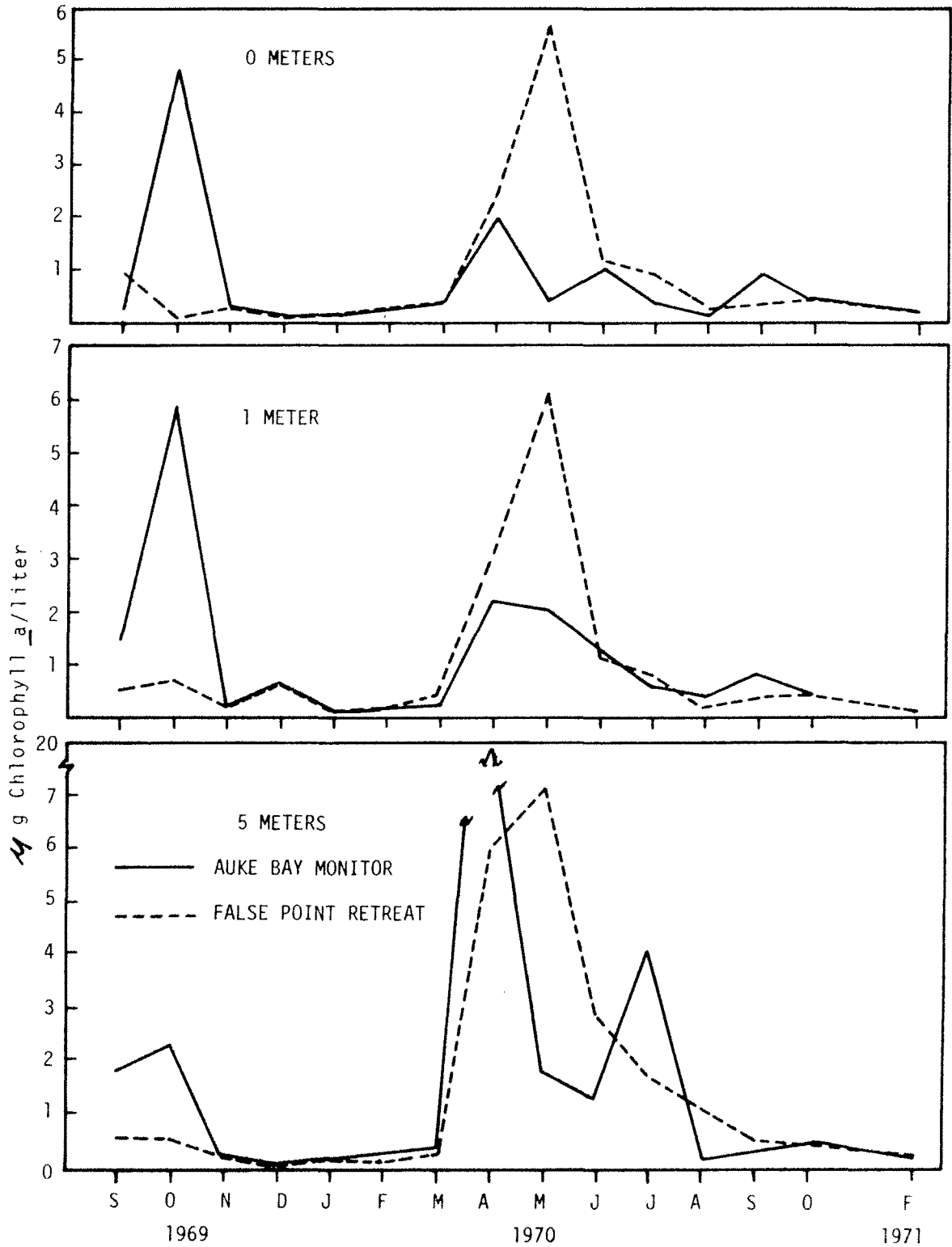
Fig. 26.--Seasonal cycle of chlorophyll a at selected depths in Auke Bay and at False Point Retreat, Alaska, September 1969 to February 1971.
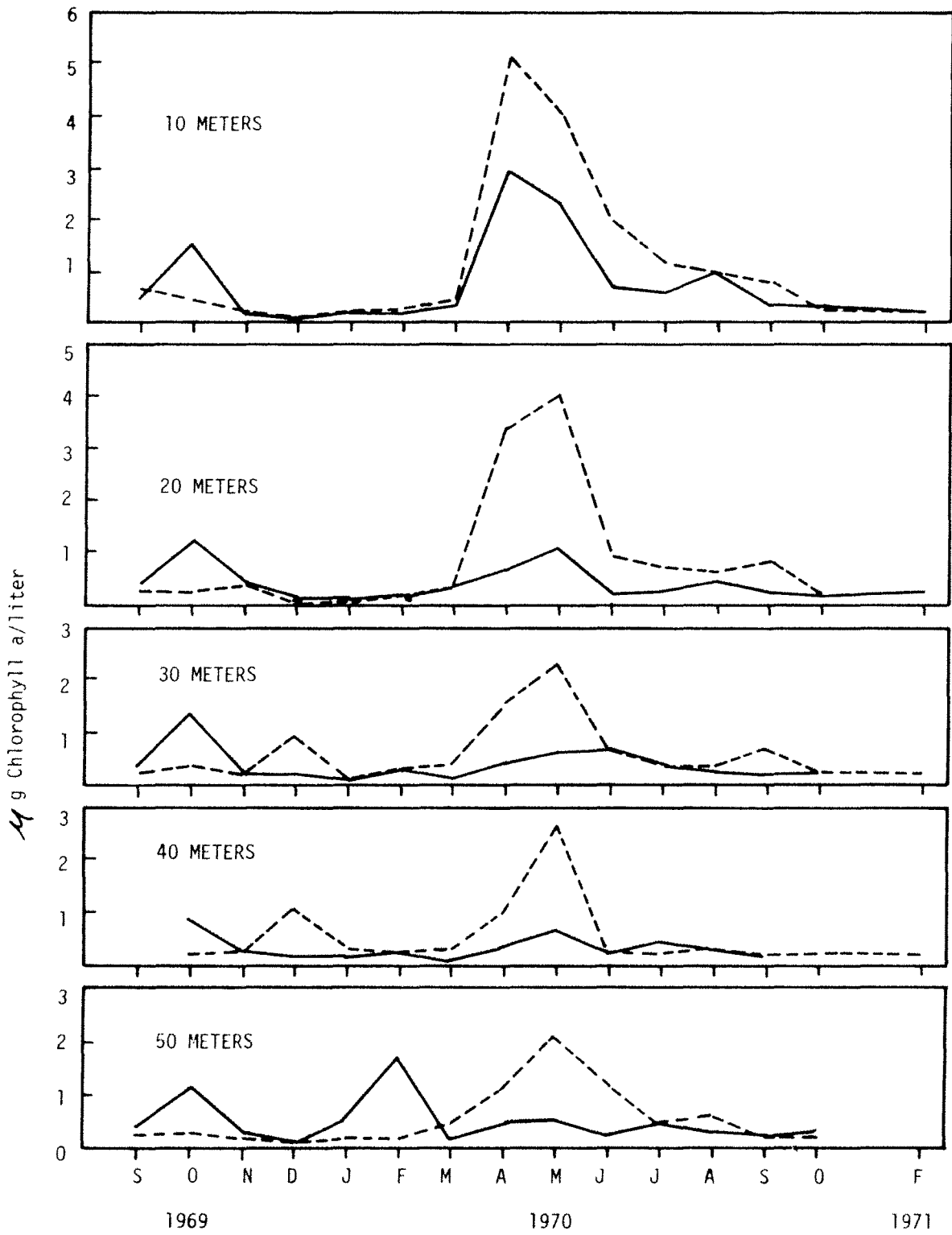
Fig. 26.--Continued

V. RESULTS OF FIELD SAMPLING PROGRAM

Seasonal Depth Distribution of Parathemisto
At False Point Retreat

Depth Distribution of Parathemisto pacifica

The number of Parathemisto pacifica collected each month and in each

sample are presented in Table 7. Parathemisto pacifica was generally

more abundant at the False Point Retreat Station than at the Auke Bay

Monitor station. Although frequently absent from the surface layers, it

was always encountered at depths of 100-200 m during the day. On all

15-day cruises, and on eight of the nine night cruises, catches of P.

pacifica in samples drawn from depths greater than 200 m did not differ

significantly from samples drawn from 200 m. Catches in samples

from below 200 m were statistically greater than in samples from

less than 200 m only on the night cruise of February 1970

(T_d=0.5208, $T_{.95}$=0.4060, pseudo-t test for difference of means

(Ostle, 1963)). Considering all data, it appears reasonable to

conclude that P. pacifica normally resides at depths less than 200 m.

During the day, Parathemisto pacifica were not uniformly distributed

in the upper 200 m. From September to April, adult and subadults were

more numerous between 100 and 200 m than between 0 and 100 m. Juveniles

apparently did not live as deep as adults and subadults, and dominated

the shallow portion of the population. Frequently the smallest

individuals were those taken in the shallowest samples. In May, almost

all of the population was small juveniles; about a fourth of the population

was within 15 m of the surface; and half of the population was between 50 and

100 m. During June and July, juveniles made up the major portion of the

population, and appeared to be concentrated between the seasonal thermocline

TABLE 7.--Daytime and nighttime depth distribution of Parathemisto pacifica in samples collected monthly at False Point Retreat, September 1969 to February 1971 (Numbers are the total counts for the sample; p = presence indicated by catches in surface phytoplankton samples)

Sample depth (m)[a]	1969						1970								1971
	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	March	April	May	June	July	Aug.	Sept.	Oct.	Feb.
Daytime samples															
T-0	16	3	45	0	0	p	0	0	8	0	0	1	1	p	0
50-0	23	4	0	0	0	0	0	0	19	24	56	22	4	0	0
100-0	40	17	3	8	0	0	0	1	31	11	61	71	25	0	0
200-0	50	132	37	13	19	12	9	5	32	40	32	44	51	44	5
300-0	..	..	..	13	19	10	9	3	27	25	32	25	38	86	5
400-0	..	..	40	15	22	6	10	4	36	25	16	59	53	45	7
500-0	..	..	..	10	8	10	4	5	14	29	38	53	46	52	6
600-0	47	104	32	21	18	7	4	2	85	34	37	63	45	37	4
Nighttime samples (2-4 hours after sunset)															
T-0	..	..	2	..	0	5	0	3	..	6	76	16	..	2	..
50-0	..	..	1	..	5	4	2	1	..	14	120	40	..	23	..
100-0	..	..	20	..	8	2	11	1	..	23	52	38	..	28	..
200-0	..	..	25	..	16	4	6.5[b]	1	..	10	78	61	..	39	..
300-0	..	..	..	..	20	10	9	0	..	26	41	31	..	44	..
400-0	..	..	38	..	9	9	5	10	..	8	32	20	..	35	..
500-0	..	..	..	..	17	15	5	5	..	10	17	20	..	24	..
600-0	..	..	23	..	13	6	7	4	..	11	15	20	..	12	..

[a]Depth of sample is depth from which vertical tow with 1/2-m NORPAC net started. T = bottom of surface thermocline or 15 m when thermocline was absent. All tows were from starting depth to surface.

[b]Mean of two samples, one with 8 and one with 5 P. pacifica.

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and 50 m in the daytime. Although juveniles still predominated in August, the population appeared to be concentrated between 50 and 100 m, and by September, the daytime concentration had returned to the 100-200 m depths. Daytime depth may be dependent upon both the age of the individual amphipod and on hydrographic conditions.

At night, Parathemisto pacifica were always encountered in the upper 50 m, and on two of the nine night cruises they appeared to be absent from the upper 15 m; they appeared to be absent from the upper 15 m during 7 of the 15-day cruises. The lower limits of the nighttime distribution were not as clearly evident as the lower daytime limits, suggesting that either not all P. pacifica migrate equally or that not all P. pacifica migrate each day. Assuming that the midpoint of a sample interval represented the population's depth level, estimates of diel excursions ranged from 25 m for June to 150 m for February and April. Apparently, the youngest juveniles, which make up most of the June to August population, migrate over less distance than the subadults and adults which make up most of the winter populations. The upper limit of night distribution does not appear dependent on the presence or absence of the seasonal pycnocline, although there is a tendency for most of the population to remain below the pycnocline during the summer. During the winter, the depth of P. pacifica concentration was more variable than in summer.

Moonlight and cloud cover have been reported to influence the depth distribution of oceanic fish and zooplankton (Raymont, 1963 Woodhead, 1966). During seven of the nine night cruises, cloud cover was 7-8 octa; 4 octa and 1 octa cloud cover occurred during the April and February 1970 cruises. On two relatively clear nights, Parathemisto pacifica were as abundant or more abundant in the shallow samples than in the deep samples.

Cloud cover and intensity of sunlight do not seem to be related to the daytime depth of Parathemisto pacifica. Parathemisto pacifica, like P. libellula, sometimes shows strong phototropism. On one occasion, in 1965, over 90,000 P. pacifica were captured at a depth of 70 m with an experimental trap using light as an attractor. On calm sunny days, P. pacifica frequently is seen swimming and often entrapped at the water surface. Incident sunlight was measured at the water surface with a submarine photometer on 13 of the 15-day cruises. Ranking the cruises by brightness of day and by catch of P. pacifica in the shallow or first sample did not give a significant correlation. Surface catches of P. pacifica were recorded on the 3 dullest days and the 3 brightest days and accounted for six of the eight cruises on which P. pacifica were either collected or observed at the surface.

Depth Distribution of Parathemisto libellula

Table 8 presents the numbers of Parathemisto libellula taken each month at the False Point Retreat Station. Although abundance varies greatly, P. libellula was present at all times, with peak abundance in the late spring and early summer and minimum numbers in late winter and early spring. Except for May through July, the daytime depth of P. libellula was below 100 m, generally between 200 and 300 m. The May population was predominantly small juveniles. Probably all these juveniles were above 100 m in the day, most were above 50 m and a third of the population was above 15 m. The depth distribution in May was very similar to that of P. pacifica, but by June the P. libellula appeared to have reached a size and stage where all but a very small portion of the population were at a depth of between 100 and 200 m during the day. By September,

TABLE 8. --Daytime and nighttime depth distribution of Parathemisto libellula in samples collected monthly at False Point Retreat, September 1969 to February 1971 (Numbers are the total counts for the sample; p = presence indicated by catches in 2-m Isaacs-Kidd midwater trawl samples)

Sample depth (m)[a]	1969				1970										1971
	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	March	April	May	June	July	Aug.	Sept.	Oct.	Feb.
Daytime samples															
T-0	0	0	0	0	0	0	0	0	5	0	0	0	0	0	0
50-0	0	0	0	0	0	0	0	0	7	0	2	0	0	0	0
100-0	0	0	0	0	0	0	0	0	13	0	1	0	0	0	0
200-0	0	0	1	0	0	0	0	0	15	22	35	6	8	0	0
300-0	..	..	..	2	2	1	2	0	12	21	24	12	7	6	2
400-0	..	..	0	0	0	1	0	0	18	23	14	11	13	0	4
500-0	..	..	..	0	1	4	2	0	8	20	16	12	19	7	1
600-0	4	3	18	2	0	6	3	0	42	19	26	4	10	2	3
Nighttime samples (2-4 hours after sunset															
T-0	..	..	0	..	0	0	0	0	..	p	2	0	..	1	..
50-0	..	..	0	..	2	p	1	p	..	20	1	0	..	5	..
100-0	..	..	1	..	3	1	3	1	..	31	11	7	..	9	..
200-0	..	..	0	..	2	4	1	1	..	15	5	10	..	9	..
300-0	..	..	..	..	1	4	2	0	..	20	11	40	..	12	..
400-0	..	..	27	..	2	6	6	1	..	21	8	6	..	12	..
500-0	..	..	..	..	3	5	2	0	..	17	11	7	..	5	..
600-0	..	..	0	..	0	5	1	0	..	17	22	15	..	6	..

[a]Depth of sample is depth from which vertical tow with 1/2-m NORPAC net started. T = bottom of surface thermocline or 15 m when thermocline was absent. All tows were from starting depth to surface.

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daytime residence was between 200 and 300 m, where it apparently remained for the rest of the year.

Night distribution of Parathemisto libellula was examined on nine cruises. With the possible exception of November 1969, P. libellula had moved into the upper 100 m on each occasion. A significant portion of the population was found between the surface and 50 m. Although previous unpublished data from a 1964-65 Isaacs-Kidd midwater trawling program in Lynn Canal consistently recorded P. libellula at depths of 20 m and less at night, in only three of my samplings were P. libellula above the depth of the seasonal pycnocline. The difference between depth of the daytime distribution and the depth of most individuals at night indicates an upward movement of 150 and 200 m each night, approximately twice that of P. pacifica.

The deep distribution of Parathemisto libellula during the day in southeastern Alaska is at variance with previous reports that this species seeks surface waters, especially on bright days (Dunbar, 1946). Mean day and night catches were not significantly different once sampling had extended to the depth at which the amphipods were concentrated. This indicates that although the 1/2-m net may not have been effective for estimation of true population densities, there was no evidence for a day-night differential in ability to escape the net, and further that the catches are representative of population densities for given depth intervals.

Neither day nor night distributions appeared influenced by weather, sea state, incident light, or cloud cover conditions. In the False Point Retreat data, daytime depth appeared to be a function of age and/or season. The youngest juveniles occurred at the shallowest depths, and

as they grew during the summer they moved to deeper waters. Maximum daytime depth is possibly associated with the weak thermocline recorded between 200 and 300 m. The data available are inadequate to determine the environmental factors, either alone or in combination that may set maximum depth for Parathemisto libellula. I suspect it is more dependent upon the physiological capabilities of the amphipod to migrate upward and feed successfully at night than to a physically observable feature. This conclusion is based primarily on the observations that none of the physical and chemical features observed at depth are outside or near the extremes of the ranges at which either P. libellula or P. pacifica are normally found.

Statistical Evaluation of Depth Distributions of Parathemisto at False Point Retreat

The discussions of the preceding sections were based on evaluation of the raw data presented in Tables 7 and 8. The small catches, especially of Parathemisto libellula, and the sampling technique of vertical tows without closing nets leave considerable room for doubt. For this reason, the data were evaluated by comparison with a hypothetical model which reflects the trends indicated in the raw data.

Hypothetical models based upon prior knowledge of the data have strengths and weaknesses. Their strengths lie in the facts that they can be made to portray closely suspected patterns and that they may be designed to accept the sampling scheme actually used. This results in easier handling of the data, and the use of relatively easily computed statistical tests. Their major weakness is that an erroneous model has a high probability of being accepted as statistically correct (type II or beta error). The probability of committing a type II error can usually

be lowered by increased numbers of observations (degrees of freedom).
I was not able to obtain replicate samples for each month's data;
therefore, all data were combined to increase the degrees of freedom.

The basic model for the depth distribution of Parathemisto required
the following assumptions:

1. Zero catches from the surface downward represent true absence of
a species until a postive catch is obtained.

2. Zero catches from depths below a positive catch represent random
variation about a low mean, and the species would be represented in
replicate hauls from the same depth.

3. The amphipods have a statistical Poisson distribution. On a
given date, catches exceeding twice the mean or greatly less than one
half the mean may be assumed to be from another population if they fall
outside the 95% confidence interval for the mean, and a χ^2 test indicates
nonrandom sample deviation.

4. Catches may be expected to increase with depth of sampling until
the maximum depth of the population is exceeded. Average catch will not
increase in samples drawn from below the maximum depth of the species.

5. Chi-square test for goodness of fit is adequate to evaluate the
model. A cumulative χ^2 greater than χ^2 p = 0.95 justifies rejection of
the null hypothesis of no deviation from the model. Degrees of freedom
are determined by the number of expected positive catches in the model.

The model and statistical comparison were applied to the Parathemisto
pacifica data drawn from Table 7. Days and nights were evaluated
separately after deletion of exceptional or anomalous catches. The model
was accepted for the day catches (Table 9), but rejected for the night
catches (Table 10). Because the raw data for P. pacifica appeared to have

TABLE 9.--Hypothetical depth distribution of Parathemisto pacifica at False Point Retreat by month in daytime samples. The number of animals expected is based on the positive samples, acceptable deviation from the means of Poisson distribution and Chi square tests for goodness of fit on trial distributions

Sample depth (m)	1969				1970										1971
	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	March	April	May	June	July	Aug.	Sept.	Oct.	Feb.
						Expected catches									
T-0	19.50	3.50	1.00	0.00	0.00	0.33	0.00	0.00	8.00	0.00	0.00	1.00	2.50	0.33	0.00
50-0	19.50	3.50	1.00	0.00	0.00	0.33	0.00	0.00	26.50	27.40	39.00	58.00	2.50	0.33	0.00
100-0	45.60	17.00	1.00	13.33	0.00	0.33	0.00	3.33	26.50	27.40	39.00	58.00	43.00	0.33	0.00
200-0	45.60	118.00	36.33	13.33	17.20	9.00	7.20	3.33	26.50	27.40	39.00	58.00	43.00	44.50	5.40
300-0	..	..	..	13.33	17.20	9.00	7.20	3.33	26.50	27.40	39.00	58.00	43.00	44.50	5.40
400-0	..	..	36.33	13.33	17.20	9.00	7.20	3.33	26.50	27.40	39.00	58.00	43.00	44.50	5.40
500-0	..	..	..	13.33	17.20	9.00	7.20	3.33	26.50	27.40	39.00	58.00	43.00	44.50	5.40
600-0	45.60	118.00	36.33	13.33	17.20	9.00	7.20	3.33	26.50	27.40	39.00	58.00	43.00	44.50	5.40
						Deviation from expected catches									
T-0	3.50	0.50	(a)	0.00	0.00	0.33	0.00	0.00	0.00	0.00	0.00	0.00	1.50	0.33	0.00
50-0	3.50	0.50	1.00	0.00	0.00	0.33	0.00	0.00	7.50	3.40	17.00	(a)	1.50	0.33	0.00
100-0	5.60	0.00	2.00	5.33	0.00	0.33	0.00	2.33	4.50	(a)	(a)	13.00	18.00	0.33	0.00
200-0	4.40	14.00	0.67	0.33	1.80	3.00	1.80	1.67	5.50	(a)	7.00	14.00	7.00	0.50	0.40
300-0	..	..	..	0.33	1.80	1.00	1.80	0.33	0.50	2.40	7.00	(a)	5.00	(a)	0.40
400-0	..	..	3.67	1.67	4.80	3.00	2.80	0.67	9.50	2.40	(a)	1.00	10.00	0.50	1.60
500-0	..	..	..	3.33	9.20	1.00	3.20	2.33	12.50	1.60	1.00	5.00	3.00	7.50	0.60
600-0	1.40	14.00	4.33	7.67	0.80	2.00	3.20	1.33	(a)	6.60	2.00	5.00	2.00	7.50	1.40
x^2	2.41	3.46	5.899	7.60	6.67	3.43	4.83	3.96	13.34	2.53	10.05	7.17	13.68	3.53	0.96

Total x^2 = 89 52; p~0.41

df = 87; df = n - 1; n = (97 expected positive samples less 9 rejected samples)

[a]Sample rejected from analysis because it was judged to be outside the 95% confidence limits for the Poisson mean.

TABLE 10. --Hypothetical depth distribution of <u>Parathemisto pacifica</u> at False Point Retreat by month in nighttime samples. The number of animals expected is based on the positive samples, acceptable deviation from the means of Poisson distributions, and Chi square tests for goodness of fit on trial distributions

| Sample depth (m) | 1969 | 1970 | | | | | | | |
	November	January	February	March	April	June	July	August	October
				Expected catches					
T-0	1.50	0.00	6.89	1.00	2.14	9.83	55.80	30.75	2.00
50-0	1.50	12.50	6.89	1.00	2.14	9.83	55.80	30.75	32.17
100-0	26.50	12.50	6.89	7.25	2.14	9.83	55.80	30.75	32.17
200-0	26.50	12.50	6.89	7.25	2.14	9.83	55.80	30.75	32.17
300-0	..	12.50	6.89	7.25	2.14	9.83	55.80	30.75	32.17
400-0	26.50	12.50	6.89	7.25	2.14	9.83	55.80	30.75	32.17
500-0	..	12.50	6.89	7.25	2.14	9.83	55.80	30.75	32.17
600-0	26.50	12.50	6.89	7.25	2.14	9.83	55.80	30.75	32.17
				Deviation from expected catches					
T-0	0.50	0.00	1.89	1.00	0.86	3.83	20.20	14.75	0.00
50-0	0.50	7.50	2.89	1.00	1.14	4.17	(a)	9.25	9.17
100-0	6.50	4.50	4.89	3.75	1.14	(a)	3.80	7.25	4.17
200-0	1.50	3.50	2.89	0.75	1.14	0.17	22.20	(a)	6.83
300-0	..	7.50	3.11	1.75	2.14	(a)	14.80	0.25	11.83
400-0	11.50	3.50	2.11	2.25	(a)	1.83	23.80	10.75	2.83
500-0	..	5.50	8.11	2.25	2.86	0.17	(a)	10.75	8.17
600-0	3.50	1.50	0.89	0.25	1.86	1.17	(a)	10.75	(a)
X^2	7.470	15.18	18.12*	5.84	9.75	3.89	21.34*	22.84*	11.27

Total X^2 = 115.70; p<0.001

* indicates p<0.05

df = 59; df = n-1; n = (68 expected positive samples less eight rejected samples)

[a] Sample rejected from analysis because it was judged to be outside the 95% confidence limits for the Poisson mean.

a high variance, the data were transformed by the square root of (n + 1) for further evaluation (Table 11). This transformation may have been too extreme, for when tested by Chi square for no difference among depths of sampling, the null hypothesis was accepted. This means that the assumption could be made that all samples came from the surface in spite of the high frequency of zero catches at the surface and down to 100 m in the daytime samples collected during the winter months.

The *Parathemisto pacifica* data were also examined with a nonparametric ranking test. The daytime catches were found to have a high correlation between depth of sample and sample rank when the shallowest sample was assigned rank 1, and the lowest catch assigned assigned rank 1 (Table 12). With the exception of the November, June, and July cruises, catches from below 100 m ranked higher (mean rank 5.7) than catches from above 100 m (mean rank 2.5). Ranks of samples from all levels below 100 m did not differ significantly from a mean of 5.7, justifying the conclusion that on all occasions, the *P. pacifica* were above 200 m during the day, and that most of them were below 100 m. The high number of ties above 100 m precluded statistical evaluation of possible variation or correlation of catch size with depth for the first three samples. On the basis of these ranking tests, the proposed model was accepted for the daytime catch data. The ranking tests for nighttime catches (Table 13) indicated a significant correlation of catch with depth of sampling for all data but not for individual cruises. The correlation appears to be due to a higher frequency of low ranks in the first two sampling intervals. The implication is that most of the *P. pacifica* move upward at night from the day depth, but that the magnitude of the rise is not consistent nor is there any apparent correspondence with the daytime distributions and rankings.

TABLE 11. --Transformed data ($\sqrt{n + 1}$) and X^2 values for deviation from a normal mean for daytime and nighttime distribution of Parathemisto pacifica collected monthly at False Point Retreat, southeastern Alaska, September 1969 to February 1971

Sample depth (m)	1969				1970										1971
	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	March	April	May	June	July	Aug.	Sept.	Oct.	Feb.
Daytime samples															
T-0	4.12	2.00	6.78	1.00	1.00	1.00	1.00	1.00	2.00	1.00	1.00	1.41	1.41	1.00	1.00
50-0	4.99	2.24	1.00	1.00	1.00	1.00	1.00	1.00	4.47	5.00	7.55	4.80	2.24	1.00	1.00
100-0	6.40	2.00	3.00	1.00	1.00	1.00	1.00	2.41	5.66	3.16	7.87	8.49	5.10	1.00	1.00
200-0	7.14	11.53	6.16	3.74	4.47	3.61	3.16	2.45	5.74	6.40	5.74	6.71	7.21	6.71	2.45
300-0	..	..	..	3.74	4.47	3.32	3.16	2.00	5.29	5.10	5.74	5.10	6.24	9.33	2.45
400-0	..	..	6.40	4.00	4.80	2.65	3.32	2.24	6.08	5.10	4.12	7.75	7.35	6.78	2.83
500-0	..	..	..	3.32	3.00	3.32	2.24	2.45	3.87	5.48	6.24	7.35	6.86	7.28	2.65
600-0	6.93	10.25	5.74	4.58	4.36	2.83	2.24	1.73	9.27	5.92	6.16	8.00	6.78	6.16	2.24
Mean	5.92	5.20	4.85	2.80	3.01	2.34	2.14	1.91	5.30	4.64	5.55	6.20	5.40	4.91	1.95
X^2	1.156	18.233*	5.542	5.845	7.113	3.956	3.454	1.382	3.325	4.706	5.956	6.223	6.970	16.626*	2.588
Nighttime samples (2-4 hours after sunset)															
T-0	..	..	1.73	..	1.00	2.45	1.00	2.00	..	2.65	8.77	4.12	..	1.73	..
50-0	..	..	1.41	..	2.45	2.24	1.73	1.41	..	3.87	11.00	6.40	..	4.90	..
100-0	..	..	4.58	..	3.00	1.73	3.32	1.41	..	4.90	7.28	6.24	..	5.39	..
200-0	..	..	5.10	..	4.12	2.24	2.55	1.41	..	3.32	8.89	7.87	..	6.32	..
300-0	..	..	..	..	4.58	3.32	3.16	1.00	..	5.20	6.48	5.66	..	6.71	..
400-0	..	..	6.24	..	3.16	3.16	2.45	3.32	..	3.00	5.74	4.58	..	6.00	..
500-0	..	..	..	..	4.24	4.00	2.45	2.45	..	3.32	4.24	4.58	..	5.00	..
600-0	..	..	4.90	..	3.74	2.65	2.83	2.24	..	3.46	4.00	4.58	..	3.61	..
Mean	..	..	3.99	..	3.29	2.72	2.44	1.90	..	3.72	7.05	5.50	..	4.96	..
X^2	..	..	4.821	..	2.890	1.364	1.653	2.092	..	1.520	5.849	2.081	..	6.163	..

* indicates $p < 0.05$

TABLE 12. --Spearman rank correlation[a] comparison of Parathemisto pacifica catches with depth of sampling for daytime samples from False Point Retreat, southeastern Alaska, September 1969 to February 1971

Sample depth (m)	Rank	1969				1970				
		Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	March	April	June
15-0	1	1	1	8	1.5	2	2	2	1.5	1
50-0	2	2	2	1	1.5	2	2	2	1.5	3
100-0	3	3	3	2	3	2	2	2	3	2
200-0	4	8	8	6	5.5	6.5	8	6.5	7.5	8
300-0	5	5[b]	5[b]	3.5[b]	5.5	6.5	6.5	6.5	5	4.5
400-0	6	5[b]	5[b]	7	7	8	5	8	6	4.5
500-0	7	5[b]	5[b]	3.5[b]	4	4	6.5	4.5	7.5	6
600-0	8	7	7	5	8	5	4	4.5	4	7

Sample depth (m)	Rank	1970				1971	ΣR	$\overline{R}$	ΣT	r_s
		July	Aug.	Sept.	Oct.	Feb.				
15-0	1	1	1	1	2	2	27	1.93	54.5	0.880
50-0	2	7	2	2	2	2	32	2.29	30.5	.932
100-0	3	8	8	3	2	2	42	3.21	57.0	.875
200-0	4	3.5	4	7	5	5.5	89	6.36	89.5	.803
300-0	5	3.5	3	4	8	5.5	27	5.14	28.0	.938
400-0	6	2	6	8	6	8	85.5	6.11	39.25	.913
500-0	7	6	5	6	7	7	77	5.50	52.0	.886
600-0	8	5	7	5	4	4	76.5	5.46	116.25	.745
Total							..	..	439.00	.998

$r_s = 0.998 > P_{0.001}, \; 11 = 0.293$

[a]See Conover (1971, p. 246).

[b]Arbitrarily assigned rank for missing data.

TABLE 13. --Spearman rank correlation[a] comparison of Parathemisto pacifica catches with depth of sampling for nighttime samples from False Point Retreat, southeastern Alaska, November 1969 to October 1970

Sample depth (m)	Rank	1969 Nov.	Jan.	1970 Feb.	March	April	June	July
15-0	1	1	1	5	1	5	1	6
50-0	2	2	2	2	2	3	6	8
100-0	3	3	3	1	8	3	7	5
200-0	4	5	6	4	5	3	3.5	7
300-0	5	6.5[b]	8	7	7	1	8	4
400-0	6	8	4	6	3.5	8	2	3
500-0	7	6.5[b]	7	8	3.5	7	3.5	2
600-0	8	4	5	5	6	6	5	1

Sample depth (m)	Rank	Aug.	Oct.	ΣR	$\bar{R}$	ΣT	r_s
15-0	1	1	1	22.0	2.444	57	0.525
50-0	2	7	3	35.0	3.888	79	0.342
100-0	3	6	5	41.0	4.555	62	0.483
200-0	4	8	7	48.5	5.388	41.25	0.656
300-0	5	5	8	54.5	6.088	54.25	0.548
400-0	6	3	6	43.5	4.833	64.25	0.465
500-0	7	3	4	44.5	4.944	75.75	0.369
600-0	8	6	2	37.0	4.111	161.0	-0.341
Total				..	..	594.5	0.99

$r_s = 0.990 > P_{0.001, 72} = 0.441$

[a]See Conover (1971, p. 246).

[b]Arbitrarily assigned rank for missing data.

In evaluating both the model and how well the model reflects the depth distribution of Parathemisto libellula, four samples were rejected from the data. Retention of the deleted July night sample would not have resulted in rejection of the model. Also, the mean for deep catches from November were taken to be the average of the three positive samples for day and night. The Chi square test for goodness of fit did not reject the model (Tables 14 and 15), indicating that the model accurately reflected the results of the sampling technique. This model indicates that P. libellula spends daylight hours at 200-300 m during most of the year. In May juveniles were released near the surface; by June they were spending daylight hours at 100-200 m; and by September they had reached a stage where they were spending the days at 200-300 m. Although upward migration at night brings the population into the upper 50 m, only a small portion of it was above the seasonal thermocline or above 15 m during the study period. The sampling increments and frequency of sampling were inadequate to determine a reason for the apparent absence of P. libellula from the upper 15 m during the period of study, although previous investigations (Dunbar, 1946, as well as my personal experience) have observed P. libellula at the surface during both day and night collections.

Day-Night Catch Differences and Net Avoidance

Small ring trawls such as the 1/2-m NORPAC standard net are generally considered inadequate to sample quantitatively active zooplankton such as amphipods, especially those the size of Parathemisto libellula. To evaluate the possibility that the amphipods could escape the net more readily in the day than at night, I applied sign tests (Ostle, 1963) to

TABLE 14. --Hypothetical depth distribution of <u>Parathemisto libellula</u> at False Point Retreat by month in daytime samples. The number of animals expected is based on the positive catches, acceptable deviation from the means of Poisson distribution, and Chi square tests for goodness of fit on trial distributions

Sample depth (m)	1969						1970								1971
	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	March	April	May	June	July	Aug.	Sept.	Oct.	Feb.
						Expected catches									
T-0	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	11.14	1.00	0.00	0.00	0.00	0.00	0.00
50-0	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	11.14	2.00	1.00	0.00	0.00	0.00	0.00
100-0	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	11.14	3.00	2.00	1.00	0.00	0.00	0.00
200-0	0.00	0.00	0.50	0.00	0.00	0.00	0.00	0.00	11.14	21.00	20.00	9.00	11.40	0.00	0.00
300-0	..	..	..	1.00	0.75	3.00	1.75	0.25	11.14	21.00	20.00	9.00	11.40	3.75	2.50
400-0	..	..	0.50	1.00	0.75	3.00	1.75	0.25	11.14	21.00	20.00	9.00	11.40	3.75	2.50
500-0	..	..	..	1.00	0.75	3.00	1.75	0.25	11.14	21.00	20.00	9.00	11.40	3.75	2.50
600-0	4.00	3.00	22.50	1.00	0.75	3.00	1.75	0.25	11.14	21.00	20.00	9.00	11.40	3.75	2.50
						Deviations from expected catches									
T-0	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	6.14	1.00	0.00	0.00	0.00	0.00	0.00
50-0	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	4.14	2.00	1.00	0.00	0.00	0.00	0.00
100-0	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.86	3.00	1.00	1.00	0.00	0.00	0.00
200-0	0.00	0.00	0.50	0.00	0.00	0.00	0.00	0.00	3.86	1.00	(a)	3.00	3.40	0.00	0.00
300-0	..	..	..	1.00	1.25	2.00	0.25	0.25	0.86	0.00	4.00	3.00	4.40	2.25	0.50
400-0	..	..	0.50	1.00	0.75	2.00	1.75	0.25	6.86	2.00	6.00	2.00	1.60	3.75	1.50
500-0	..	..	..	1.00	0.25	1.00	0.25	0.25	3.14	1.00	4.00	3.00	7.60	3.25	1.50
600-0	0.00	0.00	4.50	1.00	0.75	3.00	1.25	0.25	(a)	2.00	6.00	5.00	1.40	1.75	0.50
x^2	0.00	0.00	1.90	4.00	3.67	6.00	2.71	1.00	11.64	6.48	6.70	7.22	8.18	8.73	2.00

Total x^2 = 70.23; p~0.72

df = 64; df = n - 1; n = (67 expected positive samples, less 2 rejected samples)

[a] Sample rejected from analysis because it was judged to be outside the 95% confidence limits for the Poisson mean.

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TABLE 15.--Hypothetical depth distribution of <u>Parathemisto libellula</u> at False Point Retreat by month in nighttime samples. The number of animals expected is based on the positive samples, acceptable deviation from the means of Poisson distributions, and Chi square tests for goodness of fit on trial distributions

Sample depth (m)	1969 November	1970							
		January	February	March	April	June	July	August	October
				Expected catches					
T-0	0.00	0.00	0.00	0.00	0.00	1.00	1.00	0.00	1.00
50-0	0.00	1.85	3.57	2.29	0.43	20.14	2.00	0.00	7.38
100-0	0.50	1.85	3.57	2.29	0.43	20.14	9.20	9.00	7.38
200-0	0.50	1.85	3.57	2.29	0.43	20.14	9.20	9.00	7.38
300-0	..	1.85	3.57	2.29	0.43	20.14	9.20	9.00	7.38
400-0	22.50	1.85	3.57	2.29	0.43	20.14	9.20	9.00	7.38
500-0	..	1.85	3.57	2.29	0.43	20.14	9.20	9.00	7.38
600-0	22.50	1.85	3.57	2.29	0.43	20.14	9.20	9.00	7.38
				Deviations from expected catches					
T-0	0.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00
50-0	0.00	0.15	3.57	1.29	0.43	0.14	1.00	0.00	2.38
100-0	0.50	1.15	2.57	0.71	0.57	10.86	1.80	2.00	1.62
200-0	0.50	0.15	0.43	1.29	0.57	5.14	4.20	1.00	1.62
300-0	..	0.85	0.43	0.29	0.43	0.14	1.80	(a)	4.62
400-0	4.50	0.15	2.43	3.71	0.57	0.86	1.20	3.00	4.62
500-0	..	1.15	1.43	0.29	0.43	3.14	1.80	2.00	2.38
600-0	(a)	1.85	1.43	1.29	0.43	3.14	(a)	6.00	1.38
χ^2	1.90	3.71	7.75	7.80	3.99	9.18	4.63	6.00	8.31

Total χ^2 = 53.27; p~0.35

df = 58; df = n-1; n = (62 expected positive samples less 3 rejected samples)

[a]Sample rejected from analysis because it was judged to be outside the 95% confidence limits for the Poisson mean.

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the difference between day and night catches of both P. libellula and
P. pacifica. The sign tests were applied to two hypothetical cases:
(1) no diel migration with the whole population near the surface and
equally susceptible to capture in all samples, and (2) diel migration
with the population concentrated at different depths day and night. The
null hypothesis of no significant differences between day and night
catches was accepted for both cases for both species (Table 16). The lack
of statistically significant differences in day and night catches
indicates that neither species differed in ability to avoid the net with
the time of day. The almost significantly greater catches of P. libellula
at night ($5\% < p < 10\%$) in the first case but not the second case may be
evidence for vertical migration. By combining all the samples from a
cruise, nighttime catches are expected to be higher than daytime catches,
because more of the sampling is within the depth range of the amphipods.
The nearly significant differences found for higher night catches of P.
pacifica ($5\% < p < 10\%$) in tows from above the level of concentration appear
to be a result both of the upward dispersal at night and a more
nearly uniform distribution at night than during the day.

Occurrence of Parathemisto in Auke Bay

Monthly records of Parathemisto libellula and P. pacifica in Auke
Bay were made from August 1969 to October 1970 during the present study.
Additional monthly data for the period of August 1962 to January 1964 have
been published by Wing and Reid (1972). Wing and Reid sampled Auke Bay and
adjacent areas with high speed plankton nets towed at depths of 2.5, 5, 10,
and 20 m. Circumstantial evidence for diurnal migration of both P. libellula
and P. pacifica is higher frequency and slightly higher average catches in

TABLE 16. --Tests for difference (nighttime-daytime) in catches of Parathemisto at False Point Retreat, southeastern Alaska, November 1960 to October 1970. Numerical values are the mean catch per sample

| Month and year | Assuming no diel migration | | | Assuming diel migration | | | | | |
| | | | | Above distribution break | | | Below distribution break | | |
	Day	Night	Sign	Day	Night	Sign	Day	Night	
Parathemisto pacifica									
Nov. 1969	26.17	18.17	-	1.00	19.50	+	36.33	45.60	+
Jan. 1970	10.75	11.00	+	0.00	0.00	0	13.33	12.50	-
Feb. 1970	5.62	6.88	+	0.00	6.89	+	9.00	6.89	-
March 1970	4.50	5.86	+	0.00	1.00	+	7.22	7.25	0
April 1970	2.50	2.14	+	0.00	2.14	+	3.33	2.14	-
June 1970	23.50	13.50	-	0.00	13.50	+	26.89	13.50	-
July 1970	34.00	53.88	+	0.00	53.88	+	38.89	53.88	+
Aug. 1970	42.25	53.88	+	1.00	30.75	+	48.14	30.75	-
Oct. 1970	33.00	25.88	-	0.00	2.00	+	52.80	29.29	-
p(r)			p>0.25			p>0.25			0.05<p<0.10
Parathemisto libellula									
Nov. 1969	3.17	4.67	+	0.20	0.25	+	18.00	13.50	-
Jan. 1970	0.38	1.62	+	0.00	0.00	0	1.00	1.85	+
Feb. 1970	1.50	3.12	+	0.00	0.00	0	0.75	3.57	+
March 1970	0.88	2.00	+	0.00	0.00	0	3.00	2.29	-
April 1970	0.00	0.38	+	0.00	0.00	0	0.25	0.43	+
June 1970	13.22	17.62	+	0.00	0.00	0	21.00	20.14	-
July 1970	14.75	8.88	-	1.00	1.50	+	23.00	11.33	-
Aug. 1970	5.62	10.62	+	0.00	0.00	0	9.00	14.17	+
Oct. 1970	1.25	7.38	+	0.00	1.00	+	3.75	8.29	+
p(r)		0.05<p<0.10				p>0.25			p>0.25

TABLE 17. --Abundance of Parathemisto libellula and P. pacifica in surface 20 m of Auke Bay and adjacent waters, August 1962 to January 1964. Abundance given as number per cubic meter. Data from Wing and Reid (1972)

Sampling dates and species	Auke Bay Day	Auke Bay Night	Fritz Cove Day	Fritz Cove Night	Stephens Passage Day	Stephens Passage Night
7-15 August 1962						
Parathemisto sp. (juv.)	0.56	..	0.77	..	1.00	..
22-23 August 1962						
Parathemisto sp. (juv.)	1.04	..	0.62	..	0.83	..
1-2 November 1962						
P. libellula	0.00	..	0.00	..	0.01	..
P. pacifica	0.03	..	0.02	..	0.01	..
P. pacifica (juv.)	0.01	..	0.02	..	0.02	..
15-18 November 1962						
P. libellula	0.02	0.02	0.03	0.08	0.03	0.13
<P. pacifica	<0.01	<0.01	<0.01	0.02	<0.01	<0.01
<P. pacifica (juv.)	<0.01	<0.01	0.02	0.00	<0.01	<0.01
19-20 December 1962						
P. libellula	<0.01	..	0.01	..	<0.01	..
P. pacifica (juv.)	<0.01	..	0.00	..	<0.01	..
15-19 January 1963						
P. libellula	0.09	0.02	0.00	0.04	0.00	0.03
P. pacifica	0.02	0.00	<0.01	0.00	<0.01	0.04
P. pacifica (juv.)	0.05	0.02	<0.01	0.01	<0.01	<0.01
14-19 February 1963						
P. libellula	0.00	<0.01	0.00	0.13	0.00	0.13
<P. pacifica	<0.01	0.00	0.01	0.00	<0.01	0.00
P. pacifica (juv.)	0.00	0.00	0.00	0.00	<0.01	0.02
13-14 March 1963						
<P. libellula	0.01	..	0.00	..	<0.01	..
P. pacifica	0.00	..	0.00	..	<0.01	..
24-27 April 1963						
P. pacifica	0.00	0.00	0.00	0.00	<0.01	<0.01
Parathemisto sp. (juv.)	0.20	0.09	0.21	0.03	0.21	0.25
23-27 May 1963						
P. libellula	0.00	0.00	0.48	0.00	0.31	0.00
P. pacifica	0.00	<0.01	0.00	0.00	0.00	0.00
Parathemisto sp. (juv.)	1.39	0.76	0.19	1.94	1.32	0.71

TABLE 17.--Continued

Sampling dates and species	Auke Bay		Fritz Cove		Stephens Passage	
	Day	Night	Day	Night	Day	Night
20-26 June 1963						
P. libellula	0.13	0.58	0.00	..	0.34	0.22
P. pacifica	0.10	0.10	0.00	..	0.00	0.07
P. pacifica (juv.)	0.02	0.00	0.15	..	0.17	0.00
15-16 July 1963						
P. pacifica (juv.)	0.21	..	0.06	..	0.10	..
12-13 August 1963						
P. libellula	<0.01	0.42	0.00	0.01	0.00	0.00
P. pacifica	0.00	0.33	0.00	3.60	0.00	0.24
P. pacifica (juv.)	1.90	0.17	1.82	0.19	3.12	1.54
16-17 September 1963						
P. libellula	0.00	0.00	0.00	0.00	0.00	<0.01
P. pacifica	0.00	0.84	0.03	0.42	0.04	0.88
P. pacifica (juv.)	1.32	0.11	0.35	0.36	0.64	0.16
15-16 October 1963						
P. pacifica	0.00	0.09	0.00	0.03	0.00	0.02
P. pacifica (juv.)	0.08	0.00	0.08	0.00	0.06	0.00
13-14 November 1963						
P. libellula	0.04	0.00	0.00	0.01	0.17	0.01
P. pacifica	0.95	0.06	0.15	0.11	0.59	0.16
17 January 1964						
P. libellula	0.00	..	0.00	..	0.03	..
P. pacifica	0.01	..	0.00	..	<0.01	..
P. pacifica (juv.)	0.00	..	0.00	..	0.02	..

the night samples. Table 17 presents average catches of Parathemisto in Auke Bay and adjacent areas drawn from the data of Wing and Reid (1972, Table 4). I have reexamined some of their samples and found that except for the August 1962, April 1963, and May 1963 samples, their unidentified Parathemisto sp. are all juvenile P. pacifica.

Parathemisto pacifica occurred in Auke Bay during all sampling from
1962 to 1964 with the possible exception of March 1963. The presence
at each sampling of juveniles as well as adults and subadults indicates
continuous reproduction throughout the period. Parathemisto libellula
continuously occupied Auke Bay from November 1962 to at least March 1963.
The juvenile Parathemisto in Auke Bay during April and May of 1963 may
have been a mixture of P. libellula and P. pacifica. Parathemisto
libellula were collected in Auke Bay again in June, August, and November
of 1963. Although P. libellula was not collected in July, September, or
October of 1963, it may have remained in Auke Bay at depths below 20 m if
the August and November 1963 catches represented a resident population.

Catches of Parathemisto in the monthly samples from the Auke Bay
Monitor station for August 1969 to February 1971 have been converted to
numbers per cubic meter (Table 18) for comparison with the earlier data.
However, the sampling methods of the two programs were quite different,
which influence the conclusions to be drawn from the comparison. The
major differences in methods were: (1) the 1969-71 study sampled at
only one station, and the 1962-64 study sampled at three stations;
(2) the 1969-71 study used vertical and oblique tows with a 1/2-m NORPAC
net, and the 1962-64 study used horizontal tows with a high speed net;
(3) the 1969-71 study sampled to 50 m, and the 1962-64 study sampled only
to 20 m.

Catches of Parathemisto pacifica in the upper 15-20 m varied over a
comparable range for daytime catches of $0.00-1.15/m^3$ in 1969-71, and
$0.00-1.32/m^3$ in 1962-64. However, P. pacifica were taken only five times
in the surface layer at Auke Bay Monitor in 1969-71 compared with their
consistent occurrence in the earlier sampling. Similarily, P. pacifica

TABLE 18.-- Abundance of Parathemisto libellula and P. pacifica above and below thermocline, Auke Bay, August 1969 to February 1971. Abundance given as number per cubic meter

Sampling dates an species	Above thermocline		Depth of thermo- cline (m)^a	Below thermocline	
	Day	Night		Day	Night
22 August 1969					
P. pacifica	0.00	5.77	15	3.06	0.58
16 September 1969					
P. pacifica	0.00	..	15	3.20	..
15 October 1969					
P. pacifica	1.15	..	20	1.53	..
13 November 1969					
P. pacifica	0.00	0.34	..	0.00	0.00
17 December 1969					
P. pacifica	0.01	0.00	..	0.01	0.00
20 January 1970					
P. pacifica	0.01	0.00	..	0.00	0.15
12 February 1970	0.00	0.00	..	0.00	0.00
20 March 1970	0.00	0.00	..	0.00	0.00
13 April 1970	0.00	0.00	..	0.00	0.00
6 May 1970					
P. pacifica	0.00	..	..	5.24	..
16 June 1970					
P. pacifica	0.00	..	10	5.09	..
P. libellula	0.00	..	..	1.91	..
20 July 1970					
P. pacifica	0.00	2.04	10	0.25	4.20
11 August 1970					
P. pacifica	1.02	0.00	10	3.95	2.42
9 September 1970					
P. pacifica	0.51	..	10	1.66	..
21 October 1970					
P. pacifica	0.00	0.00	15	0.00	0.58
9 February 1971	0.00	..	..	0.00	..

^{a} Tows taken vertically from bottom of thermocline or 15 m if no thermocline was present (November-May).

occurred less frequently in nighttime catches in the surface layer, although they did occur in Auke Bay at night on three occasions when the day samples were negative. Catches made below the thermocline (10-20 m) were more consistent and higher $(0.00-5.24/m^3)$ when P. pacifica were present in Auke Bay. No Parathemisto pacifica were taken in any collections in February, March, or April of 1970, and in February of 1971. Parathemisto libellula were taken in Auke Bay only once on the 1969-71 study but during the 1962-64 study were almost continuously present in Auke Bay.

Because environmental data were not collected during the 1962-64 sampling period, reasons for the differences in presence and abundance of Parathemisto in Auke Bay during that period and in the later sampling of 1969-71 cannot be hypothesized. It appears that the earlier period was definitely more favorable for P. libellula than 1969-71. Parathemisto pacifica seem to have been equally abundant in Auke Bay during the summers of both sampling periods. However, where P. pacifica were present in Auke Bay throughout the winter of 1962-63, they were absent in late winter of 1969-70.

The depth distribution of Parathemisto in Auke Bay is probably related to but not controlled by the depth of the surface layer. The surface layer is characterized by the seasonal pycnocline, and as such, has strong gradients of both salinity and temperature from May through late September. During this period Parathemisto pacifica were more numerous below the pycnocline (as determined by the bottom of the thermocline) during the day; on at least two samplings in the same period, they appeared to move into the surface layer at night. During the fall and winter when no thermocline exists, the depth distribution of

Parathemisto may be more uniform, with a large portion of the population occurring in the upper 15 m and occasionally at the surface in the daytime.

Distribution of Parathemisto in the Southeastern Bering Sea During the Summer of 1969

Three species of Parathemisto: japonica, pacifica, and libellula occur in the Bering Sea (Bowman, 1960; Fukuchi, 1970; Sanger, 1974). Parathemisto japonica occurs in the eastern Bering Sea, probably as a rare expatriate accompanying intrusions of western subarctic water (Sanger, 1974) since its population centers are in the northern Sea of Japan, the Okhotsk Sea and the western Bering Sea (Bowman, 1960). In the summer of 1969, Fukuchi (1970) found P. japonica as far east as about 169°W in the southern Bering Sea. Parathemisto japonica was apparently absent from the same general area in the summer of 1971 (Sanger, 1974).

Parathemisto libellula and P. pacifica occur commonly in the southeastern Bering Sea (Bowman, 1960; Sanger, 1974), but the distribution of the two species is not well documented. In the summer of 1969 (May-September), the Red Salmon Investigations of the Auke Bay Fisheries Laboratory collected zooplankton samples in Bristol Bay and the most southeastern portion of the Bering Sea--all sampling was east of longitude 166°W and south of latitude 58°30'N (Figure 27). Although an attempt was made to cover the same station grid as used in previous investigations of the area, the number of stations occupied, the number of samples taken and the individual areas sampled varied greatly from week to week (Table 19).

The zooplankton samples were taken with 20-cm Bongo array with 0.33-mm mesh nets. All tows were oblique, from bottom, at 1.5 knots for 3-5 minutes. Subsequent examination of flow meter and bathykymograph records indicated

TABLE 19.--Collection data for Parathemisto libellula and P. pacifica from Bristol Bay and southeastern Bering Sea, May to August 1969

Date and station[a]	Depth (m)	Temperature (°C)		Species	Number and life stages
		Surface	Bottom		
19 May					
I8	42	1.20	0.92	P. libellula	1 juvenile
20 May					
E8	80	3.85	2.57	P. pacifica	2 adults
26 May					
B4	112	4.69	3.47	P. pacifica	5 juveniles, adults
C5	105	5.65	3.32	P. pacifica	5 juveniles
29 May					
H8	50	2.80	1.39	P. libellula	2 juveniles
5 June					
E 10	75	5.55	3.28	P. pacifica	1 subadult
18 June					
G 12	65	6.00	3.96	P. pacifica	1 juvenile
19 June					
I14	45	4.15	3.59	P. libellula	1 juvenile
I12	50	3.60	2.84	P. libellula	1 juvenile
J12	10	4.90	4.42	P. libellula	2 juveniles
J10	35	4.80	4.32	P. libellula	4 juveniles
20 June					
E8	80	8.00	2.80	P. pacifica	7 juveniles, subadults
14 July					
J12	42	10.50	5.00	P. libellula	1 juvenile
G 10	47	8.50	4.75	P. libellula	1 juvenile
15 July					
I10	40	9.70	4.97	P. libellula	1 juvenile
G8	60	10.76	3.70	P. libellula	6 juveniles
				P. pacifica	1 adult
E8	71	11.30	2.90	P. pacifica	1 adult
18 July					
BC9.8	28	10.20	6.50	P. pacifica	3 juveniles, adults
D9	65	12.23	3.40	P. pacifica	24 juveniles, adults
19 July					
DE9.10	73	11.39	3.18	P. pacifica	5 juveniles, adults
22 July					
ZA6.15	50	>10	>7	P. pacifica	1 subadult
A6	58	>10	>7	P. pacifica	17 Juveniles, adults
AB6.3	65	>10	>7	P. pacifica	6 juveniles, adults
25 July					
BC9.14	42	>10	>7	P. pacifica	1 juvenile
BC9.17	47	>10	>7	P. pacifica	2 juveniles, adults
2 August					
EF12.12	60	10.70	6.48	P. pacifica	1 adult
8 August					
G8	60	10.80	3.90	P. libellula	3 juveniles
9 August					
I10	30	9.00	7.70	P. libellula	1 juvenile
12 August					
J12	50	10.30	5.30	P. libellula	2 juveniles
26 August					
BC9.11	30	10.20	9.81	P. pacifica	4 juveniles, adults

[a]See McLaughlin, P. A. (1963).
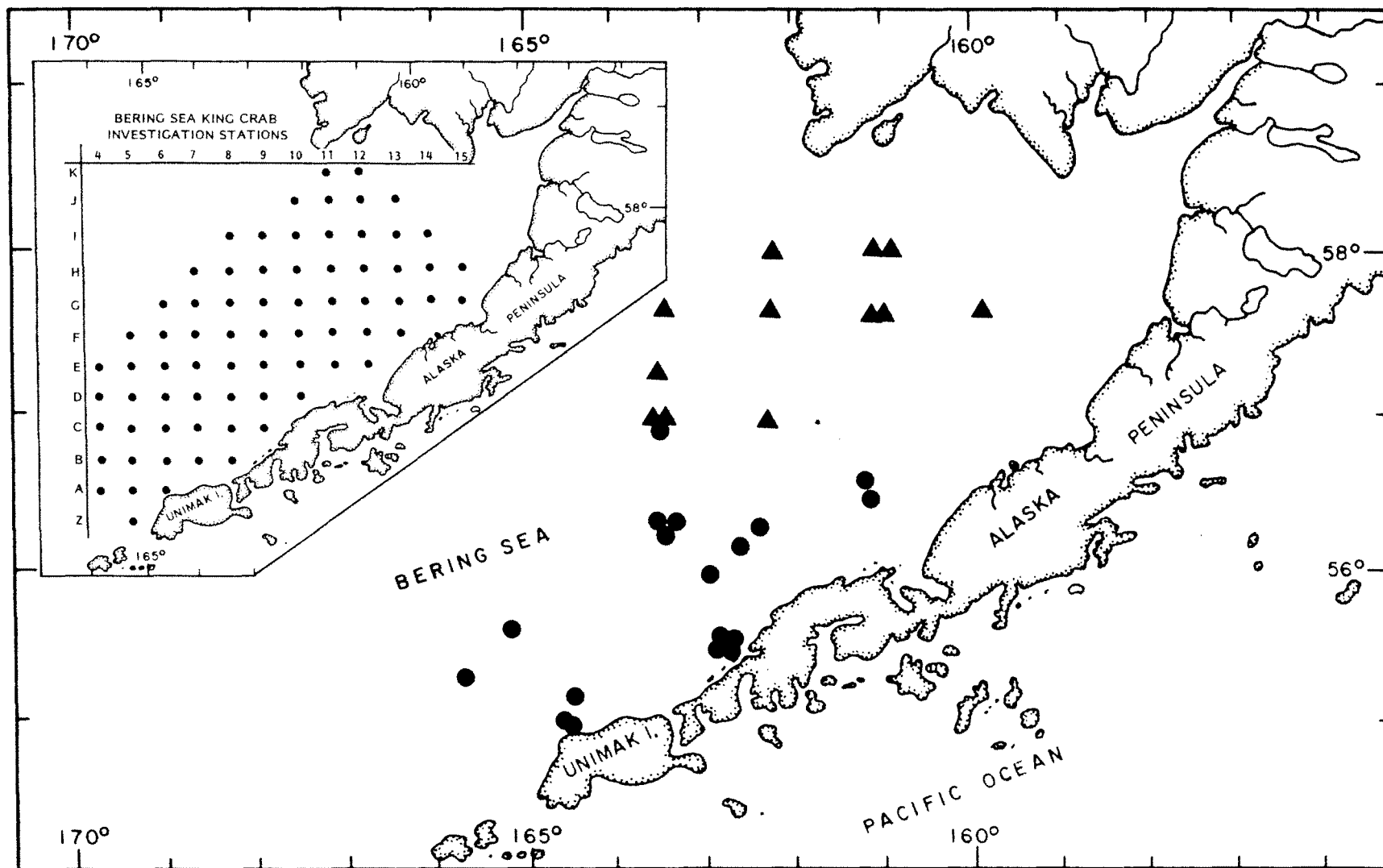
Fig. 27.--Distribution of Parathemisto libellula and P. pacifica in Bristol Bay and the southeastern Bering Sea, May to September 1969 (▲ = P. libellula, ● = P. pacifica).

that the data were not quantitative enough to determine zooplankton numbers or biomass on either a square-meter or cubic-meter basis.

At my request, all amphipods found in the 1969 Bristol Bay zooplankton samples were removed. Of 249 samples taken, 30 contained Parathemisto, with an average of 3.8 per positive sample (range 1-24, total 113 specimens). The distribution of stations at which P. libellula and P. pacifica were collected is given in Figure 27.

Only juvenile P. libellula were taken in the Bristol Bay area in the summer of 1969. Possibly in this portion of the Bering Sea, P. libellula has a 1-year life cycle, with brood release in late April or early May as in southeastern Alaska at approximately the same latitude. The possibility of late summer reproduction and a 2-year life cycle in the northern Bering Sea is indicated by an August 1893 collection of a brooding female from south of Saint Matthew Island (60°N) (Bowman, 1960).

Adults and juveniles of Parathemisto pacifica were found in all sets of positive samples, and gravid females appeared in all except the late June samples. The presence of mature adults and juveniles in all sets of samples indicates continuous reproduction from late May through August and probably later.

The distributions of the two species within Bristol Bay appear to be separate (Figure 27). Only one station (G-8, July 15) from near the center of the area yielded both species (six juvenile Parathemisto libellula and one adult P. pacifica). Parathemisto libellula was found in the northern and central portions of the area, and P. pacifica appeared restricted to a band approximately 110 km wide along the north coast of Unimak Island and the Alaska Penninsula. Water depths through the distributional areas of both species varied from 30-112 m. It would

seem that difference is not associated with water depth.

A comparison of hydrographic conditions at the time of sampling for those stations at which Parathemisto were collected showed that P. pacifica was not taken in May at temperatures below 2.5° C at the bottom or 3.2° C at the surface (Table 19). The maximum surface temperature at which P. pacifica were found in July was 12.2° C in 65 m of water with a bottom temperature of 3.4° C. On the other hand, P. libellula were taken in May in areas with surface temperatures of 1.2° C and bottom temperatures of 0.9° C. Warmest surface temperatures at positive P. libellula stations were 10.8° C in July when 3.7° C water was found along the 60-m bottom. Warmest bottom temperature for a positive P. libellula station was 7.7° C at 30 m in August.

Unfortunately, all the samples were oblique tows from bottom to surface, thus making it impossible to document the depth at which the amphipods were captured or concentrated. It appears that Parathemisto pacifica were restricted to waters which did not cool significantly below 3° C. Very likely the upper thermal limits of P. pacifica were never reached. Parathemisto libellula do not appear to be restricted by the lowest Bering Sea-Bristol Bay temperatures but were limited to waters with a maximum temperature at the bottom near 8° C and surface temperatures near 11° C.

Distribution of Parathemisto in the Southeastern Chukchi Sea in the Fall of 1970

Three species of Parathemisto: abyssorum, libellula, and pacifica, have been reported in the Chukchi Sea (Bowman, 1960; Wing, 1974). Parathemisto abyssorum appears to have a southern limit at about 71°N in the Chukchi Sea, and appears rarely in waters less than 100 m deep (Bowman,

1960). Although they may be found at lesser depths, and potentially could be transported south through the Bering Straits into the Bering Sea and North Pacific Ocean, all records of P. abyssorum in the Pacific appear to be misidentified P. japonica or P. pacifica (Bowman, 1960). Bowman believes that the failure of P. abyssorum to become established in the Pacific is a result of the combined shallowness of the Bering Strait crossing, the predominantly northward transport through the Bering Strait, and an inability to compete successfully with its morphologically similar congeners, P. japonica and P. pacifica (Bowman, 1960).

Although Parathemisto pacifica were not found in the southern Chukchi Sea by Bowman (1960), seven were captured in the fall of 1970 between 69°N and 70°N during the 1970 Western Beaufort Sea Ecological Cruise (Wing, 1974). All were juveniles approximately 4 mm long, and were taken from waters of 2.2-3.5° C by vertical tows with a 1/2-m, 0.505-mm-mesh NORPAC net. One P. libellula, a 15-mm juvenile, was taken in the same manner. In Isaacs-Kidd midwater trawl samples for fish (Quast, 1974; Wing and Barr, in prep.), P. libellula was found in 6 of 20 stations.

The sparsity of data from the WEBSEC-70 samples does not justify comparison of the distributions of Parathemisto libellula and P. pacifica in the Chukchi Sea. The size of the juvenile P. libellula captured indicates that they are from a resident population with a spring brood release. The small size of the P. pacifica juveniles (approximately 4 mm) suggests that they may be the last of a summer brood. Summer temperatures from June through late August vary between 6° and 10° C (Ingham et al. 1972), and are probably adequate for P. pacifica to mature and produce two or more generations before the onset of winter. Water

temperatures throughout the remainder of the year may be inadequate for growth and reproduction. Although P. pacifica may tolerate temperatures as low as -1.6° C or lower for extended periods in the laboratory, they do not normally occur in waters less than 2.5° C. I suspect that the P. pacifica of the Chukchi Sea are an expatriate population carried north from the Bering Sea in the spring that probably dies out each winter. A subsequent WEBSEC cruise in 1971 east of Point Barrow (Figure 1) took no P. pacifica, although P. abyssorum and P. libellula were common (Cobb and McConnell, 1974).

Reproduction and Growth of Parathemisto In Southeastern Alaska

Annual cycles of growth and reproduction for Parathemisto libellula and P. pacifica were examined only in the False Point Retreat collections. The samples from Auke Bay were inadequate. Size-frequency histograms were prepared for each species using 1-mm length increments for P. libellula, and 0.5-mm length increments for P. pacifica.

Reproduction and Growth of Parathemisto libellula

No significant differences were found in the size-frequency distributions of Parathemisto libellula from day or from night collections, whether the amphipods were taken by the Isaacs-Kidd midwater trawl or the 1/2-m net. For this reason, all available samples from each month were treated as a single lot. The 1969-71 False Point Retreat data show a strong annual cycle of growth for P. libellula with a single generation per year (Figure 28). Apparently, sexual maturity occurs in March and in April. The first ovigerous females were captured in March, and the April sample contained both ovigerous and nonovigerous

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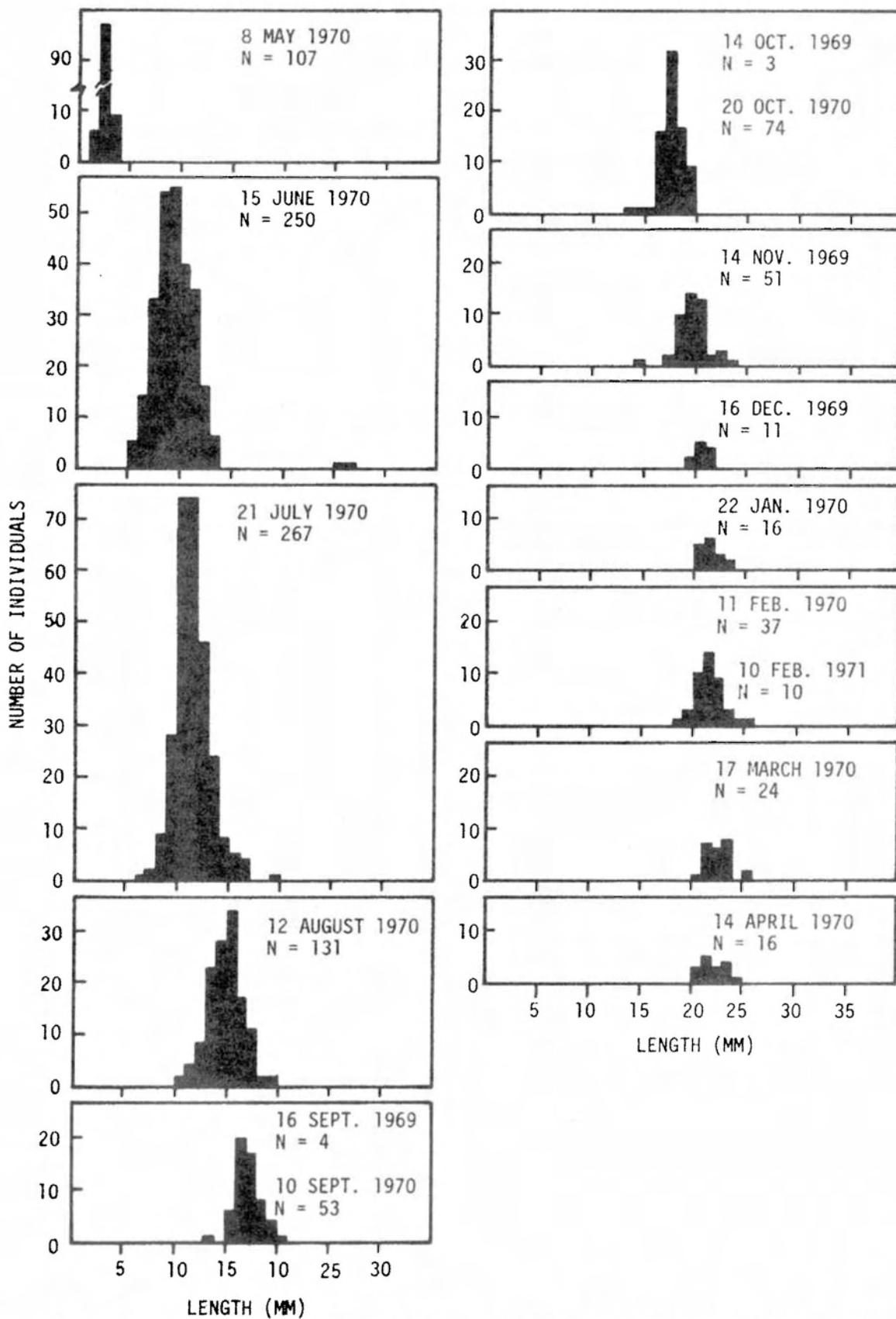
Fig. 28.--Length frequency histograms of Parathemisto libellula from False Point Retreat, Alaska. Numbers are the total in the sample.

adult females. Parathemisto libellula appears to carry the eggs and brood the early juveniles for 3-8 weeks in southeastern Alaska. Possibly, early deposited eggs develop more slowly and at lower temperatures than later deposited eggs. Sampling at the end of the first week of May captured only small juveniles.

Most of the adults died after brood release. The few adults captured after May were not ovigerous and did not produce a second later brood. No mature adults were captured after June. Captive brooding females generally died 2-5 days after brood release in the laboratory in the spring of 1972. The juveniles were 1.8-1.9 mm at brood release.

Juvenile Parathemisto libellula grow very rapidly. Collections at the end of the first week of May 1970 had a mean length of 2.7 mm and a range of 1.8-3.8 mm. By mid-June the mean was 9.2 mm, and the range was 5.0-13.0 mm. The upper and lower size limits may represent differences between early and late brood releases and/or growth rate differences due to individual variation and effects of parasites. Although no obviously parasitized P. libellula juveniles were collected in June, during subsequent months 16 P. libellula parasitized by the ellobiopsid Thalassomyces marsupii were collected. All the parasitized juveniles were in the lower 50th percentile of the month's size distribution, and 13 of the 16 were in the lower 30th percentile.

From mid-June to January, the mean monthly growth increment varied from a high of 3.4 mm to a low of 0.5 mm with an average of 1.7 mm per month. Most of the higher growth rates were in the summer and the lower growth rates in the winter. The small samples collected in the winter do not allow a reasonable estimate of winter growth rate, although observation of molting in the laboratory and a small upward shift in the

modes are evidence of continued growth.

Development of secondary sex characteristics was first noted in mid December when the male antennae began to lengthen in individuals 19-22 mm long. Females first showed signs of maturity at a larger size--they were 21-25 mm long when the oostegites first appeared. The largest mature females in March 1970 were 25 mm. A 29.5-mm female was collected in March 1972. The southeastern Alaska Parathemisto libellula thus mature at a smaller size than individuals in the Arctic populations studied by Dunbar (1942, 1957) and Bowman (1960). The Arctic males matured at about 30 mm and the females at about 35 mm. The Arctic P. libellula attain a maximum size near 60 mm (Bovallius, 1889), and appear to have a 2-year life cycle with some overlap between generations (Dunbar, 1942, 1957), in contrast to the 1-year life cycle in southeastern Alaska. Parathemisto libellula from the southern Bering Sea probably have a 1-year life cycle, while those of the northern Bering Sea and southern Chukchi Sea may be intermediate in character. Most collections of P. libellula from the Bering and Chukchi Seas are of summer juveniles. However, Bowman (1960) reports early August (1893) Bering Sea collections by the USS Albatross in which juveniles, adolescents, and maturing females were present; an ovigerous female 30 mm long was collected in the southern Bering Strait.

Reproduction and Growth of Parathemisto pacifica

Monthly length frequency data for Parathemisto pacifica were obtained in the same manner as for P. libellula except that lengths were estimated to 0.1 mm and then grouped in 0.5-mm increments for preparation of the length frequency histograms (Figure 29). The predominance of small juveniles above 100 m during the day, and above 50 m at night have biased
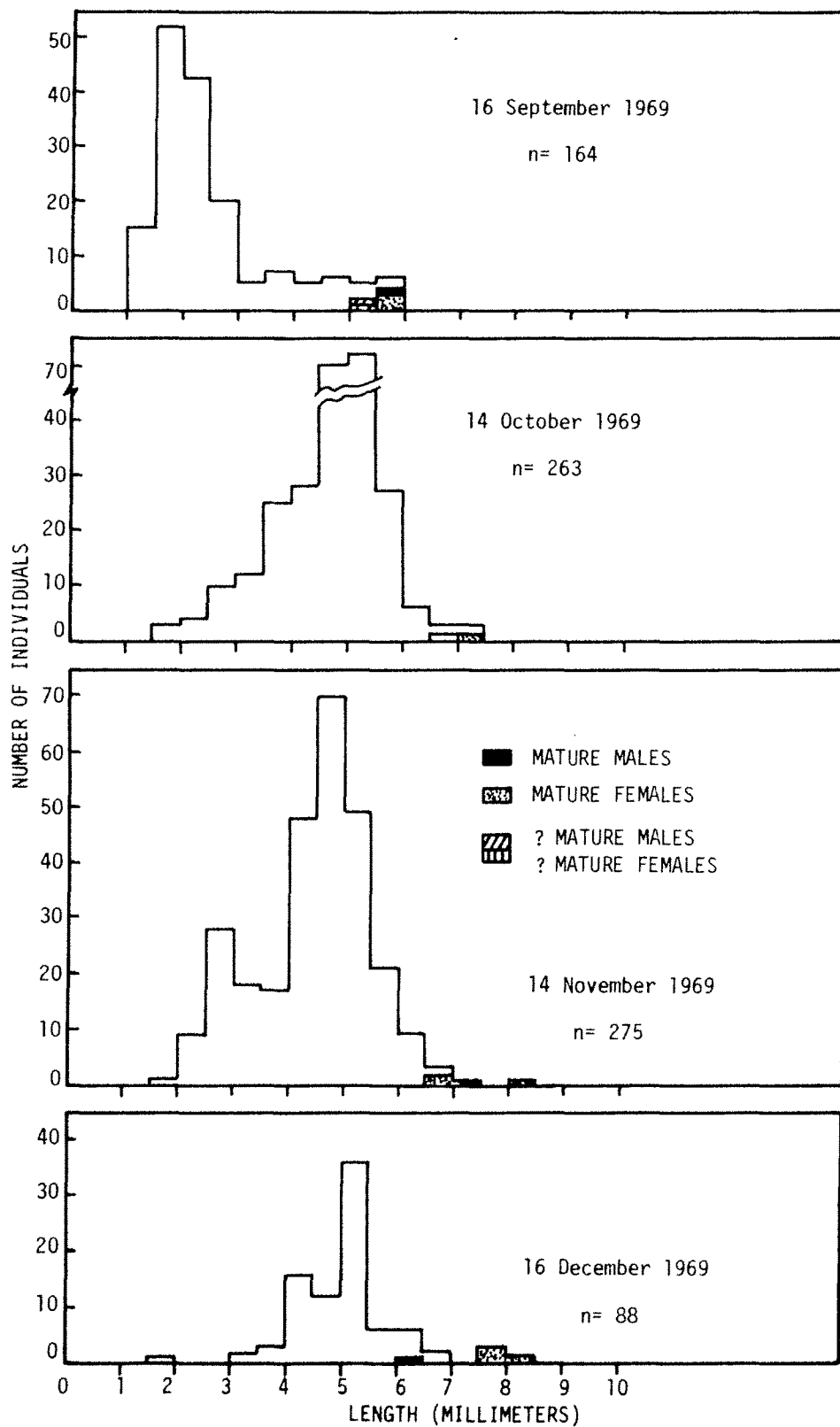
Fig. 29.--Length frequency histograms of Parathemisto pacifica from False Point Retreat, Alaska. Numbers are the total in the sample.
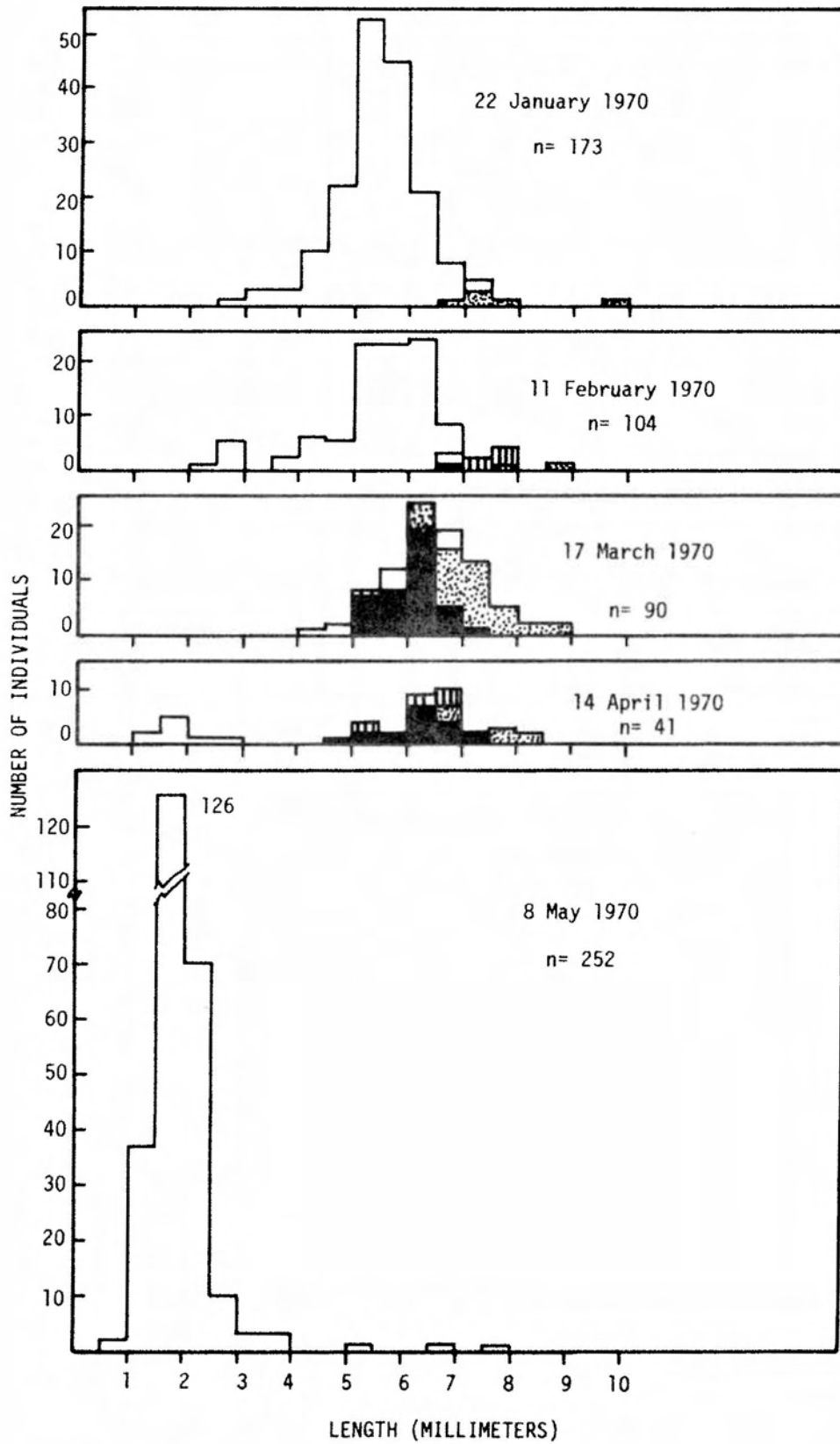
Fig. 29.--Continued
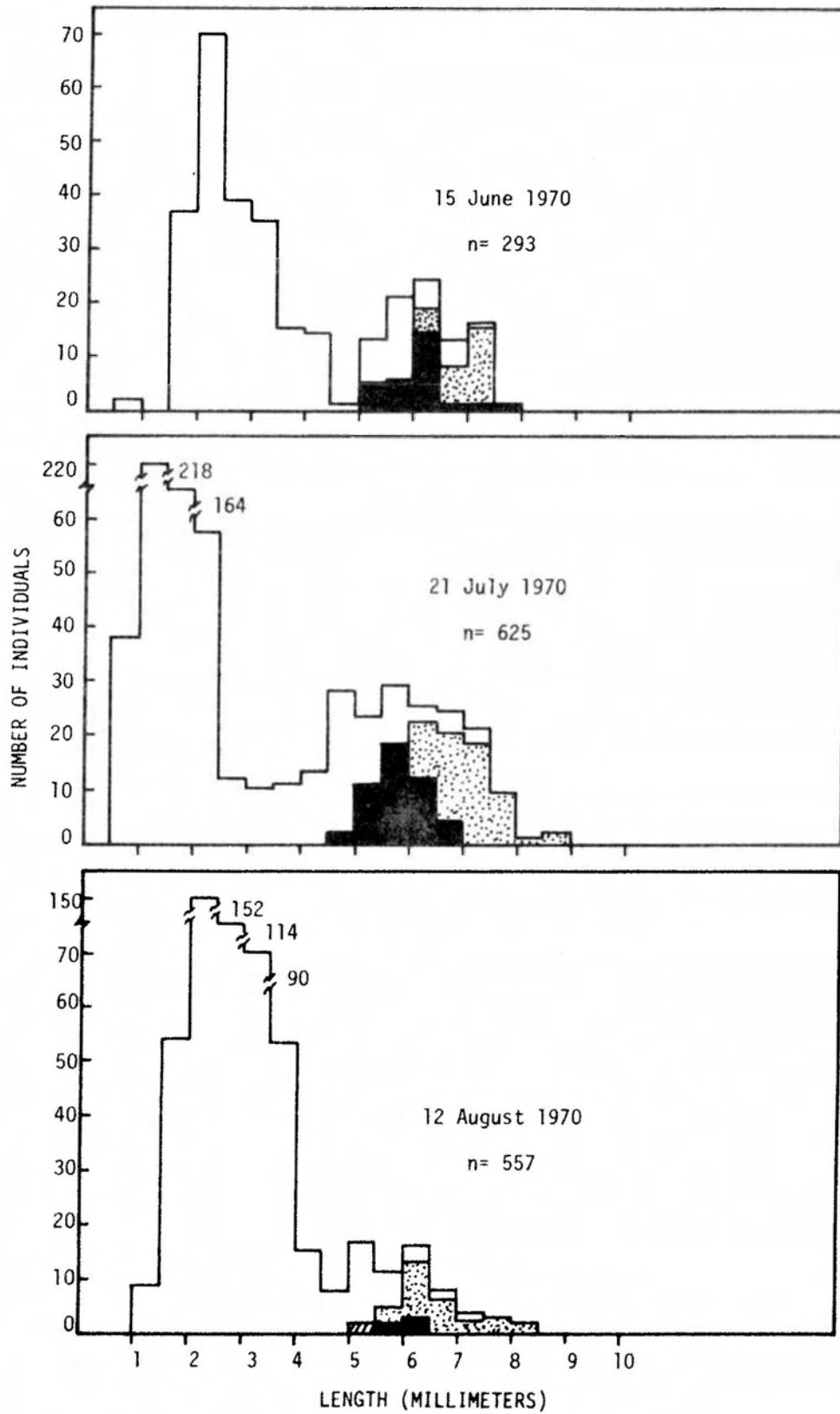
Fig. 29--Continued
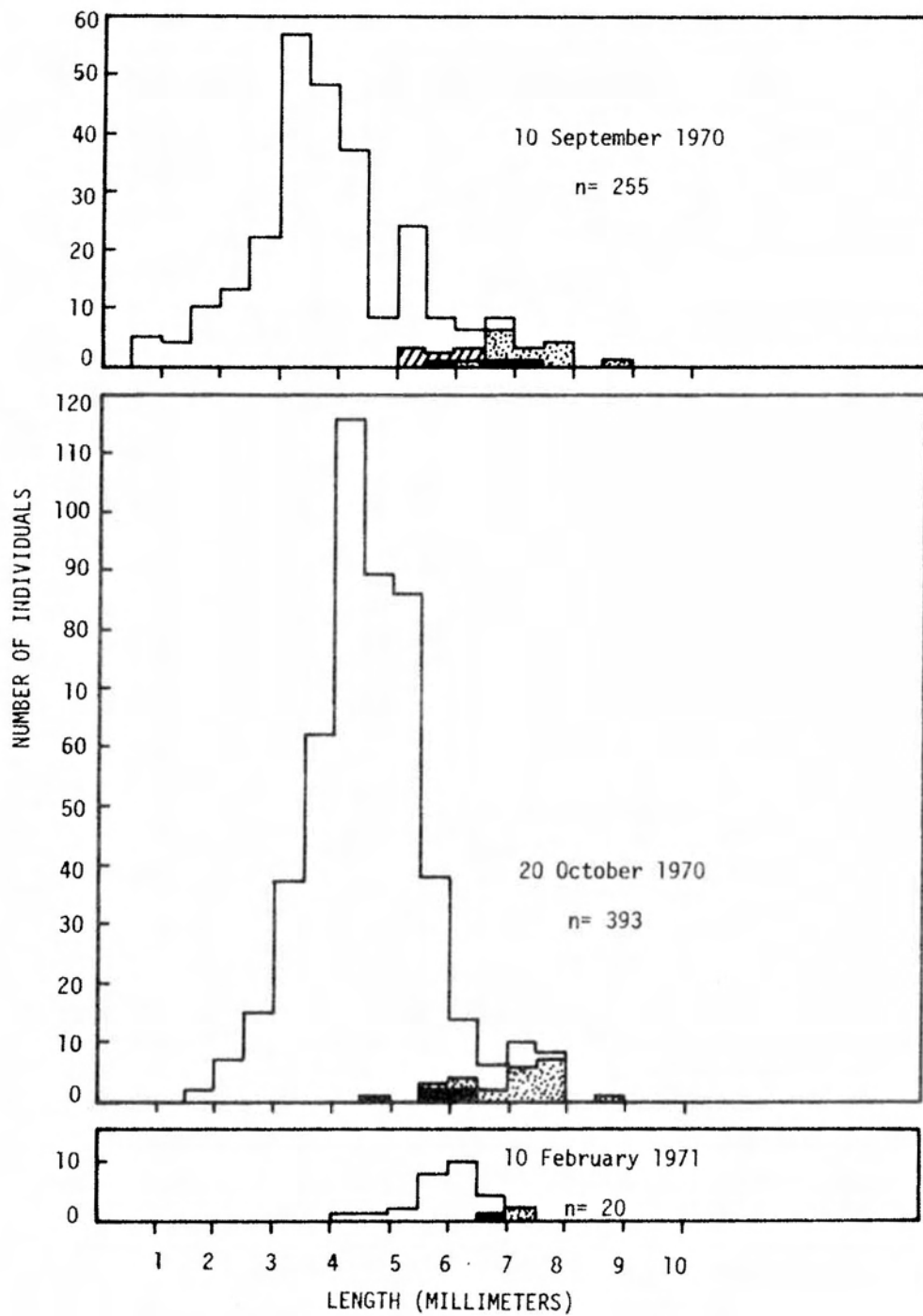
Fig. 29.--Continued

estimates of mean length when all data are considered. Omissions of data
from shallow samples to make mean length more significant did not
alter the modes of the frequency distributions. For this
reason, the following discussion is based on Figure 29 which includes all
available length data.

The reproductive cycle of Parathemisto pacifica in southeastern
Alaska is very different from that of P. libellula. Parathemisto
pacifica has multiple overlapping generations and year-round reproduction,
while P. libellula has only one generation per year. The length of
generation time and growth rates vary with season, being most rapid in
the summer. Brood release is not synchronous, as evidenced by the
continuous presence of small juveniles, adolescents, and mature or
maturing adults in all months. The proportions of each age group
differ from month to month. Small juveniles predominate during the late
spring and early summer, and adolescents predominate in the winter from
October through February. Adults predominate only in March and April.

The annual cycle of Parathemisto pacifica is assumed to begin at
about the same time as that of P. libellula. In March 1970, the P.
pacifica population was composed of subadults and adults, 4.0-8.5 mm long.
A few brooding females were captured in March. Apparently most eggs were
lost due to net damage, and the few remaining eggs had not progressed
beyond the morula stage. Sex ratio of the adults was approximately 1:1.

In mid April, although the adults and subadults still predominated,
a few juveniles 1.0-2.9 mm long were present. Four brooding females were
collected, one of which retained an apparently full complement of 41 eggs
(0.29-0.30 mm diameter). Additionally, 6 of the 15 females taken were
parasitized by the ellobiopsid Thalassomyces marsupii; these amphipods

were probably sterile.

Mortality of adults at the time of brood release is high. A major brood release occurred between the mid April and the May collections. Very few adults were taken in May, although a few may have survived to produce second broods. Further indications of heavy adult mortality are the observations that the size frequency distributions of females do not show multiple modes and that the modal size decreases during the summer. Bowman (1960) observed brooding females which were developing a second set of eggs, but the rareness of brooding females in my collections precluded application of this criterion to determine the proportion of adults which survive to produce second broods. Although my data do not preclude the possibility of female Parathemisto pacifica having multiple broods, they do show that it is not a significant feature in the reproductive cycle of P. pacifica in Alaskan coastal waters.

Beginning in May 1970, small juveniles predominated in the Parathemisto pacifica catches through August 1970, indicating continuous reproduction. The bimodal size distributions from June through September suggest high growth rates and rapid maturation. Growth and reproduction appear to decline in September or October and are at a minimum in January and February.

If the reproducing adults sampled in mid June represent the juveniles collected in early May, a generation time of less than 6 weeks is suggested, with a weekly growth increment of 1.0-1.5 mm/week. The mature females were 7.0-7.4 mm long, and the males were 6.0-6.4 mm long. Although this is a slower growth rate than shown for P. libellula, it is reasonable if a slowing of growth at maturity is accepted. Similar growth rates but earlier maturation may account for the smaller modal sizes observed in

July and August. Shorter generation time and smaller size at maturation during the summer warm periods have been observed in several Arctic and temperate zooplankton groups (Dunbar, 1968). The juveniles released in July, possibly the third generation of the summer, appeared to grow into the smallest adults, with females maturing in August at lengths of 5.5-5.9 mm. This group developed from egg to adult during the warmest period of the year. Falling temperatures in late August and September may have resulted in a longer generation time and larger size at maturity, as seen in the September and October 1970 catches (Figure 29).

Winter growth rates, as determined from the October 1969 through March 1970 collections, are low, and most individuals may overwinter as late juveniles. Although individuals in the summer populations have life spans of only 5-6 weeks, individuals captured in the winter and held in the laboratory may live over 12 weeks and have intermolt periods as long as 6 weeks. Corresponding to longer life spans at lower temperatures, females captured in winter matured at a length of about 6.5 mm. A maximum length of 9.5+ mm was recorded in January 1970.

Samples examined by Bowman (1960) were inadequate to determine generation times or growth rates for Parathemisto pacifica from more southerly areas. However, his data show the effect of temperature on size at maturity. The mean body size of mature female P. pacifica was inversely correlated with temperature over the range of 9.5-17.0° C in coastal waters of Washington, Oregon, and California. In addition, Bowman found mature males as small as 3.8 mm and mature females as small as 4.0 mm. My data are from collections over a temperature range of 2.5-12.0° C, and the temperature at depths where most adults were taken did not exceed 7.0° C. The smallest mature P. pacifica

I found were 4.5-mm long males and 5.5-mm long females collected in the late summer and early fall when temperatures at 100-m depths were highest.

Sex ratios of mature Parathemisto pacifica did not differ significantly from 1:1 from March through July. In the remainder of the collections, the number of mature individuals collected were too small to justify comparison of sex ratios, although for the record females occurred more often than males. Juveniles were not sexed. Sanger (1974) reports a 1.2:1.0 female-male ratio from the southeastern Bering Sea. Although individual samples may be predominantly male or female, the populations as a whole seem to have a sex ratio of 1:1.

Molting Frequency and Survival of Molt By Parathemisto pacifica and P. libellula

Growth of Parathemisto, as for all crustaceans, is accompanied by molting. The period of ecdysis is a major physiological event during which the animal experiences large biochemical changes and is subject to many stresses. Except for observations on copepods, euphausiids, and larval crustaceans, few data are available on the molting frequency and survival of molting in planktonic crustaceans (Lasker, 1964).

Maintenance of Parathemisto in the laboratory for experimental observations on oxygen consumption rates presented an opportunity to obtain information on molting frequency and on survival of molted animals.

The Parathemisto held in the laboratory were captured between the months of November and May, as subadults (before egg deposition in the case of females). Methods of holding the amphipods in the laboratory have been described elsewhere. The laboratory regimens of temperature,

light, feeding, etc. were not uniform and did not simulate natural conditions. My data are tenative but do indicate rates of winter molting and survival. This section summarizes observations on molting for all amphipods held in the laboratory from January 1970 through February 1973 (Table 20).

Of 77 Parathemisto pacifica kept in the laboratory, 9 molted and died and two survived 2-5 weeks beyond molting. Maximum time from capture to observed molt was 42 days. Several subadults held for 53-83 days apparently did not molt. Parathemisto pacifica exuviae are delicate and were often partially eaten by the amphipod. Most molting occurred at night, consequently some exuviae may have been completely consumed and the molt not recorded.

Of 656 Parathemisto libellula kept in the laboratory, 74 molted at least once and 4 molted twice. Thirty-three survived the first molt after captivity. None survived the second molt. Maximum time in captivity before molting was 71 days, although all but three of the amphipods which molted did so before the 50th day in captivity. Maximum time in captivity without molting was 82 days. Intermolt times for the four amphipods initiating a second molt were 22, 43, 46, and 50 days respectively.

The long periods of individual survival in the laboratory without molting indicate that molting of Parathemisto pacifica and P. libellula is not controlled by an endogenous rhythm. Molting is dependent on growth condition, and in the laboratory, conditions probably were not conducive to rapid growth. Temperature is an important exogenous control of molting frequency in euphasiids (Lasker, 1964, 1966). Holding temperatures did not appear to influence molting in

TABLE 20.--History of Parathemisto pacifica and P. libellula molting in captivity

Date captured	Number captured	Days held	Molts observed		Survived molt
			Number	At day--	
Parathemisto pacifica					
20 January 1970	4	10	0	..	..
20 March 1970	16	18-53	2	7	Yes
			1	32	No
10 February 1971	12	11-83	2	35	No
			2	42	No
28 May 1971	4	14-33	1	14	No
			1	17	No
29 December 1971	1	42	1	40	No
11 February 1972	10	7-26	1	15	No
22-23 March 1972	9	1-14	0	..	..
17 November 1972	20	2-13	0	..	..
18 December 1972	1	1	0	..	..
Parathemisto libellula					
			1	10	Unknown
			1	12	Yes
			1	20	Yes
			1	25	Yes
11 February 1970	21	2-90	1	26	Yes
			1	29	Yes
			3	30[a]	Yes
			1	35[a]	Yes
20 March 1970	1	46	2	40[a]	Yes
			1	8	Yes
			2	8[a]	Yes, no
			2	9	Yes
			2	12	Yes
10 February 1971	18	1-82	1	16	No
			1	17	No
			1	34	Yes
			1	36	Yes
			1	38	Yes
29 December 1971	11	25-49	1	49	No
			6	6	No
			1	7	No
			2	8	Yes, no
			1	15	Yes
11 February 1970	50	0-31	1	17	Yes
			1	18	No
			1	23	Yes
			2	25	Yes
			2	26	Yes, no
22-23 March 1972	155	1-70	1	29	Yes
			1	57	No
			2	2	No
			4	6	No
			2	7	No
17 November 1972	200	2-40	5	8	No
			1	22	No
			4	25	No
			3	26	No
			1	37	Yes
			1	41	Yes
			3	43	2 Yes, 1 no
18 December 1972	200	2-82	1	45	No
			1	48	No
			1	62	Yes
			1	69	No
			1	71	No

[a]One amphipod from each of these groups survived to molt a second time at 76, 78, 90, and 34 days in captivity, respectively.

laboratory Parathemisto; however, molting was apparently initiated in several instances as temperatures were being raised in oxygen consumption experiments.

Examination of molting by calendar date (Table 21) shows that molting was most frequent in late February and March. This may be a result of the collection schedule. This period also coincides with the period of maturation for the overwintering population of Parathemisto pacifica and annual sexual maturation of P. libellula. At this time, subadults of both species would be expected to undergo molting associated with sexual maturation, copulation, and deposition of eggs. Exogenous controls of the timing of molting have not been examined. Increasing day length, stabilization of falling temperature, or even endogenous rhythms cued by events of the previous fall could be involved.

Molting is a critical event for Parathemisto. In the laboratory, only 2 of 11 P. pacifica and 33 of 74 P. libellula (45%) which attempted to molt succeeded and survived. Often the amphipods died after proceeding only as far as the extraction of the head and first thoracic segment from the old exoskeleton. Some individuals proceeded through withdrawal of the head and partial withdrawal of legs and abdomen, and a smaller number completely cast the old exoskeleton before death. The 55% mortality of P. libellula and 82% mortality of P. pacifica attempting to molt in the laboratory is probably greater than under natural conditions because of unknown unfavorable factors in the laboratory. Similar high molting mortalities have been observed in attempts to raise larval crabs and shrimp (Rice and Williamson, 1970).

TABLE 21.--Numbers of Parathemisto pacifica and P. libellula molting in captivity on a given calendar day (all years combined)

Month	Day 1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31
Parathemisto pacifica																															
January																															
February							1																		1						
March													1			2									2		2				
April																															
May																															
June										1			1																		
Parathemisto libellula																															
November													2				4	2	5												
December													1				4	3													
January																										1				1	3
February		1				1										1	6	1	4	4	1		3			2	1	2			
March	1		1					3	3				2	3			1		2				1	2					1		
April																															
May	1												1					1													

Weight-Length Relationships of Parathemisto
pacifica and P. libellula

Fresh wet weight, dry weight, and length data from 17 Parathemisto pacifica and 220 P. libellula were available from collections made in southeastern Alaska between February 1971 and December 1972. Lengths ranged from 5.0 to 9.0 mm for P. pacifica and 17.0-29.5 for P. libellula. To cover a larger size range of P. libellula, the wet weight-length data of P. libellula from western Bering and Okhotsk Seas given by Lubny-Gertzik (1953) were also analyzed. Linear regressions as outlined by Sokal and Rolf (1969), were used for the limited P. pacifica and the Bering-Okhotsk Sea P. libellula data. A multiple linear regression using the BioMed BMD 02R program was used on the southeastern Alaskan P. libellula in order that days in captivity and days postmolt could be added to the regression and evaluated.

Although variances were large, the deviations from linearity were not significant and all regressions were found to be highly significant. Summaries of the analyses of variance are presented in Table 22. Summaries of the wet and dry weight regressions are given in Table 23. Figures 30 and 31 are plots of Ln (mg weight) on Ln (mm length) for Parathemisto pacifica, and of literature values for P. libellula and P. japonica.

Two exceptionally low wet weights and one dry weight value were discarded as being in error. After these deletions, the regressions of weight on length for P. pacifica were:

$$Ln \ (mg \ wet \ weight) = 2.90318 + 26583 \ Ln \ (mm \ length)$$

and

$$Ln \ (mg \ dry \ weight) = 4.64732 + 2.78999 \ Ln \ (mm \ length).$$

TABLE 22. --Analysis of variance for regressions of ln weight on ln length of Parathemisto pacifica and P. libellula from southeastern Alaska and western Bering and Okhotsk seas

SOUTHEASTERN ALASKA

P. pacifica (5-9 mm; n = 15)
Ln wet weight (mg) = -2.903 18 + 2.6538 ln length (mm)

Source variation	df	SS	MS	F	r
Size group	7	3.79140	0.54162	2.86	
Regression	1	3.41194	3.41194	53.95***	0.8167**
Deviation from regression	5	0.37946	0.06324	ns	
Within groups	7	1.32387	0.189 12		
Total	14	5.11527			

P. pacifica (5-9 mm; n = 16)
Ln dry weight (mg) = -4.64732 + 2.78999 ln length (mm)

Source variation	df	SS	MS	F	r
Size group	7	5.26489	0.75213	5.87*	
Regression	1	4.55312	4.55312	38.38***	0.851**
Deviation from regression	6	0.71177	0.11863	ns	
Within groups	8	1.02572	0.12822		
Total	15	6.29061			

P. libellula (17.0-29.5 mm; n = 220)
Ln wet weight (mg) = -3.15952 + 2.57303 ln length (mm)

Source variation	df	SS	MS	F	r
Regression	1	10.877	10.877	265.521***	0.861**
Residual	218	8.930	0.041		
Total	291	19.707			

P. libellula (17.0-29.5 mm; N=220)
Ln dry weight (mg) = -4.63885 + 2.49295 ln length (mm)

Source variation	df	SS	MS	F	r
Regression	1	10.211	10.211	140.125***	0.814**
Residual	218	15.885	0.073		
Total	219	26.096			

WESTERN BERING AND OKHOTSK SEAS[a]

P. libellula (6-22 mm; n = 14)
Ln wet weight (mg) = -3.3988709 + 2.6469728 ln length (mm)

Source variation	df	SS	MS	F	r
Regression	1	10.69626	10.69626	217.088***	0.9951**
Residual	12	0.10546	0.08788		
Total	13	10.80172			

***p 0.001; **p 0.01; *p 0.025

[a]Date from Lubny-Gertznik (1953)

TABLE 23. --Summaries of weight-length regressions for
Parathemisto libellula, P. pacifica, and
Metamysidopsis elongata

Ln weight (mg) = a + b· ln length (mm) + c· days in captivity

Species, size range and number	a	b	c
Wet weight regressions			
P. libellula[a] 6.0-22.0 mm; n = 14	-3.39887	2.64697	..
P. libellula[b] 17.0-29.5 mm; n = 220	-3.16055	2.57336	..
	-3.38265	2.60058	0.00504
P. libellula 17.0-29.5 mm; n = 181	-2.88159	2.45816	..
	-3.30202	2.56807	0.00593
P. pacifica 5.0-9.0 mm; n = 15	-2.90318	2.65830	..
Dry weight regressions			
P. libellula[b] 17.0-29.5 mm; n = 220	-4.62205	2.48818	..
	-4.71866	2.49995	0.00220
P. libellula[c] 17.0-29.5 mm; n = 181	-4.68652	2.51292	..
	-4.96134	2.57506	0.00335
P. pacifica 5.0-9.0 mm; n = 16	-4.64732	2.78999	..
M. elongata[d] 1.9-6.5 mm; n = 42	-5.436	2.77	..

[a]From data of Lubny-Gertzik (1953).

[b]Includes individuals molting in captivity.

[c]Excludes individuals molting in captivity.

[d]From Clutter and Theilacker (1971).
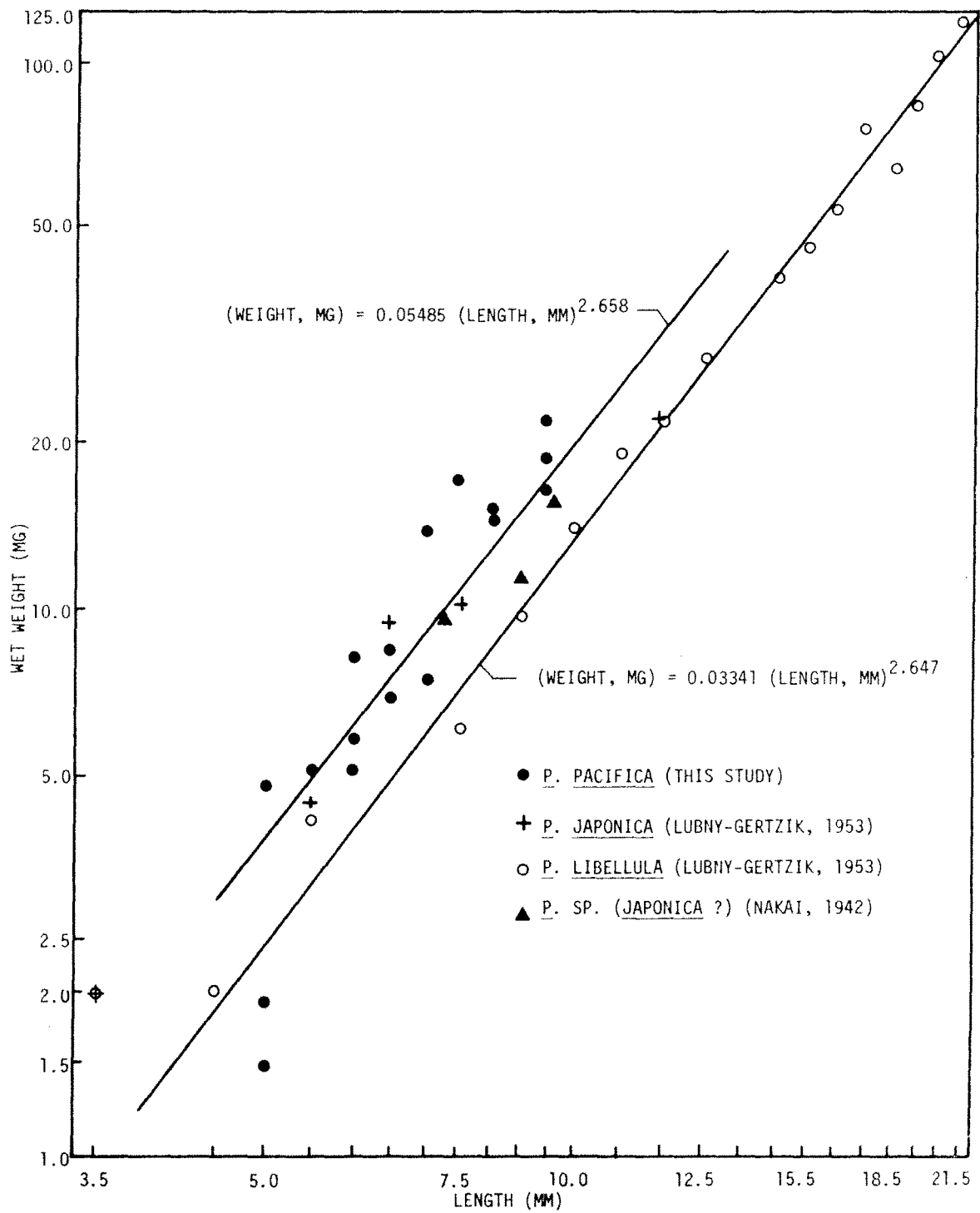
Fig. 30.--Relationship of wet weight to body length of Parathemisto libellula, P. japonica, and P. pacifica
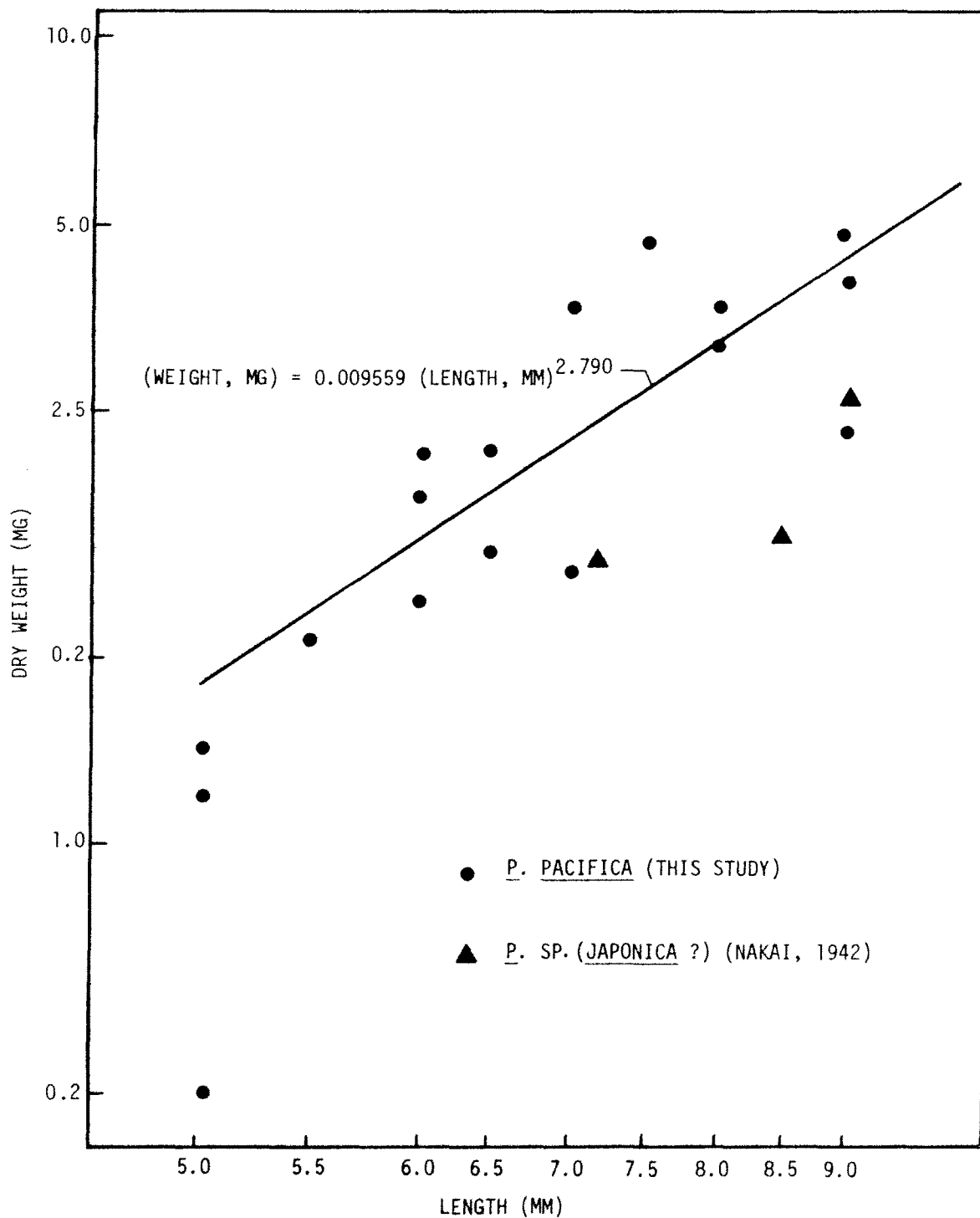
Fig. 31.--Relationship of dry weight to body length of Parathemisto
japonica and P. pacifica

For Parathemisto libellula from the Bering-Okhotsk Seas data the regression for wet weight was:

Ln (mg wet weight) = -3.39887 + 2.64697 Ln (mm length).

Disregarding the factors of days in captivity and days postmolt, the regressions for P. libellula from southeastern Alaska were

Ln (mg wet weight) = -3.15952 + 2.57303

and

Ln (mg dry weight) = -4.63885 + 2.49295 Ln (mm length).

The variance of weights at any given length were quite high; consequently, when the factors of days in captivity and days postmolt were added to the regression for the Alaskan P. libellula, no statistical differences were found between the revised regressions and the regressions without these factors. Days in captivity had a small positive coefficient (Table 23). In the data for days postmolt, 12 males and 27 females were available, and the coefficient was small and positive for wet weights, but it was negative for males and positive for females in the dry weight regression. No significant male-female differences were found, although the males had a slightly lower intercept and slightly steeper slope than the females.

The major significance of the results of these analyses, including days in captivity and days postmolt, is that no statistically measurable effects upon weights were found, and that there is a weak indication that the amphipods may have gained weight in captivity. This implies that feeding conditions of captivity, although not ideal, were not producing starving animals.

The regression coefficients for all sets of data differ from the hypothetical cubic relationship and imply allometric growth. Allometric

growth in Parathemisto, although expected, has not been previously documented. Amphipods do not have a distinct metamorphosis; however, the early juveniles are distinctly more compact and have relatively shorter legs than the adults. The change in body proportions, most distinct in P. libellula, also occurs in P. pacifica and other species of Parathemisto. Consequently, the logarithmic regression coefficients for weight on length are less than 3. The smaller individuals are heavier for their length than the larger specimens. A similar weight-length relationship has been described for the mysid Metamysidopsis elongata where the regression is

Ln (mg dry weight) = -5.436 + 2.77 Ln (mm length)

and believed attributable to orthagonal growth of appendages (Clutter and Theilacker, 1971). The 5-7 pereopods of Parathemisto spp. exhibit a distinct orthogonal growth.

The weight regression slopes for Parathemisto libellula and P. pacifica of comparable size do not differ, nor do these differ statistically from the slopes derived from the larger southeastern Alaskan P. libellula (F=0.62 vs. $F_{14,220(.95)} \sim 5.10$), when evaluated for equality of slopes (Sokal and Rolf, 1969). The lower intercepts in the wet weight regression of P. libellula may be attributable to the fact that P. libellula even as juveniles are slender compared with the same stages of P. pacifica. In Figure 30, point values for P. japonica from the data of Lubny-Gertzik (1953) and Nakai (1942) are shown. These approximate those of P. pacifica, as would be expected from the similarity of size and morphology.

Food Habits of Parathemisto in
Southeastern Alaska

Hyperiid amphipods are generally accepted as being highly predaceous. The foods of various species of Parathemisto have been reported as copepods, small compound-eyed crustaceans, and small amounts of phytoplankton with the observation that they are cannibalistic (Bigelow, 1926; Dunbar, 1942; Bowman, 1960). Observations before the initiation of this study suggested a high level of cannibalism as well as a broad overlap in the diets of P. libellula and P. pacifica from southeastern Alaska. For this reason, I assessed the diet of these two species by examining, when available, stomach contents of 50 specimens of each species from the daytime, and 50 specimens of each from the nighttime samples of each month.

The interpretation of prey composition and intensity of feeding by predaceous zooplankton and nekton collected by nets has been questioned because of the probability of capture and ingestion of prey while in the net and before preservation (Judkins and Fleminger, 1972). Additionally, many animals are known to regurgitate food when under stress of crowding in the nets and during fixation by preservative. The short time span of my net tows, generally less than 10 minutes from the depth of probable capture, and the preservation of most samples within 5-10 minutes of collections significantly reduces the probability of feeding before preservation. The time required for an amphipod to dismember prey, and the near absence of whole-bodied prey in the stomach contents may be considered as further evidence that anomalous feeding in the net did not significantly bias my observations. Regurgitation may have been a more significant factor. Approximately one-fourth of

the stomachs of both species were either empty or almost empty. However, less than 10% of the stomachs were obvious cases of regurgitation, as indicated by the presence of masticated food caught in the mandibles or other oral appendages. Thus, this material is representative of both the degree of feeding and of the types of prey consumed.

Both species feed during the day as well as at night (Tables 24 and 25). Although the percentage of full stomachs is slightly higher in the day for Parathemisto libellula, and in the night for P. pacifica, the differences are not statistically significant. Stomach contents from night catches were generally not as well digested as stomach contents from day catches, suggesting more intensive feeding for both species at night. Laboratory observations indicate that as long as 30 minutes could be required for an amphipod to consume a single prey, such as a euphausiid. Most night catches were made 2-3 hours after sunset. It is likely that a portion of the amphipods taken at night may not have had time to find and consume prey. Digestion rates of Parathemisto spp. have not been studied but may be quite slow. Small planktivorous fish such as pink and chum salmon fry (Oncorhynchus gorbuscha and O. keta) require as much as 16.5 hours to completely clear a gorged stomach at 8.5° C (Bailey, Wing, and Mattson, 1975, in press). An estimate of 15-18 hours for Parathemisto to digest completely the contents of a full stomach at 4-8° C seems a reasonable estimate. For this reason, the daytime samples taken 6-12 hours after sunrise may still retain significant amounts of food from the feeding of the previous nights.

Observations of Parathemisto libellula and P. pacifica dismembering prey in the laboratory were restricted to relatively large individuals feeding upon euphausiids and other amphipods. Parathemisto

TABLE 24.--Numbers and percentages of P. libellula with empty or full stomachs taken in daytime and nighttime trawl samples at False Point Retreat, September 1969 to May 1972

Month and year	Daytime Number stomachs	Daytime Empty Number	Daytime Empty %	Daytime Full Number	Daytime Full %	Nighttime Number stomachs	Nighttime Empty Number	Nighttime Empty %	Nighttime Full Number	Nighttime Full %
September 1969	4	0	0.0	1	25.0	..	..	..	..	..
September 1970	55	27	49.1	0	0.0	..	..	..	..	..
October 1969	3	0	0.0	1	33.3	..	..	..	..	..
October 1970	16	2	12.5	0	0.0	12	1	8.3	0[a]	0.0
November 1961	21	4	19.0	3	14.3	31	1	3.2	1	3.2
December 1969	11	3	27.3	0	0.0	..	..	..	..	..
January 1970	3	0	0.0	1	33.3	13	1	7.7	1	7.7
February 1970	12	2	16.6	6	50.0	25	1	4.0	8	32.0
February 1971	12	1	8.3	3	25.0	..	..	..	..	..
March 1970	7	2	28.6	0	0.0	17	17	100.0	0[a]	0.0
April 1970	..	..	..	..	..	3	1	33.3	1	33.3
May 1972	25	1	4.0	0	0	..	..	..	..	..
June 1970	64	9	14.1	6	9.4	60	11	18.3	0	0.0
July 1970	50	6	12.0	0	0.0	49	9	18.4	1	20.0
August 1970	24	13	54.2	0	0.0	69	22	31.9	1	1.4
Total	307	70	22.8	21	6.8	279	64	22.9	13	4.7

[a]No full stomachs were found, but those that were examined generally contained more than the stomachs collected in daytime the same month.

TABLE 25.--Numbers and percentages of P. pacifica with empty or full stomachs taken in daytime and

nighttime trawl samples at False Point Retreat, September 1969 to May 1972

Month and year	Daytime					Nighttime				
	Number stomachs	Empty Number	Empty %	Full Number	Full %	Number stomachs	Empty Number	Empty %	Full Number	Full %
September 1969	50	35	70.0	0	0.0	..	..	..	..	..
September 1970	49	32	65.3	0	0.0	..	..	..	..	..
October 1969	50	10	20.0	18	36.0	..	..	..	..	..
October 1970	55	55	100.0	0	0.0	39	12	30.8	0[a]	0.0
November 1969	50	24	48.0	1	2.0	50	10	20.0	40	80.0
December 1969	57	9	15.8	12	21.1	..	..	..	..	..
January 1970	51	10	19.6	17	33.3	49	12	24.5	0[a]	0.0
February 1970	50	13	26.0	10	20.0	50	14	28.0	7	14.0
February 1971	29	8	27.6	0	0.0	..	..	..	..	..
March 1970	14	2	14.3	0	0.0	41	26	63.4	2	4.9
April 1970	8	0	0.0	3	37.5	20	1	5.0	6	30.0
May 1972	30	5	16.6	0	0.0	0	..	..	0[a]	..
June 1970	50	12	24.0	10	20.0	53	29	54.7	0[a]	0.0
July 1970	52	3	5.8	14	26.9	47	28	59.6	0[a]	0.0
August 1970	53	21	39.6	0	0.0	50	4	8.0	10	20.0
Total	650	239	36.8	85	13.1	399	136	34.1	65	16.3

[a]No full stomachs were found, but those that were examined generally contained more than the stomachs collected in daytime of the same months.

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also may dismember smaller crustacean prey. Stomach analyses revealed that smaller prey such as copepods and even nauplii were seldom found whole. Whether or not the small crustacean prey were actually torn apart or were masticated by the mandible and gastric apparatus was difficult to observe, but I suspect that the small P. pacifica and the smallest P. libellula tear most of their prey into bite-sized pieces. Occasionally, large P. libellula were observed to ingest whole or nearly intact copepods approximately 2 mm long or less, and one 21.5 mm P. libellula was found to have ingested a nearly intact Primno sp. 2 mm long. Intact or nearly intact prey were rarely found in P. pacifica stomachs; consequently identification of prey to species was less frequent in P. pacifica than in P. libellula, although nearly twice as many stomachs of P. pacifica as P. libellula were examined.

The results of analyses of 586 Parathemisto libellula and 1,049 P. pacifica are presented in Tables 26 and 27. The empty stomachs, 15.25% of P. libellula and 17.3% of P. pacifica, were nearly equally divided among daytime and nightime catches. Calanoid copepods were the most frequently recognized food for both species, being found in 43.1% of the P. libellula and 47.6% of the P. pacifica stomachs. The other categories, although less frequently encountered, often made up more of the material in a stomach, especially if the amphipod had fed on euphausiids, amphipods, or what often had to be listed as unidentified crustacean or compound-eyed crustaceans. More than one or two nauplii rarely occurred except in the P. pacifica stomachs from August. Phytoplankton occurred with equal frequency in both species but was present in significant numbers in P. libellula only in May and June,

TABLE 26.--Types of food items found in stomachs of <u>Parathemisto</u> <u>libellula</u> taken in daytime and nighttime trawl samples at False Point Retreat, 1969-72

Month and year	Size range (mm)	Number stomachs	Number empty	Calanoids	Euphausiids	Amphipods	Nauplii	Compound-eyed crustaceans	Unidentified crustaceans	Chaetognaths	Miscellaneous	Unidentifiable animal remains	Phytoplankton
Daytime samples												
Sept. 1969	16.0-18.5	4	0	4	..	..	..	..	..	..	..	..	..
Sept. 1970	13.0-20.0	55	17	16	2	..	1	3	..	4	..	13	..
Oct. 1969	18.0-19.5	3	0	3	..	1	..	..	..	1	..	..	..
Oct. 1970	17.0-19.0	16	0	12	..	1	..	2	..	2	..	1	..
Nov. 1969	17.5-25.0	21	2	17	..	4	..	..	..	2	..	..	..
Dec. 1969	19.5-21.5	11	2	8	..	1	..	..	..	1	..	3	..
Jan. 1970	21.0-22.5	3	0	3	1	1	..	..	..	2	..	2	..
Feb. 1970	20.0-24.0	12	2	8	2	1	..	..	..	2	..	2	..
Feb. 1971	19.0-23.0	12	1	6	4	1	..	5	..	2	..	..	..
Mar. 1970	20.5-23.5	7	1	4	..	..	..	1	..	1	1[a]	1	..
May 1972	2.7- 4.5	25	1	..	..	..	5	..	..	..	..	23	24
June 1970	5.5-12.0	64	7	5	..	1	..	2	24	1	1[b]	..	7
July 1970	10.0-16.5	50	4	18	4	6	..	13	2	..	..	..	..
Aug. 1970	10.0-16.5	24	8	2	3	1	..	4	1	1	..	6	..
Total (day)		307	45	106	16	18	6	30	28	21	2	75	31

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TABLE 26.--Continued

Month and year	Size range (mm)	Number stomachs	Number empty	Calanoids	Euphausiids	Amphipods	Nauplii	Compound-eyed crustaceans	Unidentifiable crustaceans	Chaetognaths	Miscellaneous	Unidentifiable animal remains	Phytoplankton
						Nighttime samples							
Oct. 1970	16.0-19.0	12	1	6	5	..	..	1	1	..	..	..	..
Nov. 1969	14.0-22.5	31	1	28	..	3	..	1	..	3	..	3	..
Jan. 1970	20.0-23.0	13	1	3	1	8	..	..	..	..	..	3	..
Feb. 1970	19.0-23.5	25	1	17	12	..	..	2	1	4	2[c]	1	..
Mar. 1970	21.0-25.0	17	5	12	..	..	..	..	..	..	..	..	..
April 1970	21.5-23.0	3	0	3	..	..	..	..	..	2	..	..	..
June 1970	7.0-13.0	60	11	20	..	..	1	2	14	1	3[d] 2[a]	16	8
July 1970	9.5-16.0	49	9	5	3	2	..	12	6	1	4[a,d] 2[c]	10	..
Aug. 1970	10.0-18.0	69	15	14	2	2	..	6	7	1	..	22	..
Total (night)		279	44	108	23	15	1	24	29	12	9	55	8
Grand total		586	89	214	39	33	7	54	57	33	11	130	39
Percent[e]				43.1	7.8	6.6	1.4	10.9	11.5	6.6	2.2	26.2	7.8
Rank				1	5.5	7.5	10	4	3	7.5	9	2	5.5

[a]Cyclopoid. [b]Cladoceran. [c]Fish larvae. [d]Polychaete. [e]15.8% of the daytime, 14.8% of the nighttime, and 15.2% of the total stomachs were empty.

TABLE 27. -- Types of food items found in stomachs of <u>Parathemisto pacifica</u> taken in daytime and night-time trawl samples at False Point Retreat, 1969-72

Month and year	Size range (mm)	Number stomachs	Number empty	Calanoids	Euphausiids	Amphipods	Nauplii	Compound-eyed crustaceans	Unidentifiable crustaceans	Chaetognaths	Miscellaneous	Unidentifiable animal remains	Phytoplankton
							Daytime samples						
Sept. 1969	1.4-5.8	50	2	4	..	..	4	..	20+	..	1[a]	41	..
Sept. 1970	1.0-8.0	49	14	13	1	..	1	..	6	..	..	19	..
Oct. 1969	2.1-7.0	50	2	25+	..	..	..	8	16	..	..	4	..
Oct. 1970	3.5-7.5	55	28	27	..	..	..	9	..	..	..	..	..
Nov. 1969	2.6-8.0	50	9	20	1	..	..	4	4	1	..	11	..
Dec. 1969	1.9-8.2	57	5	35	5	..	..	5	6	2	..	3	1
Jan. 1970	2.5-7.8	51	7	41	..	..	..	4	1	..	..	..	..
Feb. 1970	2.7-7.8	50	7	29	6	..	6	4	..	..	..	2	..
Feb. 1971	4.0-7.0	29	8	9	4	..	..	4	4	1	..	..	2
Mar. 1970	4.5-7.0	14	1	7	..	..	..	3	6	..	..	..	..
April 1970	5.0-8.0	8	0	6	1	..	..	..	1	..	..	..	..
May 1972	1.5-3.5	30	4	..	..	..	1	..	..	..	..	26	26
June 1970	1.8-7.5	50	7	18	..	..	7	..	18	..	..	9	8
July 1970	1.5-8.5	52	3	30+	9	1	..	3	3	..	..	5	..
Aug. 1970	2.0-7.5	55	15	5	1	..	10%	..	20+	..	1[b]	14	..
Total (day)		650	112	269	28	1	29+	46	105	4	2	134	39

TABLE 27.--Continued

Nighttime samples

Month and year	Size range (mm)	Number stomachs	Number empty	Calanoids	Euphausiids	Amphipods	Nauplii	Compound-eyed crustaceans	Unidentifiable crustaceans	Chaetognaths	Miscellaneous	Unidentifiable animal remains	Phytoplankton
Oct. 1970	4.0-7.5	39	5	5	5	..	..	14	9	..	..	..	1
Nov. 1969	2.5-7.2	50	8	30	1	..	..	8	1	..	..	2	..
Jan. 1970	3.3-7.4	49	12	25	..	..	..	8	1	..	..	5	..
Feb. 1970	2.0-7.7	50	12	26	2	1	..	10	4	..	..	..	..
Mar. 1970	4.5-8.9	41	12	25	..	..	..	3	2	..	..	1	..
April 1970	1.5-7.5	20	0	14	1	..	..	..	..	..	..	8	2
June 1970	1.5-7.0	53	8	8	..	..	7	..	8	..	..	..	24
July 1970	1.0-7.0	47	8	3	3	3	1	1	3	..	1[b]	25	..
Aug. 1970	2.0-8.0	50	4	6	..	..	10+	2	20+	..	1[b]	40	..
Total (night)		399	69	144	12	4	18+	44	48	0	2	81	25
Grand total		1,049	181	413	40	5	47+	90	153	4	4	215	64
Percent[c]				47.6	4.6	0.6	5.4	10.4	17.6	0.5	0.5	24.8	7.4
Rank				1	7	8	6	4	3	9.5	9.5	2	5

[a]Tintinnid. [b]Cyclopoid. [c]17.2% of the daytime, 17.3% of the nighttime, and 17.3% of the total stomachs were empty.

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when P. libellula was about the same size as P. pacifica. Parathemisto pacifica although ingesting phytoplankton mostly in May and June, also ingested small amounts at other times.

The Prey of Parathemisto

Copepods

Copepods appear to be the major prey of both Parathemisto libellula and P. pacifica. In approximately one-sixth of the stomachs examined, the genus, and sometimes the species of copepod eaten were determined by means of diagnostic appendages (Table 28). Copepodites of Metridia spp. (both M. lucens and M. longa) were the most frequently recognized copepods, followed by Pseudocalanus minutus. These calanoids were the predominant copepods at False Point Retreat during the study period. Calanus finmarchicus s.l. and C. plumchrus were the third most abundant copepods in both the stomachs and in the plankton. Calanus cristatus and Euchaeta japonica are among the largest copepods found in the area, and may be better able to escape the amphipods. Although Microcalanus pusilius were not very abundant, they may have been recognized more readily than other species because they were ingested nearly intact, as were many of the smaller Pseudocalanus. Acartia spp. and cyclopoids, especially Oithona spp., were surprisingly rare in the stomachs even of P. pacifica. Possibly the Acartia spp. and Oithona spp. reside in waters shallower than the normal feeding depth of the adult and subadult P. pacifica. Juvenile P. pacifica feed mostly on small copepodites and some nauplii but dismember their prey beyond recognition. I suspect that the juvenile P. pacifica capture the Acartia and Oithona copepodites more often than were observed.

TABLE 28.--Copepods identified in stomachs of Parathemisto
libellula and P. pacifica from southeastern Alaska
and frequency of identification

Copepod species	Number of times found in stomachs of--	
	P. libellula	P. pacifica
Calanoid copepods	214	413
Metridia spp. (M. longa and M. lucens)	22	19
Pseudocalanus minutus	22	8
Microcalanus pusilius	5	0
Calanus cristatus	1	0
Calanus spp. (C. finmar-chichus s.l. and C. plumchrus)	11	5
Euchaeta japonica	1	2
Acartia sp.	0	3
Cyclopoid copepods	2	2
Copepod nauplii	7	47

In general, both species of Parathemisto appeared to feed on the
predominant copepod species and in their order of abundance in the waters
of the area but it is not possible to confirm this.

Nauplii

Food items considered to be nauplii of copepods and/or euphausiids
were difficult to determine. With a few exceptions, in which larger
amphipods had consumed whole intact nauplii, this food category was
restricted to amphipods of the 1.0- to 3.5-mm sizes. In these small
amphipods, intact nauplii were rarely found. However, their presence

was indicated by small round chitinous carapaces associated with small 2- 3-segmented appendages. On occasion, the carapaces contained a pigmented naupliar eye. Although barnacle nauplii were available as prey throughout much of the late spring and summer, they were not observed in the Parathemisto stomachs--or at least the carapaces were not ingested.

Cladocerans

Only two cladocerans, both Podon sp., were recognized in the stomach contents, one each from Parathemisto libellula and P. pacifica. Cladocerans are seasonally abundant in the surface waters of Auke Bay (Wing and Reid, 1972), and in similar small inshore bays, but were not a significant component of the zooplankton at False Point Retreat during the summer of 1970.

Euphausiids

Euphausiids were identified in 7.8% of the Parathemisto libellula and in 4.5% of the P. pacifica stomachs. Euphausiids are the second most abundant group of holoplanktonic animals in southeastern Alaska, and have a depth distribution similar to that of the Parathemisto. Although it was not possible to identify which species of euphausiids were prey of Parathemisto, it was observed that Thysanoessa raschii, T. longipes, T. spinifera, and Euphausia pacifica are all abundant in the area, and were collected with the Parathemisto. Because Parathemisto shell prey such as euphausiids, it is reasonable to assume that much of the food identified as "compound-eyed crustaceans," "unidentified crustaceans," or "unidentified animal tissue" was from euphausiid in origin.

Amphipods

Amphipods, like euphausiids, generally were shelled before ingestion, thus, it was not always possible to determine what species had been eaten. With the exception of a single unidentified gammarid amphipod from a Parathemisto libellula, the identified amphipods were hyperiids. Parathemisto libellula were found to have eaten small Primno sp. twice, to have eaten small Parathemisto pacifica 11 times, and to have been cannibals twice; on 17 occasions the prey could be only tentatively identified as a Parathemisto sp. (probably P. pacifica). Five times, P. pacifica were found feeding on small hyperiids (probable cases of cannibalism).

Compound-Eyed Crustaceans

Approximately one-tenth of the stomachs of both species contained crustacean remains with masses of ommatidia, which could not be assigned to even a specific category of crustacean. These were probably most often cases of feeding on euphausiids, but may also have included other Parathemisto as well as the larvae or juveniles of shrimp, crabs, and mysids.

Unidentified Crustaceans

Food listed as unidentified crustaceans is essentially the same as "compound-eyed crustacean" except for the absence of ommatidia. This group was characterized by large pieces of muscle with a few pieces of chitin, setae, and occasionally a few segmented appendages. Its composition is probably much the same as the previous category but may also contain a significant number of copepods, especially if large calanoids such as Calanus cristatus and Euchaeta japonica were injected

but not recognized.

Chaetognaths

The arrowworms, Sagitta elegans and Eukrohnia hamata, were found
in the stomach contents of Parathemisto libellula. Sagitta elegans was
found in P. pacifica stomachs. Specific identification was based on
the chitinous hooks from the heads of the consumed arrowworms. More
often, the presence of freshly eaten arrowworms was indicated by
short tubular segments with longitudinal muscles. Arrowworms were found
in 6.7% of the P. libellula but only in 0.3% of the P. pacifica.

Miscellaneous Foods

Cladocerans, cyclopoids, polychaetes, tintinnids, and fish larvae
were combined under miscellaneous foods in Tables 24 and 25. In
aggregate they made up less than 5% of the identified foods. One
tintinnid was found in a Parathemisto pacifica. Polychaetes were
tentatively identified twice from P. libellula stomachs by the elongate
bundles of fine setae attached to probable parapodia. Fish larvae were
found only six times in P. libellula stomachs, twice each in February,
June, and July 1970. Five of the fish larvae were elongate with long
intestinal tracts, but were too far disgested to determine species
The sixth fish larvae from the February sampling was a small
2.5-mm compact animal with a short coiled intestinal tract, large head,
and dark pigmented eyes--possibly a small cottid or hexagrammid.

Considering the ease and rapidity with which Parathemisto libellula
captured and ate fish larvae in the laboratory, the infrequency of fish
larvae in the stomach was surprising. Possibly, Parathemisto feed
primarily below the depths at which fish larvae are most abundant, or,

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alternatively, they may be too small to capture fish larvae effectively when the larvae are abundant in May and in June.

Unidentified Animal Tissue

Roughly one-fourth of the stomachs of both species of Parathemisto contained material which could only be dsecribed as animal tissue. This was most frequently the case from May through September--a time when most P. pacifica are still small and may not be ingesting the hard parts of many of their crustacean prey. Additionally, during this time of year potential soft-bodied prey such as larvaceans (Oikopleura spp. and Fritillaria borealis), and the small larvae of mollusks, echinoderms, polychaetes, and other benthic invertebrates are often abundant.

Phytoplankton

Only in May and June was algal material found in signficant amounts in the stomachs of Parathemisto libellula. Plant material was in most of the stomachs of P. pacifica in May and June. In May, the stomachs of smallest individuals of both species contained mostly amorphous masses of food which was found to contain a few broken and some intact frustules of Thalassiosira sp. However, most of the material appeared to be from sources other than diatoms. Two juvenile P. pacifica (one each December 1969 and April 1970), and four subadults (one in April 1970, one in October 1970, and two in February 1971), were also found to contain plant-like material. The phytoplankton material in the juveniles could not be identified, but small quanities of what appeared to be Thalassionema sp. were found in the subadults.

With the exception of May and June, phytoplankton does not appear
to be a significant part of the diet of either species of Parathemisto
in southeastern Alaska. It is possible that most of the material
observed in May and June came from the intestinal tracts of prey or was
accidentally ingested during heavy phytoplankton blooms. Accidental
ingestion, possibly as a response to cleaning entangled diatom chains
off the pereopods does not seem likely. Chaetoceros spp. are among
the most likely diatoms to entangle and clog plankton nets and are
quite abundant in southeastern Alaska, but were never observed in the
Parathemisto stomachs. The observed phytoplankton in Parathemisto
stomachs, Thalassiosira and Thalassionema, neither form tangled mats nor
seriously clog zooplankton nets unless the blooms are exceptionally
dense.

Dietary Overlap of Parathemisto libellula and P. pacifica

The data presented here show that the Parathemisto are basically
carnivores, feeding mostly at the second and third trophic levels.
Some phytoplankton is eaten, but except for the youngest stages,
plant material is not a significant part of the Parathemisto diet.
The degree of overlap in diets, and the potential or actual competition
for food may be evaluated by rank correlation techniques where precise
quantitative data are weak or absent (Fritz, 1974). The observed
similarity in diets of P. libellula and P. pacifica justifies evaluation
of the potential for competition.

Spearman rank correlation tests were applied to the stomach
content data after converting the occurrences to percentage of stomachs
with food. For all data, the diets of the two species were quite similar

and the null hypothesis of independence was rejected at the 0.001 level of significance using both the standard test and the test corrected for tied ranks (Table 29).

The possibility that the strong correlation of diets was due to a broad overlap when the two species were of the same or nearly equal sizes was considered by a second correlation test from which the May and June data have been deleted (Table 30). In this test, the comparison was one of Parathemisto libellula over 10 mm long with P. pacifica less than 10 mm long. Although there was some reordering of the rank of food categories, especially for P. libellula, there was still a strong correlation, with the null hypothesis of independence being rejected at the 0.005 level of significance. This implies that despite the large size difference throughout 10 months of the year, the diets of P. libellula and P. pacifica are composed of the same food items and that those foods have the same relative importance.

Although the Spearman rank correlation tests indicate a very high degree of similarity in the diets of Parathemisto libellula and P. pacifica, they do not consider possible differences in the degree of usage of food categories which may have the same rank order. Therefore, I applied a t-test for difference of means, a paired t-test, and a Wilcoxon signed rank test to the data for all months except May and June. Because the categories "compound-eyed crustaceans" and "unidentified crustaceans" are not mutually exclusive, or exclusive of amphipods and euphausiids, these four categories were combined into a "noncalanoid crustacean" category for the statistical tests. For this combination, P. libellula was found to have a relative frequency of 36.8% for all data, and 38.1% for data with May and June excluded.

TABLE 29. --Percentage occurrence and rank (corrected for ties) of food items in stomachs of Parathemisto libellula (2. 7 to 25. 0 mm) and P. pacifica (1. 0 to 8. 9 mm) from southeastern Alaska for all months

Food item	P. libellula		P. pacifica	
	Percentage occurrence	Rank	Percentage occurrence	Rank
Calanoids	43. 1	1	47. 6	1
Unidentifiable animal remains	26. 2	2	24. 8	2
Unidentified crustaceans	11. 5	3	17. 6	3
Compound-eyed crustaceans	10. 9	4	10. 4	4
Euphausiids	7. 8	5. 5	4. 6	7
Amphipods	6. 6	7. 5	0. 6	8
Nauplii	1. 4	9	5. 4	6
Cyclopoids	0. 4	11. 5	0. 2	10
Cladocerans	0. 2	13	0. 1	11. 5
Fish larvae	1. 2	10	0. 0	13. 5
Polychaete larvae	0. 4	11. 5	0. 0	13. 5
Tintinnids	0. 0	14	0. 1	11. 5
Chaetognaths	6. 6	7. 5	0. 5	9
Phytoplankton	7. 8	5. 5	7. 4	5

$r_{su} = 0.9099$; $r_{sc} = 0.8930$; $r_{0.001, 14} = 0.7420$; $N_r = 14$.

where r_{su} = Spearman rank correlation coefficient uncorrected for ties

r_{sc} = Spearman rank correlation coefficient corrected for ties

N_r = Number of ranks.

TABLE 30. --Percentage occurrence and rank (corrected for ties) of
food items in stomachs of Parathemisto libellula (9. 5 to 25. 0 mm)
and P. pacifica (1. 0 to 8. 9 mm) from southeastern Alaska
for all months except May and June

Food item	P. libellula		P. pacifica	
	Percentage occurrence	Rank	Percentage occurrence	Rank
Calanoids	51. 3	1	51. 3	1
Unidentifiable animal remains	24. 8	2	23. 9	2
Compound-eyed crustaceans	13. 6	3	11. 9	4
Unidentified crustaceans	5. 2	7	15. 5	3
Euphausiids	10. 6	4	5. 3	5
Amphipods	8. 7	5	0. 7	8
Nauplii	0. 3	10. 5	4. 2	6
Cyclopoids	0. 5	9	0. 3	10
Cladocerans	0. 0	13	0. 1	11. 5
Chaetognaths	8. 4	6	0. 5	9
Fish larvae	1. 1	8	0. 0	13. 5
Polychaete larvae	0. 3	10. 5	0. 0	13. 5
Phytoplankton	0. 0	13	0. 8	7
Tintinnids	0. 0	13	0. 1	11. 5

$r_{su} = 0.7231$; $r_{sc} = 0.6744$; $r_{0.001, 14} = 0.7420$; $r_{0.010, 14} = 0.6226$;
$N_r = 14$.

where r_{su} = Spearman rank correlation coefficient uncorrected for ties.

r_{sc} = Spearman rank correlation coefficient corrected for ties.

N_r = Number of ranks.

Parathemisto pacifica had relative frequencies of 33.2% and 33.4% for all data, and May and June excluded data respectively. The results of the three tests on these data indicate no statistically significant differences in either the ranks or the frequencies within a rank (Table 31).

In conclusion, the analyses indicate that 51-52% of the feeding Parathemisto will contain calanoid copepods, about 35% will contain noncalanoid crustaceans; 24-25% will contain unidentifiable animal material; and a small portion (generally less than 10%) will contain a variety of other foods. These groupings are not mutually exclusive: an individual amphipod, especially the larger P. libellula, may eat several kinds of prey during a single feeding session. The apparent large differences in the relative use of the less frequently consumed prey by P. libellula and P. pacifica were not statistically significant, and may be an artifact of their infrequency. However, it appears that chaetognaths may be taken more often by P. libellula, and nauplii and phytoplankton more often by P. pacifica. The latter situation may be a consequence of the smaller size and year-round reproduction of P. pacifica resulting in small juveniles which may eat phytoplankton and nauplii more readily than the adults and larger juveniles of either P. libellula or P. pacifica.

Cannibalism and Interspecies Predation by Parathemisto

The significance of cannibalism by captive zooplankton, beyond the demonstration that cannibalism is possible, is subject to debate. The stomach analyses confirmed that cannibalism occurs in nature. Definite cannibalism by Parathemisto libellula was observed twice, and

TABLE 31.--Percentage occurrence, difference (d), and rank of food items in stomachs of Parathemisto libellula (9. 5-25. 0 mm) and P. pacifica (1. 0-8. 9 mm) in southeastern Alaska for all months except May and June

Food item	Percentage occurrence		d	d^2	Rank[a]
	P. libellula	P. pacifica			
Calanoids (large)	51. 5	51. 3	0. 2	0. 04	3. 5
Noncalanoid crustaceans[b]	38. 1	33. 4	4. 7	22. 09	10
Unidentifiable animal remains	24. 8	23. 9	0. 9	0. 81	7
Nauplii	0. 3	4. 2	-3. 9	15. 21	-9
Cyclopoids	0. 5	0. 3	0. 2	0. 04	3. 5
Cladocerans	0. 0	0. 1	-0. 1	0. 01	-1. 5
Chaetognaths	8. 4	0. 5	7. 9	62. 41	11
Fish larvae	1. 1	0. 0	1. 1	1. 21	8
Polychaete larvae	0. 3	0. 0	0. 3	0. 09	5
Tintinnids	0. 0	0. 1	-0. 1	0. 01	-1. 5
Phytoplankton	0. 0	0. 8	-0. 8	0. 64	-6

N = 11

t-test of difference means	Paired t-test of differences	Wilcoxon signed rank test
t = 0. 7177	t = 0. 3105	T = -18. 0
$t_{0.05, 10}$ = 2. 228	$t_{0.05, 10}$ = 2. 228	$T_{0.05, 11}$ = 11

[a]Signed rank = Wilcoxon signed rank of difference corrected for ties.

[b]This category includes amphipods, euphausiids, compound-eyed crustaceans, and unidentified crustaceans.

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suspected cannibalism by P. pacifica five times. Having a single

generation per year and a relatively narrow size distribution range,

it appears unlikely that P. libellula derives much of its normal diet

through cannibalism in southeastern Alaska. Parathemisto pacifica,

with multiple overlapping generations and a relatively wide size

distribution range, has the potential for a greater incidence of

cannibalism. However, the manner in which P. pacifica dismembers its

food would make cannibalism more difficult to detect. On the basis

of present data, it can be concluded only that P. pacifica is

cannibalistic at least as often and possibly more often than P.

libellula in southeastern Alaska. The incidence of cannibalism by P.

pacifica, if actually higher than observed here, may approach levels

observed in populations of Parathemisto gaudichaudii in the Gulf of

Maine, and of P. libellula from Baffin Island. Of 7 P. gaudichaudii

examined by Bigelow (1926), one was a cannibal, while 4 of 20 P. libellula

examined by Dunbar (1942) were cannibals. Both of those populations are

composed of overlapping generations with large adults, and cannibalism

appears higher in these than in southeastern Alaska.

Interspecies predation in Parathemisto in southeastern Alaska

appears restricted to P. libellula preying on P. pacifica. Of the

33 times P. libellula was found feeding on amphipods, 11 were positively

identified as P. pacifica; and 17, although identifiable only as

Parathemisto sp., were probably P. pacifica rather than P. libellula.

Except for the months of May and June, all P. libellula were larger

than P. pacifica. Parathemisto libellula should be able to prey

effectively on the smaller P. pacifica from July through April and to

obtain 5-10% of its food this way. Except for the short period of May and June, predation of P. pacifica on P. libellula is unlikely.

Feeding Behavior of Parathemisto

While keeping Parathemisto in the laboratory for oxygen uptake experiments, I was able to make observations on their feeding behavior response to various prey. Material offered consisted of cut foods (small pieces of scallop, mussel, sea urchin, frozen euphausiids, frozen brine shrimp, herring, cod, or flatfish) and live zooplankton. The live food was obtained in three ways: mixed zooplankton taken in net tows, fish and crab larvae hatched in the laboratory, and small gammarid amphipods (Anisogammarus sp.) gathered intertidally.

In the laboratory, the Parathemisto usually spent most of their time lying on their sides at the bottom of the holding containers. When offered cut foods, active feeding and/or search for food did not occur unless the food pieces actually touched the amphipod. Pieces of food dropped or placed over 5 cm from an amphipod often were not found within 24 hours. Pieces of food impaled on glass probes and moved slowly in front of the amphipods at distances of 1-20 cm were not followed nor was there evidence of directed movement toward food which was either still or moving. However, if a piece of food touched the amphipod, it was readily grasped and consumed.

The grasping response is an extension and closing of the elongate 5th, 6th, and 7th pereopods. Once closed about a piece of food, the pereopods appear to be temporarily locked, and the food item is not readily released. It is possible to lift an amphipod out of the water by holding a piece of food it has just grasped. After a piece of cut

food has been seized the amphipod uses the gnathopods and the 3d and

4th pereopods to manipulate and present the food to the oral appendages

for mastication and ingestion.

If on first contact the amphipod does not successfully grasp the

food, it swims rapidly in an erratic circling pattern with pereopods 5-7

extended outward from the body. Parathemisto libellula (15-25 mm long)

usually swim in circles of 5-20-cm in diameter, while the smaller P. pacifica

swim in circles 3-10 cm in diameter, the size and direction of the circles

appear to be random. Rapid circling seldom exceeds 1 minute before the

amphipod either stops swimming and settles to the bottom of the container

or swims steadily and slowly around the container. If food is contacted

and successfully grasped during the erratic swimming phase, the amphipod

either swims a few seconds longer or immediately settles to the bottom

to consume the food.

When offered live food in the laboratory, the "search" behavior

is the same as the response to missing cut food. Movements directed

obviously towards living food were not observed. Initial, apparently

accidental contact with a potential prey results in a rapid turn in the

direction of the contact and grabbing motions with pereopods 5 to 7. If

the prey is missed, the erratic circling behavior is evoked. If the prey

is captured, it is killed and eaten, usually while the amphipod rests on

the bottom of the container.

The elongate 5th, 6th, and 7th pereopods, which characterize the

genus Parathemisto, are the primary food-capturing limbs. When extended,

they appear to be prestressed for rapid traplike closing. Opening and

spreading pereopods 5-7 to form a sweeping basket takes longer than

closing. Once the pereopods have closed about a prey, the gnathopods

and 3d and 4th pereopods appear to be used to control and manipulate the victim. Most prey appear to be killed by biting, and the gnathopods may be used in tearing and dismemberment.

Small crustacean prey such as copepods and larval forms (Pseudocalanus, Metridia, Euchaeta, Balanus nauplii, and zoeae of Cancer, Chionoecetes, and Pagurus) were quickly killed and consumed by Parathemisto libellula. These prey were consumed whole, and in the laboratory no parts were discarded. Dismemberment observed in the stomach samples of preserved field collections may have been the result of crushing and tearing by the mandibles and gastric apparatus, as well as by the action of the gnathopods.

Arrowworms (Sagitta elegans--10-30 mm) and blennioid fish larvae (5-10 mm) were readily accepted as prey by Parathemisto libellula. These elongate zooplankters were easily captured by the amphipods and seldom escaped first contact, whereas more active crustaceans often were missed or escaped. The elongate form and high susceptibility to physical damage appear to increase the vulnerability of arrowworms and fish larvae to accidental contact with and retention by the elongate pereopods. (Most of the arrowworms used in feeding were damaged by the net, and few survived beyond 6 hours in captivity). Living arrowworms captured by P. libellula struggled very little and were generally consumed within 4-5 minutes. Fish larvae hatched in the laboratory were pipetted into the amphipod containers with a wide-bore pipette. Some fish larvae survived over 2 days before capture by the amphipod. When captured, the fish larvae appeared to die almost instantaneously from the shock and pressure of the closing pereopods. Struggling

consisted of only a quivering and straightening of the body of the larval fish. The fish larva was rapidly transferred from the capture legs to the gnathopods and mouth. Whole fish larvae were consumed in less than 2 minutes from the time of capture. The amphipods made no distinction between head or tail when consuming arrowworms or fish larvae. Eating began at either end and quickly worked down the length of the prey. I could not observe the amphipod's mouth parts in action, but analysis of stomachs from field collections indicated that the mandibles cut the arrowworms into short segments. The stronger bodied fish larvae were consumed relatively intact.

Capture and killing of crustaceans over 5 mm long by Parathemisto libellula were essentially the same as described for smaller prey. Parathemisto libellula 17-25 mm long were offered 5- 10-mm long amphipods (Cyphocaris challengeri and Anisogammarus sp.), and euphausiids (Thysanoessa raschii). These relatively large prey proved difficult for the Parathemisto to hold and kill. Often amphipods and euphausiids struggled enough to escape, even when apparently completely entrapped by the pereopods of the Parathemisto. Prey amphipods, possibly because they are more compact and have a harder exoskeleton, appeared to escape more often than did the euphausiids.

If the Parathemisto was successful in subduing an amphipod or a euphausiid, a distinct pattern of feeding occurred. The prey was oriented with the ventral surface and head toward the mouth of the Parathemisto. The 3d and 4th pereopods held the prey while the gnathopods were used to dismember it. The head and thoracic appendages were pulled off and partially consumed until the thoracic cavity had been opened. Having opened the thoracic cavity, the Parathemisto then

began to pull pieces of meat from the interior of the thorax and the head. With access to the body cavity, the gnathopods continued to progressively open the ventral side of the prey, working through the thorax and the abdomen. Some but not all abdominal and thoracic appendages were consumed in the process. The dorsal exoskeleton was discarded after most of the meat in the abdomen had been removed. The discarded portions of euphasiids generally consisted of the carapace and articulated abdominal cuticle, while discarded portions of amphipods often consisted of the complete exoskeleton (less legs) as a unit.

Although the initiation of cannibalism was not observed in the laboratory, examination of Parathemisto libellula and P. pacifica which had been partially eaten by container mates, showed that entrance to the body cavity started ventrally behind the head and progressed along the ventral side of the body in the same manner as observed when the Parathemisto fed on other amphipods.

The time required to consume amphipods and euphausiids was much longer than that for small crustaceans, fish larvae, and arrowworms. On one occasion, a 20-mm Parathemisto libellula was offered a 10-mm Anisogammarus that had been injured by a strong pinch in the midbody with forceps. Despite the size difference and the crippled state of the prey amphipod, one-half hour was required for the Parathemisto to subdue and kill the Anisogammarus. An additional full hour was spent dismembering and consuming the small amphipod before the exoskeleton was discarded.

Response to mixed prey selections was observed only for Parathemisto libellula. Mixtures of arrowworms, euphausiids, amphipods, and copepods were offered. The arrowworms, Sagitta elegans, were

captured and consumed on the first day. Several euphausiids, Thysanoessa raschii, were taken on the second and third days. The copepods, Euchaeta japonica and Metridia longa, and the amphipods, Cyphocaris challengeri, escaped capture for over 4 days. These laboratory observations indicate that P. libellula is better adapted to prey on elongate easily killed prey such as arrowworms and fish larvae than on the more abundant copepods and euphausiids. Copepods and euphausiids are the most numerous foods found in stomach analyses, probably because they are the most available foods and because the chitinous exoskeletons are not easily digested and therefore more often remain to be identified by the observer.

Lipid Content of Parathemisto libellula

Lipids are a major form of stored energy reserves in marine organisms. Seasonal variation of lipid content in zooplankton from high latitude and polar regions may be related to either the reproductive cycles or the need to survive extended periods of low food supply (Littlepage, 1964). Lipid content and composition may also vary with amount and type of food (Lee, Nevenzel, and Paffenhofer, 1971) and the length of period of starvation (Lee, Hirota, and Barnett, 1971). Lipid storage in Parathemisto appears to be primarily in the digestive diverticula, a pair of caeca fused to the midgut wall, which vary greatly with the amount of stored lipids (Bowman, 1960). In small P. japonica, stored lipids may approach 40% of dry weight (Nakai, 1942), but data on other sizes and species are lacking.

I attempted to obtain data on the seasonal variation of lipid content for Parathemisto pacifica and P. libellula from March to

December 1972. Parathemisto pacifica were not collected in sufficient quanttities for the analyses planned, but adequate numbers of P. libellula were obtained during 4 months. Samples were taken in March at Point Retreat, using the 6-foot Isaacs-Kidd midwater trawl towed at 50-m depth. Samples from October 1972 were taken at the junction of Stephens Passage and Fredrick Sound with the 60-cm Bongo nets towed obliquely from 250 m to the surface. Samples for November were taken with the Bongo nets at the mouth of Berners Bay, and at Outer Point near Auke Bay. The single December sample was taken at Outer Point with a 1-m NORPAC net towed at 25-m depth.

The amphipods were frozen in labeled plastic bags immediately after capture and held frozen until analysis in August 1973. Power failures and other mishaps resulted in the samples being thawed and refrozen several times. Because of these inadvertent accidents, the resulting data may be unreliable and the conclusions based on them may be invalid.

Total lipid contents of one-half of each sample were determined by a modification of the Folch method (Folch, Lees, and Stanley, 1957). One-half of each sample was homogenized in a blender with 25 ml of 2:1 chloroform-menthol solution. The homogenate was then filtered into a separatory funnel through a fat-free filter, and the homogenating flask was rinsed once with 12.5 ml of the chloroform-menthol solution. After filtration, 5.75 ml of 0.9% aqueous NaCl solution was added to the extract; the mixture was shaken and allowed to stand for 90 minutes until two phases had formed. The lower phase (chloroform and lipid) was then drawn off and blocked up to 25 ml with reagent grade chloroform. This final solution was then placed in a tared aluminum

weighing pan and evaporated overnight in a fume hood at room temperature (22° C). The following morning the dried pans were weighed on a microbalance to obtain the total lipids extracted.

The half of each sample not extracted was used to obtain estimates of wet and dry weight. The total sample was weighed wet before extraction, one-half of the amphipods removed for extraction, the remaining half reweighed wet, then dried for 1-3 days at 90° C. This may have been an excessively high temperature for drying, and may have given an underestimate of dry weights through a loss of some volatile organic compounds. The ratios of the final dry weights to the original wet weights were used to estimate the dry weights of the extracted samples.

The resulting total lipids as percent of dry weight show considerable variation between replicate samples (Table 32). There is no apparent difference between sets of samples indicative of significant temporal variation in the total lipids of Parathemisto libellula. If there is a temporal variaton, it has been obscured by analytical errors.

The values for total lipids (7.79-19.15%) fall within the range of total lipids for other macroplankton such as euphausiids (Littlepage, 1964; Morris, 1971; Pierce et al., 1969), littoral mysids (Clutter and Theilacker, 1971; Morris, 1973), and sergestid shrimp (Donaldson, 1973) but well below the 39.6% reported by Nakai (1942) for Parathemisto sp. (? P. japonica). Although Nakai's specimens were 1.46 mg average weight compared to the 15-41 mg average weights in my material, states of maturity or feeding habits may have been different. Brooding females were not included in my material for March, and the October-December specimens were late juveniles. Although it is tempting to attribute the

Table 32. -- Total lipid contents of Parathemisto libellula from south-
eastern Alaska samples, March-December 1972

Date sample taken	No. P. libellula analyzed	Wet weight (g)	Dry weight (g)	Weight lipids (g)	Lipids (% dry weight)
22 March	36	6.887	1.076	0.122	11.38
23 March (1)	28	5.875	0.678	0.090	13.31
23 March (2)	28	4.424	0.541	0.081	14.89
23 March (3)	26	7.309	1.064	0.095	8.96
17 October (1)	25	4.173	0.506	0.083	16.42
17 October (2)	25	3.587	0.532	0.073	13.72
17 October (3)	28	4.031	0.610	0.088	14.37
14 November (1)	25	3.296	0.423	0.081	19.15
14 November (2)	23	2.482	0.357	0.097	16.66
17 November	14	0.766	0.188	0.024	12.89
18 December	27	3.818	0.561	0.044	7.76

differences between my values and Nakai's to species differences, the
variance in reported values in the literature for other zooplankton is
too large and the effect of other factors too strong to warrant such a
comparison.

VI. RESULTS AND DISCUSSION OF
PHYSIOLOGICAL STUDIES

Respiratory Metabolism of Parathemisto libellula

Oxygen uptake rates of whole animals are an integrated response to physiological state and environment. Respiration rates of invertebrates are most responsive to thermal changes; but other biological, chemical, and physical factors also alter respiration rates. Age, sexual maturity, size, nutritional state, seasonal and circadian rhythms, diel light cycles, light intensity, light wavelength, various chemicals, crowding, disturbance, etc. have been demonstrated to affect the oxygen consumption rates of crustaceans under experimental conditions (Wolvekamp and Waterman, 1960; Lockwood, 1967; Buikema, 1972). The present investigations on the respiration rates of Parathemisto were designed primarily to examine the effect of temperature changes and possible accommodation by P. libellula and P. pacifica to such temperature changes. It was not always possible to assure uniform experimental conditions; therefore, factors other than temperature had to be taken into account and evaluated. The additional factors examined were: (1) variations in experimental techniques, (2) weight, (3) sex, (4) variations in salinity, (5) proximity to molting, (6) proximity to death, and (7) time in captivity. The following sections will present the results of observations on the respiration rates of P. libellula at temperatures of -1.6° C to 17° C and a discussion of the relationship of the additional factors (vide supra) to the respiration rates of P. libellula.

A stepwise linear regression was applied to the respiration data for Parathemisto libellula using the BioMedical computer program package BMD 02R. Multiple linear regressions obtained from such programs give a least squares best fit regression in which the appropriate independent

variables are chosen and entered into the regression in the order of their squared correlation coefficients (Afifi and Azen, 1972). The program used here added variables successively until the correlation of the regression and the dependent variable (oxygen consumed/hour) was no longer improved by at least 0.01%.

For the 16 subsets of data (8 wet weight and 8 dry weight) to which the stepwise regression was applied, the sequence in which the independent variables were added into the regression was fairly consistent (Table 33). Temperature and weight were the most important variables for predicting oxygen consumption rates. The narrow range of salinity $(30.7-32.4^{\circ}/_{\circ\circ})$ had the third strongest correlation with respiration. Days in captivity and days allowed for acclimation were the 4th and 5th ranking variables. In two subsets, days in captivity and in one subset, days of acclimation were insufficiently correlated with respiration rate to be considered for inclusion into the regressions. In general, the inclusion of salinity was a modest improvement to the regressions, and days of captivity and days of acclimation were of minor, almost insignificant value in predicting the respiration rates. Tables 34 and 35 present the regression coefficients and their standard errors for each of the subsets regressed.

Response to Variations of Experimental Technique

Most of the data on oxygen consumption were collected using the Gilson respirometer in the dark with the shaker set for 70 cycles per minute, and during the hours of 0900-1700. To test whether the continuous shaking, darkness, and time of day were influencing the observations, a sequence of experiments at 4° C comparing day and night,

TABLE 33. --Ranks of importance of five variables in wet and dry
weight regressions for respiration rates of
Parathemisto libellula over six temperature ranges

Variable[a]	Temperature range (° C)							
	-1.6 to 2.0	-1.6 to 5.0	-1.6 to 17.0	-1.6 to 17.0[b]	-1.6 to 17.0[c]	-1.6 to 16.0[d]	10.0 to 17.0	10.0 to 17.0[b]
Wet weight regressions								
Temperature	2	1	1	1	1	1	2	2
Weight	1	2	2	2	2	2	3	1
Salinity	3	3	3	3	3	5	1	3
Days in captivity	5	4	4	4	4	3	..	5
Days of acclimation	4	5	5	5	5	4	4	4
Dry weight regressions								
Temperature	2	1	1	1	1	1	2	2
Weight	1	2	2	2	2	2	1	1
Salinity	4	3	3	4	4	5	3	4
Days in captivity	..	4	4	3	3	3	4	5
Days of acclimation	3	5	..	5	5	4	5	3

[a]Mean ranks: temperature = 1.38; weight = 1.75; salinity = 3.12;
days in captivity = 4.06; days of acclimation = 4.44.

[b]Data from experiment at 10.5°C excluded.

[c]Females only.

[d]Males only.

TABLE 34. --Regression relationships of log oxygen consumption rate ($\hat{Y}$) of __Parathemisto libellula__ to log wet weight (X_{ww}), log dry weight (X_{dw}), temperature (X_t), salinity (X_s), days in captivity (X_c) and days of acclimation (X_a)

Temperature range (° C)	Regression equations	N	Equation no.
-1.6 to 2.0	$\hat{Y} = -2.04904 + 0.59477X_{ww} + 0.05497X_t + 0.05028X_s - 0.00015X_c + 0.00288X_a$	87	1
	$\hat{Y} = -0.92342 + 0.53626X_{dw} + 0.05271X_t + 0.02975X_s + 0.00000X_c + 0.00352X_a$	87	2
-1.6 to 5.0	$\hat{Y} = -2.47226 + 0.44141X_{ww} + 0.05560X_t + 0.07468X_s - 0.00042X_c - 0.00048X_a$	225	3
	$\hat{Y} = -1.41658 + 0.41405X_{dw} + 0.05764X_t + 0.05168X_s - 0.00025X_c - 0.00083X_a$	225	4
-1.6 to 17.0	$\hat{Y} = -2.79225 + 0.44736X_{ww} + 0.03365X_t + 0.08474X_s + 0.00086X_c - 0.00152X_a$	348	5
	$\hat{Y} = -1.34583 + 0.47728X_{dw} + 0.03784X_t + 0.04706X_s + 0.00074X_c - 0.00000X_a$	348	6
-1.6 to 17.0[a]	$\hat{Y} = -2.38677 + 0.53900X_{ww} + 0.03270X_t + 0.06548X_s + 0.00122X_c - 0.00156X_a$	338	7
	$\hat{Y} = -0.68899 + 0.56269X_{dw} + 0.03760X_t + 0.02206X_s + 0.00108X_c + 0.00020X_a$	338	8
-1.6 to 17.0[a] (females only)	$\hat{Y} = -2.23162 + 0.56694X_{ww} + 0.03202X_t + 0.05888X_s + 0.00043X_c - 0.00033X_a$	241	9
	$\hat{Y} = -0.82549 + 0.58816X_{dw} + 0.03819X_t + 0.02519X_s + 0.00064X_c + 0.00056X_a$	241	10
-1.6 to 16.0[a] (males only)	$\hat{Y} = -0.92832 + 0.51212X_{ww} + 0.03103X_t + 0.02325X_s + 0.00071X_c - 0.00339X_a$	97	11
	$\hat{Y} = +1.37276 + 0.36718X_{dw} + 0.03118X_t - 0.03127X_s + 0.00027X_c - 0.00330X_a$	97	12
10.0 to 17.0	$\hat{Y} = -4.77696 + 0.43511X_{ww} + 0.02238X_t + 0.15397X_s + 0.00000X_c - 0.00938X_a$	99	13
	$\hat{Y} = -2.87867 + 0.51282X_{dw} + 0.02728X_t + 0.09975X_s - 0.00071X_c - 0.00704X_a$	99	14
10.0 to 17.0[a]	$\hat{Y} = -4.28419 + 0.61261X_{ww} + 0.02890X_t + 0.12253X_s + 0.00108X_c - 0.00884X_a$	89	15
	$\hat{Y} = -1.49952 + 0.73868X_{dw} + 0.03681X_t + 0.04134X_s + 0.00024X_c - 0.00538X_a$	89	16

[a]Data from 10.5°C excluded.

TABLE 35.--Regression statistics for oxygen consumption rate relationships of Parathemisto libellula
(See table 34)

Equation no.	Degrees of freedom	Standard error of estimate	Multiple[a] correlation coefficient	F[b]	Standard errors of estimate for partial regression coefficients				
					X_w	X_t	X_s	X_c	X_a
1	81	0.1112	0.6737	13.462	0.13268	0.01414	0.04231	0.00141	0.00288
2	82	0.1079	0.6922	18.862	0.10491	0.01223	0.04187	..	0.00262
3	219	0.1120	0.7710	64.218	0.07899	0.00351	0.02414	0.00047	0.00199
4	219	0.1109	0.7762	66.384	0.06877	0.00345	0.02537	0.00047	0.00198
5	342	0.1234	0.8287	149.996	0.06129	0.00133	0.01904	0.00036	0.00177
6	343	0.1214	0.8370	200.594	0.05630	0.00136	0.02022	0.00035	..
7	332	0.1224	0.8321	149.423	0.06410	0.00133	0.01928	0.00037	0.00174
8	332	0.1193	0.8414	160.995	0.05857	0.00137	0.02065	0.00035	0.00169
9	235	0.1225	0.8506	123.211	0.07950	0.00157	0.02349	0.00060	0.00195
10	235	0.1176	0.8634	137.653	0.06786	0.00150	0.02378	0.00057	0.00187
11	91	0.1186	0.7504	23.454	0.18468	0.00352	0.04962	0.00064	0.00471
12	91	0.1198	0.7441	22.572	0.15517	0.00371	0.05512	0.00065	0.00481
13	94	0.1208	0.6809	20.315	0.09319	0.00479	0.02875	..	0.00333
14	93	0.1187	0.6985	17.724	0.09897	0.00487	0.03332	0.00083	0.00330
15	83	0.1186	0.7307	19.012	0.10517	0.00512	0.03049	0.00087	0.00333
16	83	0.1134	0.7578	22.387	0.11010	0.00523	0.03497	0.00083	0.00318

[a]$P < 0.010$ for all $R_{y \cdot x}$.   [b]$P < 0.001$ for all F.

in the dark with and without shaking, and light without shaking was performed. The light source was a 100-watt frosted incandescent bulb placed 30 cm above the respirometer. During the experiments, the respirometer was filled with an aqua-colored antifreeze-tapwater solution set for -10° C. Total oxygen consumed at the end of 6 hours was recorded for each condition (Table 36). Because the same group of animals was used for all six experiments, paired t-tests (Ostle, 1963) were used to evaluate for significant differences, and F-tests (Ostle, 1963) to assess changes in variance due to conditions. Neither the t-tests nor the F-tests resulted in rejection of the null hypotheses of no effect due to altering the experimental conditions. The shaking may have had a marginal effect when combined with the bright light, compared to the dark and no-shaking conditions. The slightly lower rates observed under the no-shaking conditions may be due to a lag in the diffusion of oxygen into the water and/or carbon dioxide absorption by the KOH wicks, either of which would result in low manometer readings. The lack of significant differences in these experiments indicates that: (1) the continuous shaking at 70 cycles per minute was not raising the respiration rate, (2) there is no inherent diurnal rhythm in the respiration rates, (3) high light intensities comparable to or above that that the amphipods would experience at the surface on a bright day do not affect the respiration rates, and (4) the respiration rates of the individual amphipods did not change over the 6-day period in which the experiments were performed.

Parathemisto libellula's lack of diel rhythm, lack of response to continuous high light or continuous low light levels, and insensitivity to the shaking of the respirometer are very much like that of Euphausia

TABLE 36. --Oxygen consumption rates (μl O_2/6 hours) for <u>Parathemisto libellula</u> subjected to five variations of experimental technique[a] in daytime (0900-1700) and nighttime (2100-0300). Six experiments were run

P. libellula No.	Daytime				Nighttime	
	1 Dark, shaking	2 Light, shaking	3 Dark, no shaking	4 Light, no shaking	5 Dark, shaking	6 Dark, shaking
1	62.3	52.8	51.6	47.8	67.5	70.5
2	49.5	45.5	48.2	39.2	55.1	54.7
3	54.0	57.5	57.2	52.9	..	..
4	64.0	72.2	..	..	..	..
5	..	..	47.2	44.4	68.1	61.7
6	58.2	48.8	43.5	41.1	62.5	70.1
7	45.2	39.3	38.9	32.0	61.6	62.4
8	62.2	65.5	53.4	48.9	65.1	65.9
9	96.8	95.5	..	..	..	..
10	48.7	64.8	49.8	55.8	61.2	40.5
11	48.1	52.5	36.3	40.5	52.5	55.2
12	..	..	..	..	53.2	51.0

Paired t-tests

Pair	t_D	$t_{(0.05,\ n-1)}$
1 vs 2	0.063	2.262
3 vs 4	0.539	2.306
5 vs 6	0.203	2.306
1 vs 5	1.446	2.447
1 vs 6	0.818	2.447
(5 + 6)vs 1	1.433	2.447

[a]Terminology for the five variations is as follows: dark, no light admitted; light, illuminated by 100-watt frosted bulb 30 cm above respirometer; shaking, respirometer shaker set for 70 cycles per minute; no shaking, shaker turned off.

pacifica (Pearcy, Theilacker, and Lasker, 1969).

Temperature Relationships

Respiration rates of Parathemisto libellula are most strongly correlated with temperature, and secondly with weight (Table 33). Plots of respiration rates against temperature suggest slightly different relationships at high and low temperatures and a bimodal distribution in the 7.5° C observations (Figure 32).

A single preliminary experiment in 1972 at 7.5° C had significantly lower mean respiration rates than had been observed at 5° C and at 10° C. Consequently, when respiration experiments were resumed in the winter of 1972-73, a sequence of six determinations of respiration rates was made on one group of amphipods. Using the temperature sequence of 5° C, 7.5° C, 10° C, 7.5° C, 5° C, and 5° C, the individual oxygen comsumptions for 6-hour periods were compared by graphic plots (Figure 33) and analyzed statistically with paired t-tests and F-tests for mean temperature effects and effects on variance (Table 37). The null hypothesis of no significant mean effect due to temperature or between experiments was rejected only for the comparison of 5° C and 10° C 6-hour oxygen consumptions $(t=5.97 > t_{.975,7} = 2.37)$. The null hypothesis of equal variances was rejected only for the comparison of the first (5° C) and second (7.5° C) experiments in the series, although in the second experiment the variance was the largest of the series. The data are not conclusive but do indicate that individual animals were responding differently during the rising temperature phase of the experimental series. During the falling temperature phase, individual variance appeared strongest at 5° C.

TEMPERATURE (°C)

```
        -2.400          1.600           5.600           9.600           13.600
               -.400            3.600           7.600          11.600          15.600          17.600
-.240
-.270
-.300
-.330
-.360
-.390                                                                                    1
-.420
-.450
-.480
-.510
-.540
-.570                                                         2                       2
-.600                                                         1
-.630
-.660                                                         2                1      1
-.690                                                         2                       1
-.720                                                                                 2
-.750                            1               2         1  1            2    1      1      1
-.780                       1                               2  1           2    2      2    1
-.810                  1     1                             2  2           3    6      2    2
-.840                        1                             6              2
-.870               2 3      2                            2               2    1
-.900               1        2               1           2               1
-.930               5                        3           2                    2
-.960               5     1                  5           4               2    2
-.990      1        1 5   2 5                2           4                     1
-1.020             2 4   3 5                 1           4               2
-1.050       1     3 A  11 5                 1           3               2
-1.080             2 4  13 5                 3           2               1
-1.110         3   3 5   3 1                 2           1
-1.140      1      9 22                      2
-1.170    1  1     1 3  21 1                             2
-1.200    1  2   1   3  12 1                             1
-1.230       3   2   1 1 1                   1
-1.260    4  7       1
-1.290    6  2   2   1
-1.320       8               2                           1
-1.350    5  2   1                                       1
-1.380    2  3
-1.410    5  3       1                       1
-1.440    1  3                    1
-1.470    2
-1.500    3
-1.530       1
-1.560    3  1                    1
-1.590    2  1
-1.620
-1.650
-1.680
-1.710
-1.740
```

LOG 4/LITER O₂/MG WET WEIGHT/HOUR

Fig. 32.--Relationship of respiration rate of Parathemisto libellula to temperature. Numbers (or letters) are the numbers of observations at each point. The letters A through G represent number 10 through 16 respectively
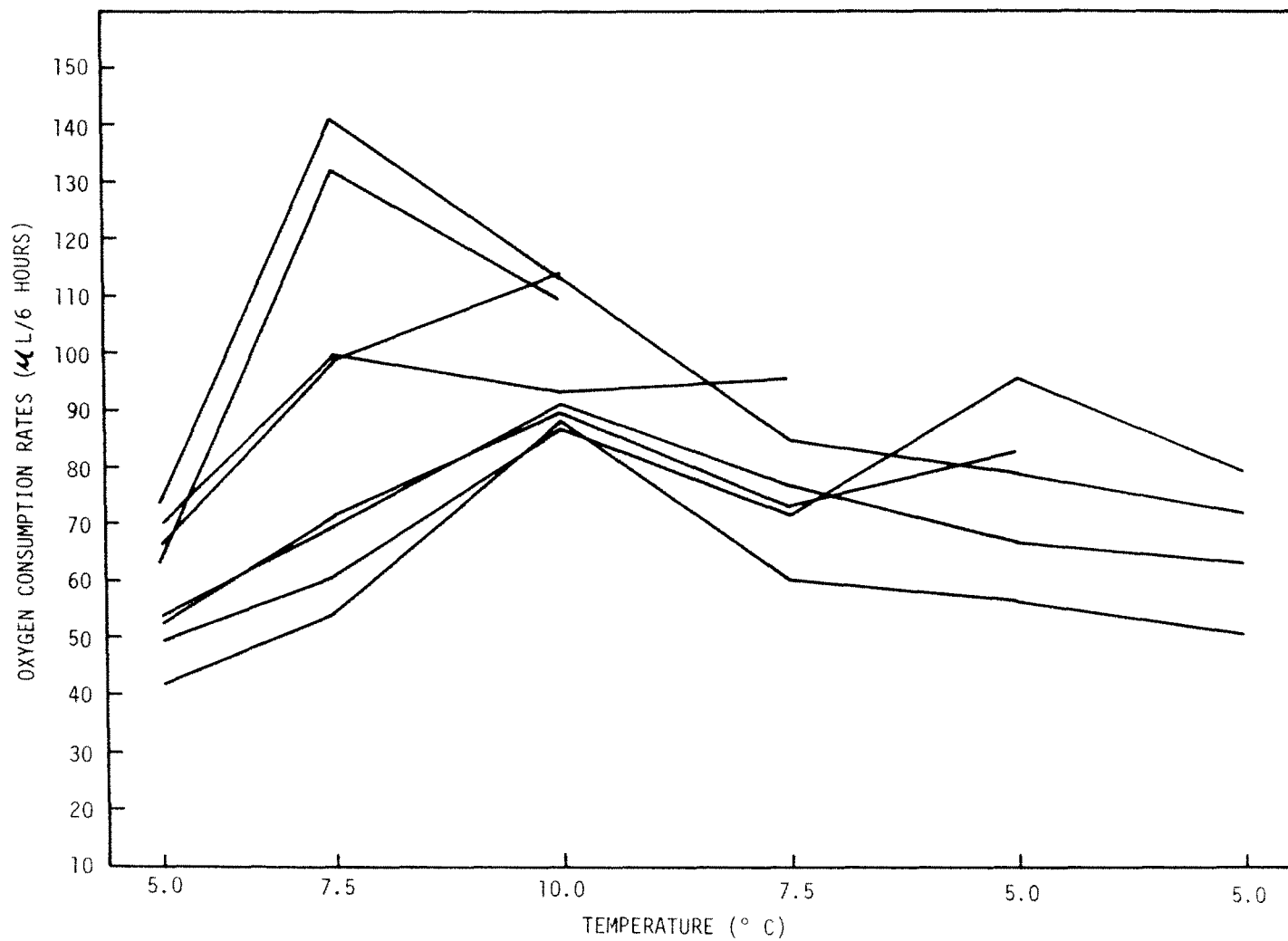
Fig. 33.--Six-hour respiration rates by individual Parathemisto libellula at 5.0°C, 7.5°C, and 10°C

TABLE 37. --Oxygen consumption rates (μl O_2/6 hours) for individual Parathemisto libellula at temperatures of 5°, 7.5°, and 10° C. Experiments performed in order numbered

P. libellula No.	1 5.0°	2 7.5°	3 10.0°	4 7.5°	5 5.0°	6 5.0°
1	62.8	131.8	109.3	..	..	..
2	41.4	54.3	87.9	59.9	56.6	50.9
3	49.3	60.5	87.6	71.7	95.5	79.0
4	52.2	71.4	89.5	72.5	82.7	80.5
5	66.5	98.5	113.9	..	..	..
6	69.8	98.7	92.7	95.6	..	..
7	52.8	69.1	90.3	76.6	66.7	63.1
8	73.2	141.3	112.7	84.5	78.9	72.0

Paired t-tests   F-test of variance

Pair	t_D	$t_{(0.05, n-1)}$	F	$F_{(0.05, n_1, n_2)}$
1 vs 2	1.371	2.365	8.510*	5.12
1 vs 3	5.973*	2.365	1.311	5.12
2 vs 4	0.225	2.571	7.137	7.15
2 vs 4 (less No. 8)	0.800	2.779	1.727	9.60
1 vs 5	1.386	2.776	1.791	9.60
1 vs 6	1.152	2.776	1.206	9.60
5 vs 6	1.302	2.776	1.409	9.60
3 vs 4	1.456	2.571	1.103	7.15
2 vs 3	0.462	2.571	6.465	7.15

*Significant at 0.05

The stepwise regression program was applied to the oxygen consumption uptake data for each sex separately and over the temperature ranges of -1.6° C to 5.0° C and 10.0° C to 17.0° C, as well as to the combined data for males and females. The data for 7.5° C were excluded from the high and from the low temperature ranges because of the biomodality and the suspicion that it represented two overlapping physiological responses to temperature change. Data from a single experiment at 10.5° C were rejected from some regressions because they are anomalously high, and appear to be outside the normal distribution for respiration rates (Figure 32).

The regression coefficients for temperature do not differ significantly for sexes (Tables 34 and 35). The trend of higher temperature coefficients in the regressions utilizing dry weights than in wet weight regressions is not statistically significant (Tables 34 and 35). Temperature coefficients of regressions for low temperature ranges (-1.6° C to 5.0° C) are 0.05271-0.05764, and are significantly higher than the temperature coefficients of 0.02890-0.03681 for the high temperature range (10.0° C to 17.0° C). The temperature coefficients for the total temperature range of -1.6° C to 17.0° C do not differ statistically from the high temperature range but are separable from the low temperature range coefficients, indicating a stronger effect of response to high temperatures than to low temperatures.

The ability of an organism or biological system to adapt to thermal changes of the environment is generally assumed to be reflected by the degree to which homeostasis is attained. Rate-temperature relationships may be expressed in terms of either the regression coefficients as has been done for the oxygen consumption rates above, or in terms of the Q_{10}

(the ratio of rates determined at temperatures 10° C apart). When
dealing with stenothermal systems, or when it is inconvenient to
determine rates at 10° C intervals, Q_{10} may be determined by the Van't
Hoff equation:

$$Q_{10} = \frac{k_2}{k_1}^{10/(t_2-t_1)} \quad \text{or}$$

$$\text{Log } Q_{10} = \frac{10}{t_2-t_1} \text{Log } \frac{k_2}{k_1}$$

where k_2 is the rate at the high temperature t_2 and k_1 is the rate at the
lower temperature t_1 (Giese, 1968). The Q_{10} for respiration from
regression is the antilogarithm of 10 times the regression coefficient
for temperature:

$$Q_{10} = \text{Antilog } 10(b_t).$$

The Q_{10}'s that can be obtained from my data are not strictly
comparable to the Q_{10}'s normally derived from acutely determined
respiration temperature studies, although the values are quite similar.
From the regressions for oxygen consumption for the Parathemisto
libellula, Q_{10} in the low temperature range of -1.6° C to 5.0° C is
between 3.366 and 3.767; in the temperature range of 10° C to 17° C, it
is between 1.945 and 2.334. Both these ranges of Q_{10} are considered to be
representative of poikilotherms which do not regulate metabolic activity in
response to acute temperature changes. Marine crustaceans generally
show acclimation to temperature changes by a lateral shift of the
rate-temperature curve and do not rotate the curve--that is, the
response to new stable environmental temperatures is one of either
raising or lowering the total thermal response according to demands
of the animal rather than the changing relationship of the response

(Scholander et al., 1953). The lateral shift of the P. libellula respiration-rate of temperature curve is most clearly evident in the wet weight regressions (Table 34) where the constant is -2.04904 to -2.47226 for temperatures of -1.6° C to 5.0° C, and falls to -4.28419 for the 10.0° C to 17.0° C temperature range. This indicates an adjustment of lowered metabolic rates in response to acclimation to higher temperatures.

Although the rotation of the rate-temperature curves by marine crustaceans has been denied (Scholander et al., 1953), a lowering of the Q_{10} at high temperatures or a raising of Q_{10} at low temperatures is frequently observed (Kinne, 1963; Scholander et al., 1953). The significance of this change in Q_{10}'s with temperature remains unexplained but suggests that some rotation of the rate-temperature curves does occur as a partial response to high temperatures. A great many tropical and temperate invertebrates reside normally at temperatures closer to their upper lethal limits than to their lower lethal limits. Although Q_{10}'s of 2-3 are representative of nonadaptive conformation of metabolic rates to temperature changes, the ability to alter the Q_{10} from 3-4 at low temperatures to 2-3 at high temperatures may be significant in imparting survival ability during those seasons or periods when temperatures may temporarily approach upper lethal limits.

The high Q_{10}'s observed at low temperatures may not be representative or predictive of the ability of an animal to function at low temperatures. Metabolic rates of fish commonly exhibit a high upward variability at low temperatures compared to trends established by measuring rates at higher temperatures (Wohlschlag, 1964). A similar trend is shown in my data for Parathemisto libellula (Figure 32), and in the data of Scholander et al. (1953) for Arctic gammarids, and

possibly in the data of Armitage (1962) for the Antarctic <u>Orchomonella</u> <u>chiliensis</u>. Although causes of this excess upward variability remain unexplained, it should allow at least a portion of any population to remain active at temperatures below normal.

No previous work has been done on the metabolic response of planktonic amphipods to temperature changes. Three studies on benthic gammarids (Krog, 1954; Scholander et al., 1953; Armitage, 1962) have examined the temperature responses of polar benthic gammarids. These demonstrated that metabolic compensation to low temperatures was by increased respiration rates when compared with extrapolated curves for temperate amphipods. The Arctic gammarids were able to tolerate broad temperature ranges, and exhibited some compensation to temperature changes, but were primarily conformers at low temperatures. The Antarctic gammarid, <u>Orchomonella</u> <u>chiliensis</u>, also tolerated a wide temperature range (-1.8° C to 12.0° C), but was a regulator at low temperatures (-1.8° C to 6.0° C) and a conformer at higher temperatures. The planktonic hyperiid, <u>Parathemisto</u> <u>libellula</u>, seems comparable to the Arctic gammarids in its responses to temperature, appearing to be a strict conformer at temperatures less than 5° C and a partial regulator at temperatures above 10° C. Upper tolerance limits of <u>P</u>. <u>libellula</u> are also similar to the Arctic gammarids, in that the upper lethal limit appeared to be in the range of 15° C to 18° C. I had high mortalities in all attempts to maintain <u>P</u>. <u>libellula</u> at temperatures above 14° C, and no survivors at temperatures of 18° C or above for periods of more than 24 hours.

The change of Q_{10} between 5° C and 10° C may explain the bimodal distribution and high variance of respiration rates observed at 7.5° C.

This type of distribution would be expected if one group of the experimental animals were in a high temperature mode of metabolism and the other group in the low temperature mode. Whether or not 7.5° C is a critical temperature is a moat point. A certain amount of individual and genetic variability should be expected in species that have wide geographic distributions, such that not all individuals would change modes of metabolism at precisely the same temperature.

The change of Q_{10} near 7.5° C may be related to the environmental limits and observed distribution of Parathemisto libellula, both geographically and in depth. Parathemisto libellula presently is primarily distributed in the Arctic, and in the high boreal waters of the Northern Hemisphere. The species probably evolved in and is now primarily adapted to Arctic and near Arctic conditions, where temperatures seldom exceed 7° C. The southward extension of its range into the southern Bering Sea and to southeastern Alaska requires an ability to survive for short periods in temperatures in excess of 10° C, and possibly as high as 15° C to 17° C, if P. libellula remains at the surface. As was found in the examination of the Bering Sea samples, P. libellula was restricted to those areas where at least a portion of the water column remained below 8° C. In southeastern Alaska, although surface water temperatures exceed 8° C during the summer, below 50 m the waters are always less than 7° C. Daytime residence of P. libellula was consistently below depths at which 7-8° C were recorded, even for the youngest stages which migrated vertically the least. If the diurnal vertical migration is a feeding migration, only short excursions into the upper layers are required. If P. libellula is extending its range southward, it appears to have a limited ability to

utilize warm water environments and does not have full capacity to reside permanently in waters exceeding those of its Arctic origins.

The southeastern Alaska Parathemisto libellula may not be the southernmost members of a continuous distribution but may be the equivalent to glacial relicts that have not fully adjusted to the new environment imposed on them. Some evidence for this hypothesis can be drawn from the presently known distribution in the North Pacific. With the exception of one record off Afognak Island east of Kodiak Island (Bowman, 1960), there are no records of P. libellula from the Gulf of Alaska (Bowman, pers. comm., 1965). Isolated populations may occur in the coastal bays and sounds between Cross Sound in northern southeastern Alaska and the Bering Sea. A number of Bering Sea invertebrates and fish have eastern limits near Kodiak Island, and several fish have been observed to have a disjunct distribution, with populations in northern southeastern Alaska and the Bering Sea (1,600 km apart) and no known intervening populations (Quast and Hall, 1972).

Although the modestly high Q_{10}'s in the lower thermal range of Arctic and boreo-Arctic poikilotherms appear to be commonly known (Kinne, 1963), apparently its significance has not been explained. At first glance, it appears unlikely that an organism would regulate its metabolism at temperatures within its upper thermal range and not within its lower thermal range. Reduction of metabolic requirements at the upper limits of a range is reasonably hypothesized as an energy conservation measure. Failure to regulate metabolism and the activities it supports at low temperatures could conceivably result in failure to obtain enough food to support the organism. Unlike terrestrial poikilotherms and benthic aquatic poikilotherms, midwater plankton and

nekton must retain a certain level of activity to remain in the water column, regardless of how low both temperatures and food sources become. Polar and high latitude nekton and plankton obviously have high enough levels of activity to remain in the water column and must be metabolically adapted to survive at minimum water temperatures. With the total system adapted to the low temperatures, which seldom vary over a $10°$ C range, what would be the advantage to the animal of having Q_{10}'s of 3-5 instead of 1-2?

A possible advantage for modestly high Q_{10}'s may be hypothesized if the annual cycles of productivity in high latitude and polar regions are considered. Peak productivity occurs during the short summers, when in the Arctic temperatures near the surface may reach $5-7°$ C. Minimum productivity is obtained during the long winter when water temperatures are commonly below $0°$ C. Many Arctic invertebrates are long lived (compared to related temperate and tropical species) with life spans of two or more years (Dunbar, 1968). The long-lived Arctic invertebrates experience long periods of famine and shorter periods of feast. Low metabolic rates during the winter cold period, when food supplies are low and the organisms must live off stored energy reserves, are advantageous. Higher metabolic rates supporting higher levels of activity during the summer warm period, when food supplies are abundant, are advantageous to the point where they allow accumulation of food reserves in excess of current metabolic demands. However, if increased metabolic rates at high temperatures exceed those supportable by food supplies and/or allow no accumulation of reserves, a lowering of the metabolic rate and a lower Q_{10} would be desirable.

I believe that the temperatures at which increased metabolic rates

of polar and boreal zooplankton are no longer advantageous will approximate the normal seasonal maxima (possibly slightly above the norm) but will be below the expected extremes. Biological systems as a whole appear to have evolved to operate most efficiently within the limits of the average environmental changes, and at the same time, have evolved mechanisms to survive extreme conditions which lie within the normal variation of the environment.

Weight Relationships

Log weight entered the regressions for respiration rates as the second most important variable (Table 33). The regression coefficients for log weight ranged from 0.36718 to 0.73868 for dry weights and 0.4414 to 0.61261 for wet weights, with the best estimates judged as 0.56269 log (mg dry weight) and 0.53900 log (mg wet weight) (Tables 34 and 35). The wet and dry weight coefficients have broadly overlapping 95% confidence limits and probably do not differ significantly. Regressions of oxygen consumption rates on weight at each experimental temperature (Tables 38 and 39) differ slightly, but not significantly from those obtained from the stepwise regressions for both temperature and weight.

Confidence intervals derived from the standard errors for the regression coefficients are broad and indicate considerable variation for the individual determinations. This is probably a result of levels of activity, and it is assumed that the determinations are for average metabolic rates and do not represent basal metabolic rates. Confidence intervals for weight coefficients reported in the literature are not readily available, although my data overlap the means and have variances similar to that of Armitage (1962) for the Antarctic gammarid

TABLE ??.--*Parathemisto libellula* regression relationships for log oxygen consumption rate to log wet weight and for log weight specific oxygen consumption rate to log wet weight for various temperatures from -1.6° to 17.0° C[a]

Temperature °C	N	Wet weight (mg) Mean	SD	Oxygen consumption (μl/mg/hour) Mean	SD		a	b	SE_{est}	SE_b	r	F ratio
-1.6 to -1.5	36	145.75	37.55	0.04440	0.01486	(1)	-0.73430	0.70288	0.1288	0.18953	0.5367**	13.753***
						(2)	-0.73432	-0.29711	0.1288	..	0.2596	2.457
0.0	42	129.99	33.00	0.04945	0.01225	(1)	-0.26259	0.49730	0.0948	0.13896	0.4925**	12.807***
						(2)	-0.26258	-0.50271	0.0948	..	0.4965**	13.088***
2.0	9	173.70	28.21	0.06264	0.01311	(1)	-0.61961	0.73498	0.0966	0.45952	0.5173	2.558
						(2)	-0.61962	-0.26502	0.0966	..	0.2130	0.333
3.5	16	116.97	23.49	0.09307	0.02286	(1)	-0.53931	0.75576	0.1018	0.30900	0.5471*	5.982
						(2)	-0.53932	-0.24423	0.1018	..	0.2067	0.625
3.5 to 5.0	138	125.57	33.59	0.08974	0.02516	(1)	-0.20197	0.60576	0.1170	0.09314	0.4871**	42.300***
						(2)	-0.24198	-0.39123	0.1170	..	0.3412**	17.916***
4.0	61	108.26	17.94	0.08933	0.02272	(1)	0.18965	0.38270	0.1056	0.20499	0.2362	3.384
						(2)	0.18965	-0.61729	0.1056	..	0.3650**	9.068**
4.4 to 4.5	26	159.81	37.60	0.08191	0.02066	(1)	-0.40351	0.68341	0.0861	0.15323	0.6732**	19.891**
						(2)	-0.40352	-0.31658	0.0861	..	0.3886*	4.268
5.0	35	134.26	33.89	0.09473	0.03191	(1)	0.35195	0.33678	0.1541	0.25466	0.2243	1.749
						(2)	0.35193	-0.66321	0.1541	..	0.4129*	6.782*
7.5	24	149.30	52.20	0.10089	0.03276	(1)	0.41805	0.33284	0.1166	0.18221	0.3629	3.337
						(2)	0.41803	-0.66615	0.1166	..	0.6153**	13.306**
10.0	38	159.62	56.51	0.11288	0.03426	(1)	-0.64394	0.85073	0.1437	0.15430	0.6766**	30.397***
						(2)	-0.64396	-0.14927	0.1437	..	0.1592	0.936
10.5	10	97.19	18.46	0.21240	0.05189	(1)	Insufficient for correlation regression			..	..	0.010
						(2)	1.32579	-1.01474	0.0664	..	0.7974**	13.964*
13.5	10	109.22	35.59	0.16982	0.02947	(1)	-0.25817	0.74417	0.0652	0.17733	0.8292**	17.613**
						(2)	-0.25817	-0.25581	0.0652	..	0.4543	2.081
15.0	20	121.34	26.69	0.13749	0.03081	(1)	-0.22607	0.68842	0.1011	0.27064	0.5142*	6.470*
						(2)	-0.22608	-0.31158	0.1011	..	0.2619	1.325
16.0	17	137.63	46.02	0.19809	0.07987	(1)	0.61468	0.36469	0.1325	0.24361	0.3605	2.241
						(2)	0.61466	-0.63530	0.1325	..	0.5585*	6.801*
17.0	4	133.92	23.24	0.16739	0.01149	(1)	-0.01173	0.63931	0.0165	0.12585	0.9634*	25.807
						(2)	-0.01174	-0.36068	0.0165	..	0.8968	8.215

***P<0.001; **P<0.010; *P<0.050.

[a] (1)Regression equations for log (μl O_2/hour):log (mg wet weight); (2) regression equations for log (μl O_2/mg/hour): log (mg wet weight); where a = intercept, b = regression coefficient for weight, SE_{est} = standard error of the estimate, SE_b = standard error for regression coefficient (the regression coefficient, b, for weight-specific regressions (equation 2) is equal to the regression coefficient of the rate-to-weight regression minus 1), r is the correlation coefficient, and F is ratio for analysis of variance; SE_{est} and SE_b are the same for both regressions.

TABLE 39.--**Parathemisto** libellula regression relationships for log oxygen consumption rate to log dry weight and for log weight specific oxygen consumption rate to log dry weight for various temperatures from -1.6° to 17.0° C[a]

Tempera-ture (°C)	N	Dry weight (mg)		Oxygen consumption (μl/mg/hour)			a	b	SE_{est}	SE_b	r	F ratio
		Mean	SD	Mean	SD							
-1.6 to -1.5	36	32.33	9.82	0.20493	0.07240	(1)	-0.06243	0.56361	0.1316	0.16476	0.5060**	11.702*
						(2)	-0.06243	-0.43639	0.1316	..	0.4136*	7.015*
0.0	42	28.74	13.21	0.23244	0.06135	(1)	0.13769	0.45046	0.0868	0.09419	0.6032**	22.874***
						(2)	0.13769	-0.54954	0.0868	..	0.6781**	34.042***
2.0	9	39.89	7.65	0.27237	0.04730	(1)	-0.33306	0.85080	0.0808	0.32974	0.6972*	6.658
						(2)	-0.33306	-0.14920	0.0808	..	0.1686	0.205
3.5	16	24.07	4.08	0.44922	0.10185	(1)	-0.22720	0.90566	0.0933	0.28963	0.6413**	9.778*
						(2)	-0.22720	-0.09433	0.0933	..	0.0867	0.106
3.5 to 5.0	138	24.42	7.88	0.47125	0.15061	(1)	0.28244	0.54018	0.1135	0.07383	0.5315**	53.532
						(2)	0.28244	-0.45981	..	..	0.4711**	38.788
4.0	61	19.94	4.15	0.49852	0.15973	(1)	0.91347	0.04090	0.1086	0.15185	0.0350	0.073
						(2)	0.91346	-0.95910	0.1086	..	0.6351**	39.891***
4.4 to 4.5	26	32.43	9.08	0.40897	0.11414	(1)	0.20538	0.59432	0.0891	0.14400	0.6443**	17.034***
						(2)	0.20538	-0.40568	0.0891	..	0.4985**	7.936**
5.0	35	26.43	7.92	0.48008	0.16623	(1)	0.06210	0.71379	0.1295	0.17717	0.5742**	16.231**
						(2)	0.06210	-0.28621	0.1295	..	0.2707	2.610
7.5	24	28.29	8.11	0.52117	0.16536	(1)	0.52417	0.42494	0.1150	0.21081	0.3948	4.063
						(2)	0.52416	-0.57505	0.1150	..	0.5027*	7.441*
10.0	38	28.36	10.76	0.64206	0.19599	(1)	0.04596	0.81867	0.1284	0.11931	0.7528**	47.086***
						(2)	0.04595	-0.18133	0.1284	..	0.2456	2.310
10.5	10	17.28	3.15	1.19121	0.26329	(1)	1.20071	0.07792	0.0660	0.26244	0.1044	0.088
						(2)	1.20071	-0.92208	0.0660	..	0.7790**	12.345*
13.8	10	18.14	5.02	1.02146	0.22608	(1)	0.39510	0.68342	0.0840	0.25088	0.6937**	7.421
						(2)	0.39510	-0.31658	0.0840	..	0.4074	1.592
15.0	20	17.01	3.33	0.97289	0.20261	(1)	0.11352	0.89030	0.0918	0.26059	0.6272**	11.672**
						(2)	0.11352	-0.10970	0.0918	..	0.0987	0.177
16.0	17	21.90	6.30	1.20497	0.35529	(1)	0.67357	0.53862	0.1258	0.26553	0.4640	4.115
						(2)	0.67356	-0.46138	0.1258	..	0.4093	3.019
17.0	4	17.33	2.18	1.28452	0.03142	(1)	0.23671	0.89640	0.0111	0.11563	0.9838*	60.099*
						(2)	0.23671	-0.10359	0.0111	..	0.5352	0.803

***$P<0.001$; **$P<0.010$; *$P<0.050$.

[a](1) Regression equations for log (μl O_2/hour) log (mg dry weight); (2) regression equations for log (μl O_2/mg/hour): log (mg dry weight); where a = intercept, b = regression coefficient for weight, SE_{est} = standard error of the estimate, SE_b = standard error for regression coefficient (the regression coefficient, b, for weight-specific regressions (equation 2) is equal to the regression coefficient of the rate-to-weight regression minus 1). r is the correlation coefficient, and F is ratio for analysis of variance; SE_{est} and SE_b are the same for both regressions.

<u>Orchomonella chiliensis</u>, and of Haq (1967) for the boreo-Arctic copepods <u>Metridia longa</u> and <u>M. lucens</u>.

The relationship of oxygen consumption rates to weight at temperatures of -1.6° C to 17° C was evaluated by regressing the log O_2/hr. on log mg wet weight and on log mg dry weight with the BioMedical O2R computer program. In addition to the O_2 weight regressions for each experimental temperature, weight specific regressions (log O_2/mg/hr.:log mg) for each were obtained. The resulting regressions (Tables 38 and 39) were examined for significance by correlation coefficients and F-tests.

Regressions for log O_2/hr. on log weight were significant at 7 temperatures for wet weight data and at 10 temperatures for dry weight data. At the temperatures of 4.0° C, 7.5° C, 10.5° C, and 16.0° C the correlation of oxygen consumption and weight was not significant for either wet or dry weight data. Regression coefficients for the significant regressions ranged from 0.49730 to 0.85073 for wet weights and 0.45046 to 0.90566 for dry weights. The regressions and correlation coefficients appeared to have a large variance, therefore, the correlation coefficients for dry weight regressions were normalized and a test for homogeneity (Sokal and Rolf, 1969) was applied. The null hypothesis of homogeneity was rejected ($x^2 = 27.293 > x^2_{14(0.05)} = 23.685$ for the total set of regressions (Table 40). Because the regressions at 4.0° C and 10.5° C were the most deviant, they were deleted from the set and the test for homogeneity was reapplied. This resulted in acceptance of the null hypothesis and the conclusion that all remaining regressions were estimates from the same population and were not significantly different. This differs from the case for the Antarctic benthic gammarid <u>Orchomonella chiliensis</u>, where the regressions at different temperatures were

TABLE 40. -- Tests of homogeneity of correlation coefficients between log oxygen consumption rate and log dry weight for <u>Parathemisto libellula</u> at temperatures of $-1.6°$ to $17.0°$ C

Temperature ($°$ C)	n_i	$n_i - 3$	r_i	z_i	Weighted z_i	Weighted z^2_i
-1.6	36	33	0.5060	0.5573	18.39090	10.24924
0.0	42	39	0.6032	0.6981	27.22590	19.00640
2.0	9	6	0.6972	0.8618	5.17080	4.45619
3.5	16	13	0.6413	0.7604	9.88520	7.51670
4.0	61	58	0.0350	0.0350	2.03000	0.07105
5.0	35	32	0.5742	0.6538	20.92160	13.67854
3.5-5.0	138	135	0.4871	0.5322	71.84700	38.23697
7.5	24	21	0.3938	0.4175	8.76750	3.66043
10.0	38	35	0.7528	0.9795	34.28250	33.57970
10.5	10	7	0.1044	0.1048	0.73360	0.07688
13.8	10	7	0.6937	0.8550	5.98500	5.11717
15.0	20	17	0.6272	0.7368	12.52560	9.22886
16.0	17	14	0.4640	0.5024	7.03360	3.53368
17.0	4	1	0.9838	2.4040	2.40400	5.77921

Sums for

	n_i	n_i-3	r_i	z_i	Weighted z_i	Weighted z^2_i
N = 15	486	441	..	..	248.80970	167.66879
N = 12	415	376	..	..	242.04610	167.52086
N = 11	277	241	..	..	170.19910	129.28389

Chi square test for homogeneity

N	$\bar{z}$	χ^2	$\chi^2_{(0.05,\ n-1)}$
14 [a]	0.56419	27.293*	22.362
12 [b]	0.64373	11.709	19.675
11 [c]	0.70622	9.086	18.307

[a] Data from all temperatures.

[b] Data from temperatures $4.0°$ and $10.5°$ C omitted.

[c] Data from temperatures $3.5°-5.0°$, $4.0°$, and $10.5°$ C omitted.

significantly different (Armitage, 1962). Plots of the calculated regressions (Figure 34) and of oxygen uptake rates based on the regressions (Figure 35) for various weight Parathemisto libellula resemble Armitage's figures for O. chiliensis, but probably the resemblance is due to the high variances rather than to temperature effects on the relationship of weight to oxygen consumption rates.

Spearman rank correlation tests (Siegel, 1956) were applied to the regression to determine the degree of relationship of mean metabolic rates to temperature (Table 41). After deleting the constants for 4.0° C and 10.5° C, the correlation was marginally significant (r_s=0.573; $r_{s(12, 0.05)}$=0.532; $r_{s(12, 0.01)}$=0.661). If the regression for the combined data of 3.5° C to 5.0° C is added to the set, the correlation is still significant; but if the 3.5°-5.0° C constant is used to replace the 3.5° C, 4.0° C, 4.5° C, and 5.0° C values, the correlation is not significant. This relatively weak degree of correlation between regression or mean respiration rates with temperature appears to be a consequence of the high variance in the regression coefficients.

Regressions for Parathemisto libellula weight-specific respiration rates, log (O_2/mg/hr.)=a + (b-1) log (mg weight), were generally less significant than the regressions for log (O_2/hr.)=a + b log (mg weight) (Tables 38 and 39). Only at 0° C, 4.0° C, and 10.5° C were the weight-specific regressions more significant than the weight regressions. Values of b-1 for the significant weight-specific regression ranged from -1.01474 to -0.31658 for wet weights and 0.95910 to -0.40568 for dry weights. These values are at considerable variance for most crustacean data where the weight-specific coefficient, b-1, is usually -0.05 to
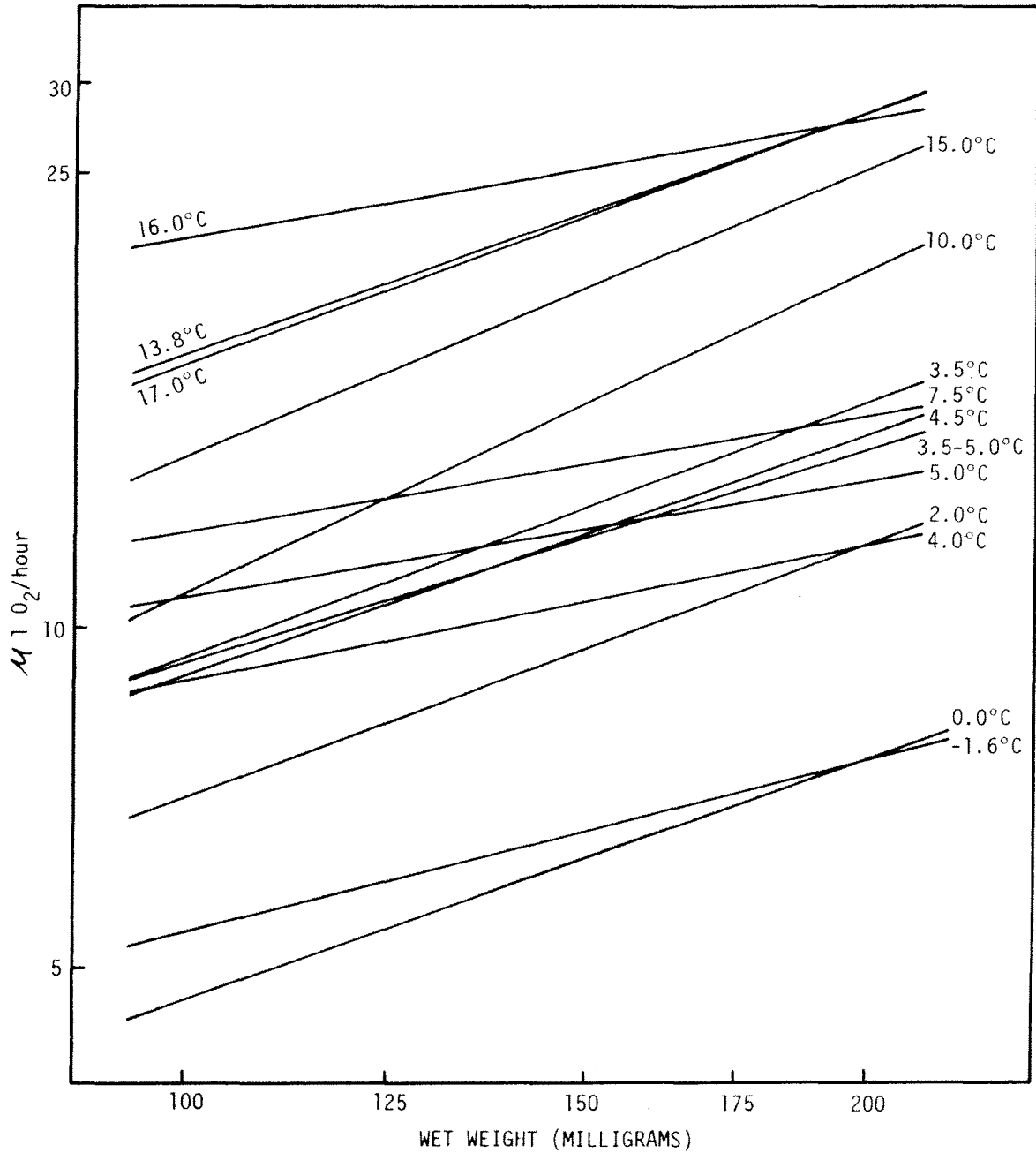
Fig. 34.--Relationship of respiration rates of Parathemisto libellula
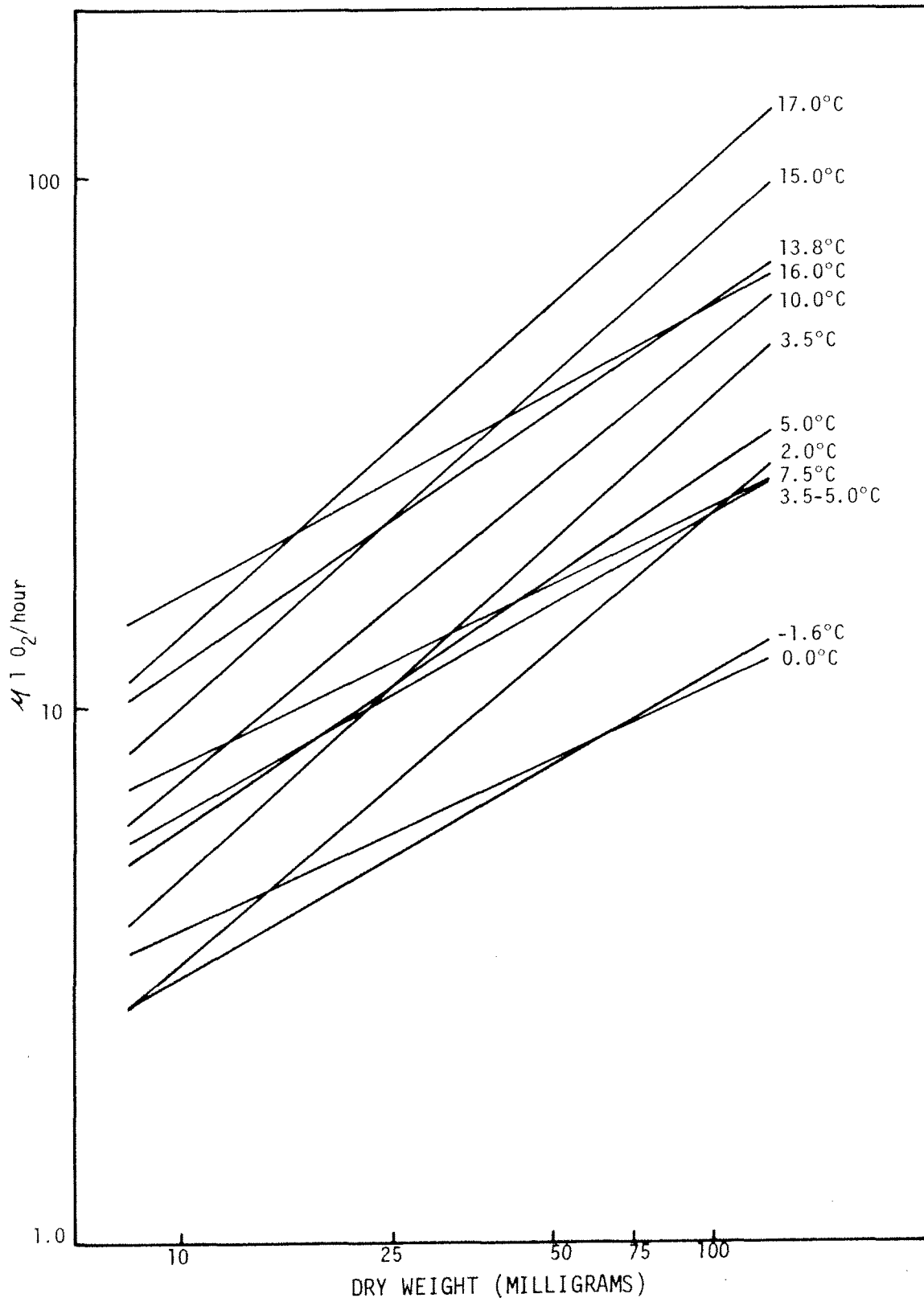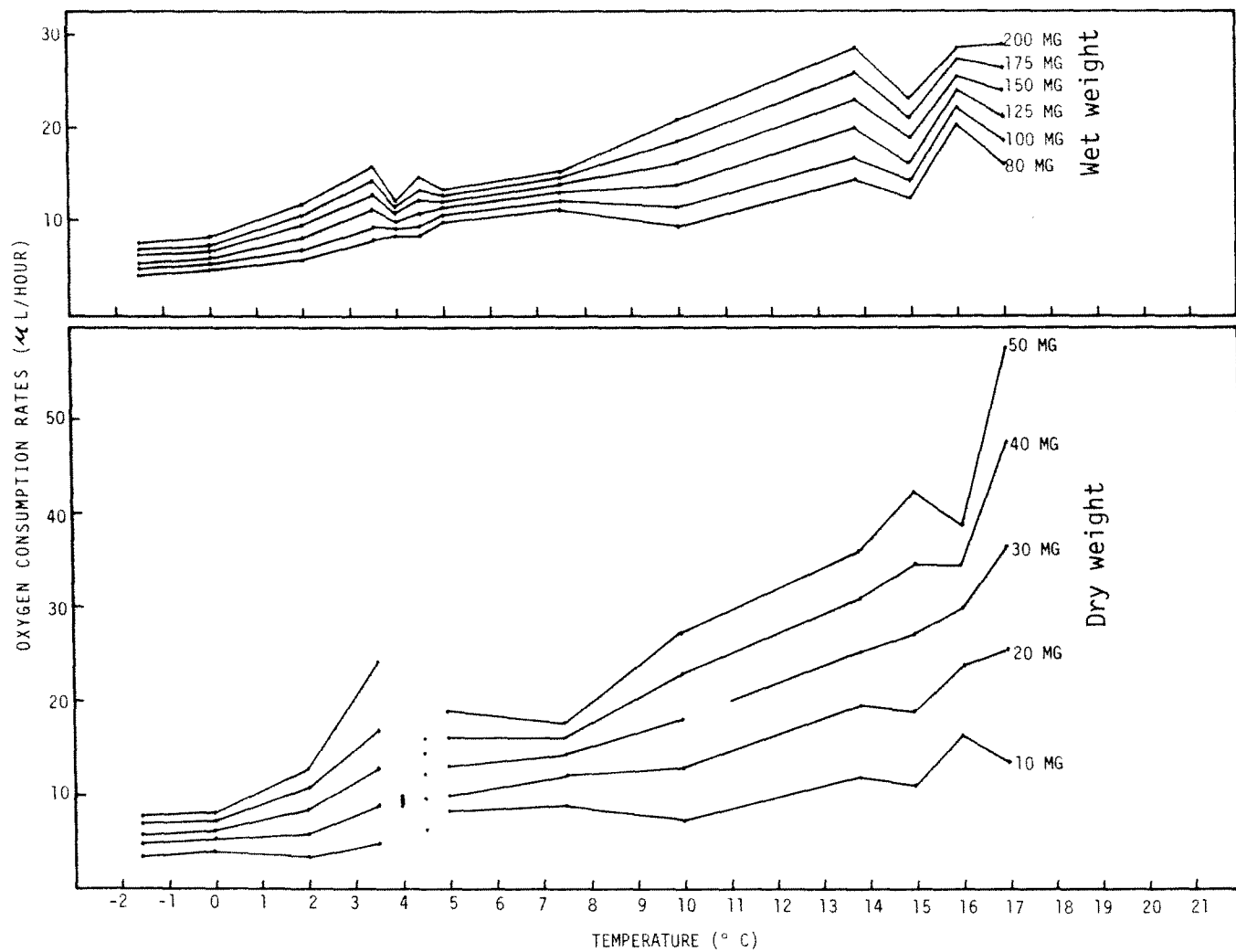to wet weight (a) and dry weight (b) at different temperatures

Fig. 34.--Continued

Fig. 35.--Relationship of respiration rate of different sized
Parathemisto libellula to temperature

TABLE 41.--Spearman Rank correlation tests for relationship between temperature and intercepts of Parathemisto libellula regressions of log oxygen consumption to log dry weight

Temperature (°C)	Rank	Intercept	Test 1[a] Rank of intercept	d	d^2	Test 2[b] Rank of intercept	d	d^2	Test 3[c] Rank of intercept	d	d^2	Test 4[d] Rank of intercept	d	d^2
-1.6	1	-0.06	2	1	1	2	1	1	2	1	1	2	1	1
0.0	2	0.13	6	4	14	6	4	16	6	4	16	5	3	9
2.0	3	-0.33	1	-2	4	1	-2	4	1	-2	4	1	-2	4
3.5	4	0.23	8	4	16	8	4	16	8	5	25	..	..	..
3.5-5.0	..	-0.28	..	..	..	..	..	..	10	6	36	7	3	9
4.5	5	0.21	7	2	4	7	2	4	7	2	4	..	..	..
5.0	6	0.06	4	-2	4	4	-6	36	4	2	4	..	..	..
7.5	7	0.52	11	4	16	..	..	..	12	5	25	9	4	16
10.0	8	0.04	3	-5	25	3	-4	16	3	-5	25	4	-2	4
13.8	9	0.39	10	1	1	..	..	..	11	2	4	8	1	1
15.0	10	0.11	5	-5	25	5	-3	9	5	-5	25	3	-5	25
16.0	11	0.67	12	1	1	..	..	..	13	2	4	10	1	1
17.0	12	0.24	9	-3	9	9	0	0	9	-2	4	6	-4	16
N	..	..	12	..	..	9	..	..	13	..	..	10	..	..

$$r_s = 1 - \frac{6(\Sigma d^2)}{N^3 - N}$$

	Test 1	Test 2	Test 3	Test 4
	0.573*	0.150	0.514*	0.479

*Significant correlation exceeding $r_{s(N)}$ 0.05

[a] Data from temperature range 3.5-5.0 omitted.

[b] Data from temperatures 3.5°-5.0°, 7.5°, 13.8°, and 16.0° C omitted

[c] Data from all temperatures.

[d] Data from temperatures 3.5°, 4.5°, and 5.0° C omitted.

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weight-specific relationships are found encompass animals of a large size range, in which the largest individuals are 10 to 20 times heavier than the smallest (see Table 4, Wolvekamp and Waterman, 1960), although in some cases it may be evident where the largest is 3 to 4 times heavier than the smallest (Pearcy, Theilacker, and Lasker, 1969). In this study on respiration rates at given temperatures, the weights of the largest amphipods were seldom as much as twice the smallest. It appears that given the high variation of respiration rates, a doubling of size is too narrow a range to determine meaningful weight-specific relationships for metabolic rates.

Log O_2/hr. on log weight regressions for each sex were obtained at temperatures of 3.5° C to 5.0° C, 7.5° C, 10.0° C, and 16.0° C (table 42). The dry weight regressions for females were not significant at 7.5° C and for wet weights were not significant at 7.5° C and 16° C. For males, the regressions were significant only for the 3.5° C to 5.0° C data for dry weights. Wet weight regressions for males were not significant at 7.5° C and 16° C. In the remaining cases, where a valid comparison could be made between regression coefficients for the two sexes, low degrees of freedom and high standard errors for the coefficients give broadly overlapping 95% confidence limits. Thus, although the females tend to slightly higher regression coefficients, it is concluded that there is no difference in the weight-oxygen consumption relationships for males and females.

For many crustaceans, respiration on weight regression coefficients are in the range of 0.67 to 1.0 log weight (Wolvekamp and Waterman, 1960). For a wide variety of zooplankton, the regression coefficients are correlated with the temperature of the habitat (Ikeda, 1970). Boreal

TABLE 42.--<u>Parathemisto</u> <u>libellula</u> regression relationships for log oxygen consumption rates: log weight for males and females[a]

Temperature (°C)	Males				Females			
	N	a	b	F ratio	N	a	b	F ratio
For regressions using wet weight								
16.0	8	2.01057	-0.31691 0.64096	0.224	9	-0.32457	0.78787 0.29268	7.246*
10.0	9	-0.73024	0.94468 0.98862	113.622*	29	-1.08293	1.03416 0.17361	35.483*
7.5	14	-1.10865	1.07930 0.55416	3.793	10	0.26492	0.39300	0.824
3.5-5.0	50	-0.16235	0.57780 0.24110	5.743*	88	-0.29584	0.62504 0.09965	39.414*
For regressions using dry weight								
16.0	8	1.68696	-0.24421 0.58019	4.599	9	0.23631	0.87392 0.18539	22.23*
10.0	9	0.41707	0.58956 0.20779	8.050	29	-0.02134	0.85355 0.13530	39.801*
7.5	14	-0.15697	0.6991 0.44701	2.446	10	0.50610	0.42893	1.020
3.5-5.0	50	0.35175	0.50698 0.16019	10.016*	88	0.22894	0.56891 0.08228	47.811*

*$P < 0.05$.

[a]Log (μl O_2/hour) = a + b log (mg) + e; SE_b = standard error of regression coefficient.

zooplankton as a group have regression coefficients of 0.687 for wet

weight and 0.830 for dry weight; temperate zooplankton have coefficients

of 0.722 for wet weight and 0.691 for dry weight; and tropical

zooplankton have regression coefficients of 0.446 for wet weight and

0.538 for dry weight (Ikeda, 1970). Tropical zooplankton had the

highest variances. Ikeda included Parathemisto libellula among his

boreal species. In the present study, P. libellula respiration on

weight regression coefficients are 0.539 for wet weight and 0.563 for

dry weight, and are comparable with wet weight coefficients of 0.455

to 0.665 for Orchomonella chiliensis (Armitage, 1962) and dry weight

coefficients of 0.37 to 0.48 for Metridia longa and M. lucens (Haq,

1967). Apparently, these primary polar crustaceans have respiration

to weight relationships similar to those of tropical zooplankton.

Salinity Relationships

Salinity was the third ranking variable entered into the

respiration regressions (Table 33). In two of eight wet weight

regressions and in four of eight dry weight regressions the large standard

errors do not allow the separation of the salinity regression coefficient

from zero with 95% confidence (Tables 34 and 35). The entry of salinity

as the third ranking variable of the metabolism regression was not

expected. Salinities during the experiments ranged only from 30.70 to

32.40°/oo. The positive regression and correlation of respiration

rates and salinities appear to be artifacts of the experimental

technique. Salinities were negatively correlated with experimental

temperatures, days of captivity, and acclimation time, and were

positively correlated only with weight and oxygen uptake. In most subsets, the correlations were weak and not significant. The estimated regression coefficients for salinity which differ significantly from zero vary by a factor of three or more in regressions using dry weights, and vary by a factor of nearly seven in regressions using wet weights, and have large standard errors. For this reason there is not much confidence in the estimated coefficients, although the positive correlation of salinity and respiration rates seems real and valid.

Salinity changes are recognized to affect the respiration rates of invertebrates through their effect on osmotic and ionic balances. Adaptation of metabolic rates to salinity changes are not well documented, although three basic patterns have been described (Kinne, 1964): (1) increased rates at low salinities and lowered rates at salinities above the normal environment, (2) increased metabolic rates at both lower and higher salinities than normal, and (3) metabolism rates unaffected by salinity changes. The gammarid amphipods, Gammarus locusta and G. duebeni, and most other crustaceans examined have the first type of response (Kinne, 1964). Both of these amphipods, and most of the other crustaceans listed by Kinne (1964) for the first form of metabolic response to salinity changes, are euryhaline estuarine species. Stenohaline crustaceans may have a fourth type of response--lowered metabolic rates at lowered salinities, such as was reported for the crab Maja verrucosa (Schawbe, 1933) and for the copepod Calanus finmarchicus (Marshall and Orr, 1955). Most experimental work on the relationship of respiration rates to salinity changes have used large

changes of salinity (on the order of 25% seawater or roughly $8^\circ/_{oo}$ or more), although marine stenohaline animals are reported to be sensitive and possibly intolerant of change of 2-3% seawater (0.7 to $1.0^\circ/_{oo}$) (Bullard, 1964; Hopper, 1960).

Parathemisto libellula may experience salinity changes from near $34^\circ/_{oo}$ to $28^\circ/_{oo}$ during the course of diurnal migration, depending upon depth of daytime residence and time of year. This is nearly four times the range of salinities at which the laboratory experiements were performed. If the positive coefficients for salinity are valid, this suggests that during upward migration from high salinity and low temperature depths to low salinity and high temperature surface waters, the effects of changing temperature and salinity may counteract and result in a nearly constant metabolic rate. This would be analogous to the counteracting effects of temperature and hydrostatic pressure on the respiration of the shrimp, Systellaspis debilis, which appears to maintain a constant metabolic rate during migration from low temperatures and high pressures to high temperatures and low pressures (Napora, 1964). Using the regression equation:

$$\log O_2 \text{ hr.} = -2.38677 + 0.53900 \log \text{ (mg wet weight)} + 0.3270 \text{ (T}^\circ \text{ C)} +$$
$$0.06548 \text{ (S}^\circ/_{oo}),$$

a 100-mg amphipod would require 11.07 µl O_2/hr. at depths where the salinity was $34^\circ/_{oo}$ and temperature 4.5° C. Assuming a constant salinity and a 9.5° C surface temperature, the upward migrating amphipod would require 16.91 µl O_2/hr. at the surface, whereas at $31^\circ/_{oo}$ and 9.5° C it would require only 10.71 µl O_2/hr. It appears possible for a $2\text{-}3^\circ/_{oo}$ salinity drop to more than compensate for a 5° C temperature rise.

Response to Time in Captivity, Acclimimation Time,

Molt Cycle, and Moribundity

Days in Captivity

Days in captivity was the fourth ranking variable to be entered into the stepwise regressions for oxygen consumption rates (Table 33). The regression coefficients for days in captivity are small and have large standard errors. For half of the subsets the standard errors are larger than the coefficients (Tables 34 and 35). For only three subsets the coefficient may be distinguished from zero, with 95% confidence limits. The three exceptional subsets all contain data from one experiment at 10.5° C which gave exceptionally high oxygen consumption rates (Figure 32).

Abnormally high respiration rates are a common experience when freshly caught plankton are used. Ikeda (1970) observed that the respiration rates of the copepod Calanus cristatus and the euphausiid Thysanoessa inermis declined during the first 4 days of captivity, before stabilizing. This initial high metabolism just after captivity may partially explain the high rates I observed at 10.5° C for Parathemisto libellula. This group of animals had been in captivity only 5 days and had been subjected to a 7° C temperature rise. Subsequent experiments with the same group of animals at 13.8° and 16.0° C gave lower rates than the initial 10.5° C rates. Consequently, the 10.5° C data have been excluded from data comparisons.

Holding Parathemisto libellula in the laboratory from 0 to 80 days had little or no observable effect on respiration rates. If there was an initial

high respiration shortly after capture, rates apparently were stablized within 6 days.

Acclimation Time

Most investigations of temperature-respiration relationships of aquatic invertebrates utilize acutely determined respiration-temperature curves. In these cases, the animals are subjected to relatively large temperature changes within a short period of time, after which they may or may not be allowed to acclimate to the new temperature before respiration rates are observed. Nonmigrating and many shallow-dwelling zooplankton are seldom if ever subjected to temperature changes in excess of a few tenths of a degree per day. Zooplankton which migrate daily may experience large temperature changes within a few hours. In the tropical regions, vertically migrating shrimp may experience as much as 14° C change when moving from 400 m to the surface (Napora, 1964; Donaldson, 1973). At midlatitudes, the temperature changes within the upper 400 m may be of the same order of magnitude although of lower means. In boreal and polar waters, the temperature differences are seldom as extreme, and the waters may be seasonally isothermal. In southeastern Alaska coastal waters, temperatures at depths of 300-400 m remain at 4-5° C throughout the year, and surface waters may vary from winter lows of 2° C to summer highs of 10-12° C; thus, zooplankton migrating daily would seldom experience more than a 6° C change. High Arctic zooplankton migrating within the upper 200 m would experience a similar 6° C temperature change during the summer in moving from -1.5° C waters at 150-200 m to summer surface waters of 4-7° C. Dwelling in the upper water column, with an Arctic and sub-Arctic distribution, Parathemisto libellula

would experience near isothermal waters in the winter and as much as 6° C temperature change in the summer during its diel migration.

When this study was initiated, little was known about the depth distribution or extent of diel migration by Parathemisto libellula. For this reason the amphipods were assumed to be near-surface dwellers, which means they might have a limited diel migration and would not be expected to experience large daily changes of temperature but could experience a sizable seasonal change of temperatures. Such animals may be assumed to alter metabolic rates slowly by acclimation during a slow temperature rise but may not tolerate large rapid changes. In the laboratory, the temperatures were changed at the rate of 1° C per day, and at least one additional day was allowed for adjustment before respiration rates were determined. In some cases, the amphipods were held at the new experimental temperature for varying periods of time and the respiration rate was again measured. If acclimation is a time-dependent process, and if the amphipods do acclimate to temperature changes, metabolic rates should be correlated with time allowed for acclimation; and regressions of metabolic rate at the new temperatures on time should be a measure of the rate of acclimation. In theory, this experimental design should more closely approximate the normal course of events than determination of respiration rates and acclimation by the acutely determined respiration-temperature curves.

Acclimation time was the fifth ranking variable to be entered into the stepwise regressions for oxygen consumption rates (Table 33). As in the case for days in captivity, the regression coefficients for days of acclimation are small and have large standard errors and with exception of the regressions for 10-17° C cannot be distinguished from zero at

the 95% testing level. Also, the sign of the coefficient is not consistent between the wet and dry weight regressions for the same data sets (Tables 34 and 35). It was concluded that acclimation time lacked statistical significance in the present data.

Although acclimation time was not a significant factor for the observed metabolic rates, there was an indication of an acclimation effect or trend. The majority of observations were made at temperatures near or above the temperatures at which the amphipods were captured. For an amphipod to acclimate to higher temperatures, it should lower the metabolic rate and thus have a negative regression coefficient for acclimation to elevated temperatures and conversely a positive acclimation coefficient for raising metabolic rates at temperatures below the norm. Respiration regressions for temperatures above 10° C had negative coefficients for acclimation times and were the only coefficients that differed significantly from zero. In the dry weight regressions, the coefficient for acclimation is positive only for that subset of data entirely at temperatures below that of capture.

Molt Cycle

Little is known about the relationship of molt cycle to the respiration rates of nondecapod crustaceans. In decapods, whole animal and isolated tissue oxygen consumption rates are elevated for a period of time before and after molt (Edwards, 1950; McWhinnie, and Kirchenberg, 1962), and the oxygen consumption rate is increased in tissues from intermolt animals by application of ecdysome (McWhinnie et al., 1972). Attempts to correlate molting cycles with oxygen consumption rates for nondecapod crustaceans such as barnacles have been unsuccessful (Costlow

and Bookhout, 1958) or not attempted (at least not reported).

Twenty-three of the 125 amphipods used for respiration rate studies molted in the laboratory. Fifty-seven respiration rates were obtained for these amphipods; 33 before the day of molting, 4 on the day of molting, and 20 after the day of molting. The stepwise regression program was applied to these observations to examine the correlation between oxygen consumption rates and days before molt, days after molt, and the combination of days before and/or after molt. After the regression program had accounted for the effects of temperature, weight, salinity, acclimation time, and days in captivity, the partial correlations remaining for proximity to molt were not signficant (Table 43), even though regression coefficients were computed. In all cases, the standard errors of the regression coefficients were larger than the coefficient, implying that the coefficients did not differ from zero. The trend for respiration to increase at time of molt is present, but it is not significant compared to the other factors of temperature, weight, and salinity.

Death was often associated with molting of captive amphipods. Of 23 amphipods which molted in captivity and which were used in respiration studies, 8 died the same day as molting, 7 survived 1-67 days after molting; and 8 were intentionally sacrificed. The stepwise regression analysis was applied to respiration data for the 15 amphipods which died before they were to be sacrificed. Time, or "days before death," was more strongly correlated with respiration rates than either time before or after molt; however, the regression coefficients did not differ significantly from zero (Table 44).

TABLE 43. --Regression coefficients for relationship between days premolt or postmolt and oxygen consumption rates of Parathemisto libellula[a]

N	Regression coefficient	Standard error of coefficient	Partial[b] correlation coefficient
	Days premolt[c]		
57	(1) +0.00079	0.00223	+0.06427
	(2) (d)	(d)	-0.00468
	Days postmolt[c]		
24	(1) -0.00107	0.00172	-0.19176
	(2) -0.00093	0.00167	-0.13018
	Days from molt (premolt or postmolt)[c]		
57	(1) -0.00115	0.00129	-0.12571
	(2) -0.00029	0.00157	-0.02631

[a]Regression coefficients are for estimate of log (μl O_2/hour) after stepwise multiple regression coefficients for temperature, log weight, salinity, and acclimation time were computed; equations (1) are for regressions using wet weight, (2) for regressions using dry weights.

[b]Partial correlation coefficients are for correlations before inclusion in the regression.

[c]Includes observations on day of molting.

[d]Insufficient correlation to compute the regression coefficient.

TABLE 44.--Regression coefficients for relationships of days from
molt and days before death to oxygen consumption rates of
Parathemisto libellula[a]

Days	N	Regression coefficient	Standard error of coefficient	Partial[b] correlation coefficient
For regressions using wet weight				
Premolt	23	([c])	([c])	+0.45779
Before death		+0.00187	0.00309	+0.14983
Postmolt	11	-0.00267	0.00330	-0.23112
Before death		+0.00519	0.01748	+0.28605
For regressions using dry weight				
Premolt	23	([c])	([c])	+0.53619
Before death		-0.00045	0.00366	+0.03089
Postmolt	11	-0.00288	0.00310	-0.23112
Before death		-0.00601	0.01741	+0.28605

[a]Regression coefficients are for estimate of log (μl O_2/hour) after stepwise multiple regression coefficients for temperature, weight, salinity, and acclimation time were computed.

[b]Partial correlation coefficients are correlation before inclusion in the regression.

[c]Insufficient correlation to compute the regression coefficient.

Moribundity

Moribund animals may exhibit anomalous metabolic rates. Their deviation from the norm may be dependent upon the degree and cause of moribundity and should be correlated to time from actual death. Although obviously moribund amphipods were not used for respiration studies, it was not always possible to separate lethargic animals from moribund animals.

For this reason records were kept of the dates of death for all experimental animals and the probable cause of death.

One hundred thirty nine measurements of respiration rates were made on Parathemisto libellula that died before they were to be sacrificed. The causes of death were mostly unknown. The stepwise regression was applied to these data with the same results as in the regressions for molting animals. The regression coefficients for days before death are negative, showing a slight increase in respiration rate as death approaches. However, the coefficients are very small, with standard errors larger than the coefficients (Table 45), and contribute only a small increase for the significance of the regression. They cannot be considered significantly different from zero.

The regression coefficients for days in captivity, days allowed for acclimation, days from molt, and days before death all are small and do not differ significantly from zero. Separately or in aggregrate they do not provide sufficient information to alter conclusions on the relationships between respiration rate and temperature, weight, and/or salinity.

Respiration Rates of Parathemisto pacifica

The attempts to determine the respiration rates of Parathemisto pacifica were not overly successful. Few animals were available for respiration studies in the winters, and summer juveniles did not survive in the laboratory. Oxygen uptake rates of individual animals were generally insufficient to be distinguished from the inherent variability of the Gilson respirometer used. Only three determinations were made successfully for individual animals, two of those are suspiciously high. Six experiments using two to nine animals in a respiration flask were successful. Table 46 presents the results of

TABLE 45. --Regression coefficients for relationship between time before death and oxygen consumption rates of Parathemisto libellula[a]

N	Regression coefficient	Standard error of coefficient	Partial[b] correlation coefficient
For regressions using wet weight			
139	-0.00014	0.00066	-0.01872
131[c]	-0.00023	0.00075	-0.02671
For regressions using dry weight			
139	-0.00036	0.00066	-0.07023
131[c]	-0.00056	0.00074	-0.06837

[a]Regression coefficients are for estimates of log (μl O_2/hour) after regression coefficients for temperature, log weight, salinity, and acclimation time were computed.

[b]Partial correlation coefficients are correlation before inclusion in the regression.

[c]Data from experiment at 10.5° C not included.

the nine experiments between -1.6° C and 5.0° C. Oxygen uptake rates were computed as μl O_2/hr. for individual, mg wet weight, and mg dry weight and shown in plots against temperature in Figure 36. The small number of experiments and inconsistency of composition of the groups used precluded rigorous statistical treatment of the data.

The plots of respiration rates of Parathemisto pacifica versus temperature indicate both an adherence to expected trends of higher rates at higher temperatures and an approximate Q_{10} of 1.9 as reported for a number of other crustaceans by Grainger (1956) (Figure 36). The deviations from linearity and from predicted rates for a Q_{10} of 1.9 based on the mean of determinations at -1.6° C may be in part

TABLE 46. --Oxygen consumption rates of <u>Parathemisto pacifica</u> held in laboratory at temperatures between -1/6° and 5.0°C. (N = number of individuals in a respirometer flask; lengths and weights are for each individual in the flask)

| Tempera-ture (°C)	N	Length (mm)	Wet weight (mg)	Dry weight (mg)	Oxygen consumption (μl/hour) per--		
					Indi-vidual	Milligram wet weight	Milligram dry weight
-1.6	2	6.5	6.78	2.14	0.645	0.092	0.369
		7.0	7.26	1.36			
Total			14.04	3.50			
-1.6	2	6.5	6.78	2.14	0.690	0.098	0.394
		7.0	7.26	1.36			
Total			14.04	3.50			
0.0	4	6.5	6.78	2.14	0.868	0.069	0.292
		7.0	7.26	1.38			
		8.0	14.58	3.63			
		9.0	21.77	4.74			
Total			50.39	11.89			
2.0	7	6.0	8.06	1.81	1.333	0.116	0.496
		6.5	6.78	2.14			
		6.5	8.25	1.48			
		7.0	7.26	1.36			
		7.0	13.60	3.66			
		8.0	14.58	3.63			
		9.0	21.77	4.74			
Total			80.30	18.82			
4.0[a]	1	5.0	3.90	0.78	1.250	0.321	1.603
4.4	9	5.5	5.00	1.06	1.368	0.136	0.559
		6.0	5.00	2.12			
		6.0	8.06	1.81			
		6.5	6.78	2.14			
		6.5	8.25	1.48			
		7.0	7.26	1.36			
		7.0	13.60	3.66			
		8.0	14.58	3.63			
		9.0	21.77	4.74			
Total			90.30	22.00			
5.0	1	9.0	16.37	2.29	1.467	0.090	0.640
5.0[a]	1	5.0	3.45	0.72	2.933	0.850	4.074
5.0	3	6.0	5.73	1.23	2.727	0.198	0.830
		7.5	16.91	4.66			
		9.0	18.62	3.97			
Total			41.26	9.86			

[a]Oxygen uptake rates believed erroneous.
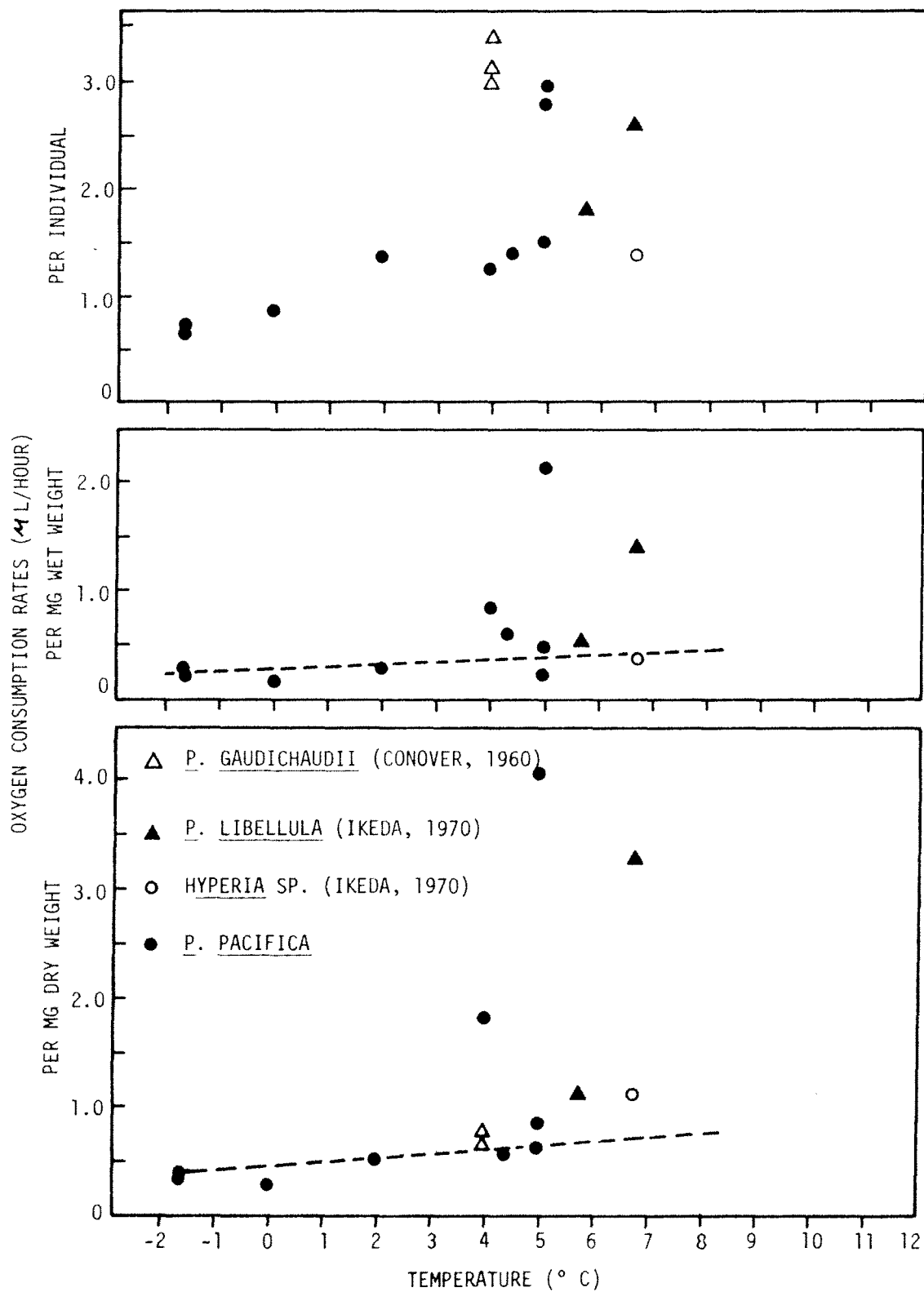
Fig. 36.--Relationships of respiration rates of three species of Parathemisto and a Hyperia sp. to temperature

attributed to the dissimilarity of experimental groups, differences in activity level, and general experimental variation.

Crowding does not appear to have been a major factor in causing variability of the results, as shown by the similarity of rates per individual at temperatures of 4° C to 5° C. The lower rates expressed in $\mu l \ O_2/mg/hr.$ may be the result of higher mean weights for some experimental groupts. Metabolic rates of marine crustaceans have a general relationship of $O_2/hr=aW^b$, with b often in the range of 0.80 to 0.95 (Zeuthen, 1953). Consequently large animals will have lower uptake rates per unit weight than small animals, and groups of animals with high mean weights may be expected to have somewhat lower uptake rates per unit weight than groups with low mean weights.

No attempt was made to control or monitor the activity level of amphipods during respiration studies. In most cases, the amphipods appeared to lie quietly on the bottom of holding containers and in the respiration flasks. However, when disturbed, the amphipods would often swim actively and become entrapped in the miniscus. Such entrapped individuals often struggled violently for an undetermined amount of time, until either resting quietly or escaping the miniscus. The high metabolic rates observed for individual amphipods at 4° C and 5° C are from amphipods found trapped in the miniscus and actively struggling at the end of the experiment.

Acclimation to lower temperatures is not evident in the limited data for Parathemisto pacifica. Although the higher rate at -1.6° C came from the same individuals and after 10 days additional accumulation, the difference is less than the expected experimental error. The determination based on three amphipods at 5° C is from a group held 17

days at -1.6° C and subjected to a 6.6° C temperature rise in less than
3 hours. The 5° C rate for this group is not above the hypothetical rate
predicted by a Q_{10} of 1.9 indicative of an absence of overshoot associated
with animals acclimated to low temperatures and then subjected to a
sudden temperature rise (Prosser, 1967).

Parathemisto pacifica has a metabolic rate not greatly different
from that of other similar-sized planktonic crustaceans from temperate
waters. Conover (1960) obtained three measurements for the uptake of
oxygen by the North Atlantic P. gaudichaudii (reported as Euthemisto
compressa) at 4° C which do not differ significantly from my P.
pacifica rates, although Conover's specimens averaged larger than
those used in this investigation (Figure 36). Ikeda (1970) reports a
pair of observations on similar-sized P. libellula at 5.5° C to 6.8° C
for the southern Bering Sea. These appear to be from active animals
and may not be representative of average metabolic rates (Figure 36).

Starvation Tolerances of Parathemisto

In boreal and polar epipelagic communities, annual production is
strongly seasonal, being high in the spring and summer and low in the
winter. In such areas it would be advantageous for zooplankton to be
able to accumulate and store large energy reserves for use during the
winter months (Littlepage, 1964). Lipids, especially wax esters, appear
to be the major form of energy storage for many planktonic crustaceans
(Lee, Nevenzel, and Paffenhoffer, 1971). Although considerable
data have been accumulated on lipid contents and composition and less
data on the utilization rates of various fractions (Lee, Hirota, and Barnett,
1971), few attempts have been made to determine how long zooplankters may

actually survive starvation and how the ability to withstand starvation
conditions may influence geographical distribution.

Parathemisto libellula and P. pacifica were captured with a 6-ft.
Isaacs-Kidd midwater trawl towed at 15- 20-m depth for 30 minutes at
False Point Retreat on the nights of February 11, 1970, and March 20, 1970.
Twenty-one P. libellula were captured on the first cruise and 25 P.
pacifica and 1 P. libellula on the second cruise. Each species was
divided into two lots--an experimental group to be starved and a
control group to be fed. The experimental animals were placed in
individual containers of 0.54 micron millepore filtered seawater. The
controls were placed in individual containers of unfiltered seawater and
fed with either live zooplankton or "cut food" two or three times a week.
Water in the containers (1-quart jars with 300-500 ml of water) was
changed twice a week. All containers were kept on an open flow table
in which the temperature was usually 6.4° C to 7.5° C, depending upon
ambient temperatures in the building and the temperature of incoming
seawater. No attempt was made to control light cycles.

Daily records were kept on temperatures, molting, mortality, and
the general response of individual amphipods to stimuli of touch, sudden
change in light intensity, and agitation. Moribund animals were identified
as being no longer able to swim to escape or to capture food. Death was
determined when the heart was no longer beating and appendages
did not move when touched. Moribund animals, although still having some
physiological activity, were considered ecologically dead.

Survival time for 19 Parathemisto libellula and 19 P. pacifica are
given in Table 47. Minimum survival time for P. libellula was 12 days,

TABLE 47. --Survival times of starved and fed Parathemisto libellula and P. pacifica held in laboratory at 6.4°-7.5° C

Experimental group no.	Days in captivity before--			
			Death[a]	
	First molt	Second molt	Ecological	Physiological
Parathemisto libellula				
Starved				
1	10	..	12	13
2	26	..	36	36
3	30	..	36	37
4	..	..	36	37
5	20	..	37	38
6	..	..	37	38
7	..	..	40	41
8	12	..	42	43
9	..	..	42	45
10	29	..	42	46
11	30	..	56	59
Fed				
1	..	..	32	34
2	..	..	32	35
3	..	..	32	35
4	25	..	36	36
5	30	76	76	77
6	40	..	76	77
7	35	78	78	78
8	40	90	90+	90+
Parathemisto pacifica				
Starved				
1	..	..	5	7
2	..	..	7	8
3	..	..	8	8
4	..	..	9	10
5	..	..	9	10
6	..	..	16	18
7	..	..	18	21
8	..	..	22	22
9	7	..	22	22
10	..	..	23	26
11	..	..	26	27
12	..	..	26	29
13	7	..	35	43
Fed				
1	..	..	18	21
2	..	..	22	22
3	..	..	24	24+
4	..	..	30	34
5	..	..	46	46
6	..	..	53	53+

[a]Ecological death: moribund and no longer capable of feeding or swimming. Physiological death: cessation of heart beat and other visually observable body movements.

and the maximum survival for starved P. libellula was 56 days. Minimum survival of P. pacifica was 5 days, and maximum survival of starved P. pacifica was 35 days. All controls of P. libellula survived over 31 days with one individual surviving over 90 days. This individual evidently died while molting. Maximum survival of the P. pacifica controls was in excess of 53 days. Actual date and cause of death of this last P. pacifica are not known.

Two of the Parathemisto pacifica starved group molted successfully on the 7th day of the experiment (Table 47). Six of the starved P. libellula and five of the controls completed successful first molts during the experiments. However, the three control P. libellula which attempted a second molt in captivity did not survive. The longest period before molt was 40 days after capture and the between-molt periods were 43, 46, and 50 days.

The starvation tolerance of the two species of Parathemisto may be estimated from the maximum days of survival. The condition of the animals before initiation of the experiments is not known and it is possible they may not have all started with the same amount of bodily reserves. The ranges of survival times (12-56 days for P. libellula and 5-35 days for P. pacifica are evidence that the individual amphipods did not have equal food reserves.

The maximum survival of P. pacifica subjected to starvation was 35 days or 7 weeks. Heart beat and small leg movements were observed for an additional 8 days. This was the longest period any of the amphipods were observed to be in a moribund or an ecologically dead state before ceasing all signs of life.

Maximum survival of starved Parathemisto libellula was 56 days before becoming moribund. This is 21 days longer than for P. pacifica and approximately the same difference as between median days before death (19 days). These observations imply that although P. pacifica can survive long periods of food deprivation comparable to those observed for the mesopelagic copepod Gausia princeps (Lee, Hirota, and Barnett, 1971), P. pacifica has a lower starvation tolerance than its larger congener, P. libellula. However, neither species of Parathemisto appears to have the ability to survive a complete winter without some nutrient intake.

The temperatures during the starvation experiment were $3°$ C to $4°$ C above those that the animals would have experienced in nature, thus, metabolic requirements may have been somewhat higher than normal. Parathemisto pacifica has a metabolic rate Q_{10} near 1.9, and P. libellula has a Q_{10} near 3.5, as determined from oxygen consumption rates within the temperature range of $-1.6°$ to $5.0°$ C. With these Q_{10}'s, a $3°$ C lowering of temperatures to $4.4°$ C would lower the metabolic rates and hypothetically allow P. pacifica to survive up to 42 days of starvation and P. libellula to survive up to 82 days. This is still inadequate to survive a winter from November through March in southeastern Alaska, where water temperatures average $3°$ C to $4°$ C in the winter.

Under Arctic conditions, where winters are nearly 8 months long and water temperatures $-1.5°$ C or lower at the surface, hypothetical starvation survival times for the two species are 2 months for Parathemisto pacifica (58 days), and nearly 5 months for P. libellula (152 days). Although neither species appears to have the ability to survive a complete winter without supplemental food, P. libellula appears to have an advantage in

that it may have to feed or find food less often during the period when food is least abundant. This advantage for winter survival may be in part attributed to the higher Q_{10} of P. libellula and its lack of metabolic adjustment or acclimation at low temperatures; that is P. libellula has a greater reduction in its metabolic requirements during the winter than P. pacifica. Whether or not the two species differ in ability to accumulate and store food reserves is not known. Parathemisto libellula has total lipid contents (7.79 to 19.15% of dry weight) comparable with those of euphausiids and similar-sized planktonic crustaceans. Comparable data are not available for P. pacifica. Parathemisto japonica, a species very similar to and often confused with P. pacifica, is reported to have a total lipid content of 39.6% dry weight (Nakai, 1942). If P. pacifica accumulated comparably high lipids as energy reserves, it appears likely that it is not the relative amounts of lipids stored but the rate at which they are used that imparts the differences in starvation tolerance of P. libellula and P. pacifica.

V11. COEXISTENCE OF PARATHEMISTO LIBELLULA AND P.
PACIFICA IN ALASKAN COASTAL WATERS

An objective of this study of the biology of Parathemisto libellula
and P. pacifica has been to develop a better understanding of congeneric
coexistence of marine zooplankton. Closely related species, especially
congeneric species, are potential competitors for those environmental
resources which may limit population growth. Competition in biological
systems has been defined by Milne (1961) as "the endeavor of two (or more)
animals to gain the same particular thing, or to gain the measure each
wants from the supply of a thing when that supply is not sufficient for
both (or all)." Under current ecological concepts "two species cannot
coexist unless their limiting factors differ and are independent" (Levin,
1970); thus, competing species should not be able to maintain permanent,
coexisting populations. Sympatric congeneric species may coexist by
occupying different habitats and/or niches which minimize competition
such that competitive exclusion is not evident within the area of
sympatry.

The concept of the niche and the principle of competitive exclusion
have been the subject of numerous published reviews, symposia, and
debates, due in large part to the ambiguity of definitions (Hardin, 1960;
Whittaker et al., 1973). Because the concepts are generalizations
derived from many and varied specific observations, it is unlikely that
a firm definition of niche acceptable to all ecologists will be attained.
For the purposes of this work, habitat, niche, and ecotope are
distinguished as proposed by Whittaker et al. (1973). The habitat is
conceived as the range of physical environments occupied by a species;
the niche as the intracommunity role of a species; and the ecotope as

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the combined niche and habitat. Thus, a species' population responses to the physical and chemical variables of its environment describes its habitat. Similarly, a species' relationships and responses to other species within a biological community describe its niche. The ecotope may then be considered as a hypervolume describing the full range of environmental variables to which the species is adapted.

Parathemisto pacifica and P. libellula may be sympatric over 3,000 km of the Alaskan coast from southeastern Alaska (56° N) to the southern Chukchi Sea (70° N). Although coastal zooplankton surveys are not available for most of the area east of Kodiak, Alaska, there is sufficient information to assume a continuous distribution of P. pacifica. Bowman (1960) found P. pacifica in the Bering Sea, south of the Alaska Peninsula, and eastward to British Columbia. I have collected P. pacifica throughout southeastern Alaska and have recorded it from lower Cook Inlet, Alaska, while Sanger (1973) found P. pacifica in the central Gulf of Alaska. Surface currents flow westward (Dodimead, Favorite, and Hirano, 1963) in the unsampled area between Cape Spencer and Kodiak Island. The absence of P. pacifica in the unsurveyed area is unlikely. The assumption of a continuous distribution for P. libellula is not as well founded. Other than my records from southeastern Alaska (predominantly inside waters north of 56° N), the only record of P. libellula from the Gulf of Alaska is off Afognak Island east of Kodiak (Bowman, 1960). If the southeastern Alaska P. libellula are not glacial relicts, the intervening populations between Cape Spencer and the Bering Sea must exist along the unsurveyed coastal areas.

Sympatric distributions only imply habitat coexistence, because the three dimensional and temporal variation within the area of sympatry are

not considered. The pelagic portions of marine ecosystems are generally physically and chemically uniform over broad areas on horizontal planes, but may exhibit strong vertical variations, especially within the upper few hundred meters. Habitat (spatial) coexistence of sympatric zooplankton requires that the coexisting species occupy the same depth ranges at the same times of the year. Both Parathemisto pacifica and P. libellula reside permanently in the upper portions of the water column throughout the year. My data are inadequate to critically examine the question of vertical segregation in the Bering and Chukchi Seas; however, there was no evidence of either species being excluded from areas occupied by the other by reason of lack of sufficient water depth. In southeastern Alaska the sampling method was designed to examine potential vertical segregation. Parathemisto pacifica was encountered from the surface downward to an approximate lower limit of 200 m; P. libellula was encountered from the surface to an approximate lower limit of 300 m. The physical habitat of P. pacifica is contained within the habitat of P. libellula. Where these two species are sympatric they do coexist in the same habitat.

Within the common habitat, Parathemisto pacifica and P. libellula show some partial diel and seasonal segregation concerning the portions of the habitat within which they may be most concentrated. During the 1969 to 1970 sampling at False Point Retreat in southeastern Alaska P. pacifica adults and subadults were generally shallower than P. libellula by 50-100 m during the daylight hours. Small juveniles of P. pacifica were above both the P. libellula and the larger P. pacifica, providing a further segregation of the two species, except for the May-June period when populations of both species were almost totally small,

shallow-dwelling juveniles. Evidence for the diel segregation being only partial is in the mixed catches of both species at depths less than 100 m in material used for the physiological studies and by observations of both species at the surface during daylight sampling in the 1972 MARMAP program.

Partial seasonal segregation of Parathemisto pacifica and P. libellula results from the different daytime depths and differences in reproductive life histories. The short generation span of P. pacifica, year-round reproduction, multiple overlapping generations, and daytime residence of juveniles above the adults result in at least a portion of the population of P. pacifica near the surface at all times of the year. In contrast, P. libellula has but a single generation per year in southeastern Alaska and generally a daytime residence below its congener from July through April.

Having established that Parathemisto libellula and P. pacifica share a common habitat when they are sympatric, it becomes pertinent to ask whether or not they actually compete for a common niche. Unlike benthic and terrestrial animals, competition for niches by zooplankton appears to be limited to trophic competition. The spatial uniformity of the chemical and physical environment provides little opportunity for selection of microhabitats in which the individual animals or populations of a species may control a definable physical space. Nor do most zooplankton present behavioral patterns or displays which may function to maintain an optimal spacing within the water mass. Although some zooplankton, including P. gaudichaudii, can assimilate dissolved organic compounds (McWhinnie and Johanneck, 1966) and a number of zooplankton species excrete or release amino acids (Webb and Johannes, 1967),

dissolved organic compounds have yet to be shown to be directly related to the abundance or distribution of carnivorous zooplankton. Competition between P. libellula and P. pacifica by control of chemical concentrations through either uptake or excretory rates, in the same manner as phytoplankton may compete for nutrients, appears unlikely. It is probable that for predaceous zooplankton, such as the various species of Parathemisto, competition and/or niche segregation is a function of differing abilities to utilize available prey.

Parathemisto libellula and P. pacifica are potentially strong competitors for prey. Both feed primarily upon calanoid copepods and euphausiids, along with other available zooplankton. The comparison of prey species consumed and the relative diets did not show statistically significant differences, although the large P. libellula appeared to consume more chaetognaths, fewer nauplii, and fewer phytoplankton than P. pacifica. Except for the months of May and June, P. libellula from southeastern Alaska were all larger than the largest P. pacifica, and potentially able to take larger prey than the P. pacifica. It is reasonable to assume that P. libellula over 10 mm long could capture and kill adult calanoids and subadult euphausiids more effectively than P. pacifica (always less than 10 mm long). Because both species commonly dismembered their prey, it was not possible to determine whether or not they fed on the same or similar prey species but of different sizes. If there is a difference in size of prey captured, some trophic niche separation is also possible as a consequence of the difference in reproductive cycles of the two Parathemisto.

Lack of competition or evidence for competition for food may be the result of extremes in abundance of either the prey or the predators.

Experimental studies have shown that in the case of superabundance of food, intraspecific competition does not occur, and that at least hypothetically if food is so sparsely distributed that all individuals have an equal chance of finding it, ompetition will not be evident (MacPhee, 1961). The case for intraspecific competition may apply to pelagic ecosystems and interspecific competition. In temperate and high latitude regions, primary productivity and first-level secondary productivity are strongly seasonal, with maxima in the spring and minima in the late winter. This seasonality results in alternating periods of abundant and scarce food supplies. During May and June, when both Parathemisto libellula and P. pacifica are of similar size, have the same depth distribution, and are feeding on the same sized prey, food supplies may be superabundant and so potential competition is minimized. By autumn, when the two amphipods differ greatly in size and have differing daytime depths, food supplies may be so sparsely distributed that mechanisms for reducing competition are not fully evident. By late winter the densities of both the amphipods and their prey are at an annual low, possibly so low that prey captured by either species is a random event with little effect upon the chances of other individuals to obtain food.

The annual decline of the two Parathemisto populations may be the result of factors other than food supply. This study has not dealt with the environmental factors that limit population size, but two aspects may be considered: (1) predation and (2) physiological inability to cope with the extremes of the physical-chemical environment.

Predation on Parathemisto was not measured in this study. A number of animals have been observed to feed on Parathemisto in southeastern Alaska and the Bering Sea, including salmon (Oncorhynchus spp.), trout

(Salvelinus malma), rockfish (Sebastes spp.), herring (Clupea harengus), and shrimp (Pasiphaea pacifica). Although not specifically documented for Alaskan coastal waters, whales, seals, and other fishes of the area may feed upon Parathemisto--as indicated from observations in the Atlantic, Arctic, and Antarctic (Gray and McHardy, 1967; Lambert, 1960; Dunbar, 1957; Nemoto and Yoo, 1970; Kawamura, 1970). Predation has been demonstrated as a major factor in maintaining species diversity and allowing coexistence of competitors in intertidal areas (Paine, 1966), laboratory experiments (Utida, 1953), and mathematical models (Levin, 1970). The large diversity of potential predators on Parathemisto spp. and other zooplankton may reduce populations to such levels that even during the winter, food is not a limiting factor for the amphipod populations. It has not been possible to show differential predation of the two Parathemisto; however, there are sufficient size and habitat differences to suggest that P. pacifica may be more susceptible to general predation than P. libellula. Parathemisto pacifica is both smaller and spends a greater part of the day near the surface where it would be available to shallow-dwelling salmon, herring, juvenile fish, etc. The larger P. libellula, by spending a part of the day in the 200- 300-m depths appears more susceptible to predation by deeper dwelling adult rockfishes (Sebastes spp.) and shrimp (Pasiphaea pacifica). Additionally, in southeastern Alaska P. pacifica appears more susceptible to cannibalism as a consequence of its year-round reproduction than does P. libellula. In southeastern Alaska P. libellula does not seem to be as strongly cannibalistic as in those areas where P. libellula has multiple or overlapping generations.

The physiological responses of Parathemisto to the changes of the physical-chemical habitat may be adaptive to the seasonal changes in food supply and secondarily apply to the question of coexistence. The major physical cycle of the habitat has been shown to be the annual temperature cycles, in which temperatures are lowest during the winters, when food density is lowest. Both species of Parathemisto tolerate and actively feed in the full range of temperatures experienced in Alaskan coastal waters. Optimal or preferred temperature ranges appear to differ. Parathemisto pacifica, especially as juveniles, are more frequently found associated with water temperatures above 7° C to 8° C and less frequently with water temperatures below 3° C than are P. libellula. These differences in distribution compared to water temperatures may be related to the differences observed in starvation tolerance and respiratory Q_{10}'s. When held at temperatures of 6° C to 7° C, P. libellula tolerated up to 56 days starvation while P. pacifica tolerated only 35 days starvation. Within the range of -1.6° C to 5° C, P. libellula has a Q_{10} of 3-5 and P. pacifica has a Q_{10} near 1.9. Possibly P. libellula not only has an inherently greater tolerance of starvation but under low temperature conditions when food supplies are apt to be least, it is able to lower its metabolic requirements more than P. pacifica.

The greatly lowered metabolic requirements in response to low temperatures by Parathemisto libellula may be an adaptation to the environmental conditions of its Arctic origins, but also, it may have an effect of partially removing P. libellula from competition for food when prey are least available. Parathemisto pacifica, with relatively higher metabolic requirements and possibly by maintaining a higher level of activity, is able to obtain enough food to maintain growth and reproduction

during the winter by a few individuals in a small but declining population. Also, the shallow daytime distribution of P. pacifica may be adaptive to winter survival because calanoid copepodites and euphausiid larvae tend to have shallower distributions than adult and subadult calanoids and euphausiids.

The differing strategies of the two Parathemisto for surviving the seasonal paucity of food are similar to that described by Haq (1967) for the calanoid copepods Metridia longa and M. lucens in the Gulf of Maine. Metridia longa has high lipid reserves (25-35% dry weight) and low respiratory rates while M. lucens has low lipid reserves (1-5% dry weight) and high respiratory rates. At 5° C, Haq estimated that M. lucens would tolerate only 2-3 days starvation, while M. longa would tolerate up to 2 months starvation.

The relationships of lipid storage and respiratory rates observed for Metridia longa and M. lucens differ somewhat from that observed for Parathemisto. Parathemisto libellula total lipids are 8-20% of dry weight. No data are available for lipids from P. pacifica, but the comparable P. japonica may have up to 49% dry weight as lipids (Nakai, 1942). At low temperatures, P. libellula has lower metabolic rates than P. pacifica by reason of its higher Q_{10}. The Metridia examined by Haq (1967) do not appear to have significantly different Q_{10}'s. The difference in starvation tolerance at low temperatures between P. libellula and P. pacifica is a function of the differing temperature-respiration rate relationships, whereas in the comparison of M. longa and M. lucens the difference is due to the differing abilities to accumulate and store energy reserves.

The winter survival strategies of the two pairs, Parathemisto libellula--P. pacifica and Metridia longa--M. lucens are analogous to the terrestrial comparison of bears and wolves. The first member of each pair survives winter by lowering its metabolic demands and/or storing energy reserves to tolerate semi-starvation. The second member of each pair survives by maintaining a high level of activity and capturing sufficient prey to assure survival of at least a portion of the population.

Investigations of coexistence mechanisms in zooplankton have tended to emphasize the importance of size differences implying food differences (Hutchinson, 1951), vertical segregation (Donaldson, 1973), and seasonal segregation associated with differing reproductive capabilities (Jeffries, 1962). Generally, it is assumed that if one of these three mechanisms is not evident, one of the other two is functioning. However, at least in the case of freshwater diaptomid copepods, any two of the mechanisms may be simultaneously evident (Sandercock, 1967). Less attention has been given to the suggestion by Riley (1963) that potential competitors simultaneously invading new or marginal habitats may not have accrued competitive advantages, or that competitive elimination processes are so slow between nearly equal competitors that evidence of competitive exclusion may be impossible to detect. Seasonal segregation due to differing reproductive capabilities may be a variant of Riley's proposal. Although competitive advantages may exist for stable environments, the seasonal changes reassign those advantages before exclusion of one or more of the competing species occurs.

The coexistence of Parathemisto libellula and P. pacifica in Alaskan coastal waters may be dependent upon all three of the previously emphasized

coexistence mechanisms. Except for the late spring (May-June) in southeastern Alaska and the southern Bering Sea, the two species differ greatly in size, suggesting potential of utilizing different-sized prey, although I found no definite evidence of size selectivity in prey. Partial vertical segregation during the day was evident in most months, except May and June, but not at night when most feeding probably occurs. Seasonal segregation of reproductive periods is also only partial. In southeastern Alaska and probably in the Bering Sea, both species initiate their annual reproductive cycle in May. Parathemisto libellula has only the single spring brood release, but P. pacifica with short overlapping generations continues to reproduce through the summer and to a lesser extent in the fall and early winter.

Parathemisto libellula and P. pacifica do not appear to have strong habitat and niche segregation in the areas where they are sympatric. Coexistence mechanisms do not appear to have evolved in response to an interaction of the two species. Their coexistence may be the result of inability to fully occupy a marginal habitat. Parathemisto libellula may be restricted by summer conditions, while P. pacifica appears to be limited by winter conditions along the Alaskan coast. Although P. libellula tolerates limited periods at temperatures above 7-8° C, it does not appear to be able to establish populations where temperatures rise to 10-15° C unless it has access to colder waters through vertical migration. This may be a consequence of failure to fully acclimate its metabolic rates at the warmer summer temperatures, resulting in P. libellula being unable to obtain enough food to maintain itself in spite of an abundance of food during the summer. Parathemisto pacifica appears well suited to the upper range of temperatures in the region of sympatry

but not to the lower range of temperatures. Although P. pacifica can tolerate temperatures as low as -1.6° C, it is most abundant in areas where water temperatures are seldom below 3° C. Having a high metabolic rate and low starvation tolerance, the P. pacifica population declines during the winters when food is least available. The annual temperature cycle, which passes beyond the optima of both species, and the associated cycle of food abundance appear to control population levels and allow the coexistence of P. pacifica and P. libellula in southeastern Alaska and the Bering Sea. If the records of P. libellula from the northern Gulf of Alaska and the records of P. pacifica from the Chukchi Sea are not of expatriate populations the same environmental controls probably apply in those areas.

VIII. SUMMARY

1. The planktonic hyperiid amphipods Parathemisto libellula and P. pacifica appear to be sympatric in Alaskan coastal waters from southeastern Alaska to the southeastern Chukchi Sea. This study has used field and laboratory observations to describe their habitat and aspects of their ecology and physiology which allow them to coexist in this area.

2. Parathemisto were collected monthly from September 1969 to October 1970, and in February 1971, at False Point Retreat and Auke Bay in southeastern Alaska. Supplementary collections were obtained for May-September 1969 from the southeastern Bering Sea, and September-October 1970 from the southeastern Chukchi Sea. Standard chemical and physical oceanographic observations were concurrent with plankton collections for Parathemisto.

3. The oceanography of Alaskan coastal waters is characterized by strong seasonal cycles. In southeastern Alaska the upper water column is isopycnal during the winter, with annual minimum temperatures (2.5° C to 4.0° C), maximum salinities (31-32°/$_{oo}$), and minimum standing crops of plankton in February-March. Vernal warming and stratification of the water column is initiated in April-May leading to maximum primary productivity in May followed shortly by peak zooplankton crops. Maximum water temperatures (9-14° C) and stratification occur in late August. Autumnal cooling begins in September. Minimum salinities occur in October and are associated with heavy runoff from autumn storms. Rapid cooling and storm mixing result in near isopycnal conditions by mid-November.

4. Parathemisto libellula and P. pacifica were found consistently in the upper 300 m at False Point Retreat. Parathemisto libellula occurred in Auke Bay only in June of 1970 during this study, in contrast to regular occurrence during an earlier 1962-64 study. Parathemisto pacifica was absent from Auke Bay from February to April 1970, in contrast to absence only in March in the early study.

5. Both Parathemisto libellula and P. pacifica were collected in the southeastern Bering Sea during the spring and summer of 1969. Parathemisto libellula appeared restricted to areas where the summer bottom temperatures did not exceed 8° C. Parathemisto pacifica appeared restricted to areas where May water temperatures were above 2.5° C.

6. Both Parathemisto libellula and P. pacifica were found in the southeastern Chukchi Sea in the fall of 1970, when water temperatures were generally less than 3.0° C. The P. pacifica may have been expatriates from the Bering Sea and may have been unable to survive a full Chukchi Sea winter.

7. In southeastern Alaska, juveniles of both species reside in the surface waters at shallower depths than subadults and adults. Both species have a diurnal vertical migration, with daytime depth increasing with age. Subadult and adult Parathemisto pacifica have a day depth of 100-200 m. Subadult and adult P. libellula have a day depth of 200-300 m. Both species move into the upper 50 m at night. During nine night samplings P. pacifica were found above 15 m seven times and P. libellula only twice.

8. Parathemisto libellula in southeastern Alaska has a strict 1-year life cycle with no overlap of generations, in contrast to the

2-year life cycle with partial overlap of generations in the Arctic Ocean. Eggs are deposited in the brood pouch in March. Broods are released in May with individuals about 1.8 to 2.0 mm total length. Growth of juveniles is rapid; by late June modal size exceeds 10 mm and by November mean length approximates 20 mm. Growth continues through the winter at a lesser rate with males maturing at 19-22 mm and females at 21-25 mm. Maximum observed size was a 29.5 mm female.

9. Parathemisto pacifica in southeastern Alaska has continuous reproduction, with overlapping generations. Generation span varies through the year, being longest in the winter and shortest in the mid-summer. The annual cycle of P. pacifica can be considered to begin in May with a first major brood release of juveniles 1.8 to 2.0 mm. Few if any adults survive the brood release. During the summer, successive but overlapping broods mature in 6-8 weeks. During the winter, growth and maturation of successive broods decreases. By late winter, generation time appears to be 8-12 weeks. In March, the separate broods appear to coalesce when most individuals are mature and some eggs are deposited. A few juveniles are released in April, but most are not released until May. During the summer males may mature at 4.5 mm and females at 5.5 mm. In the late spring males mature at 6.0 mm and females at 6.5 to 7.0 mm. Maximum size observed was a 9.5-mm female.

10. Parathemisto libellula and P. pacifica have similar weight-length relationships. Wet weight-length regressions for Parathemisto from southeastern Alaska are:

P. libellula Ln mg = -3.16 + 2.57 Ln mm

P. pacifica Ln mg = -2.90 + 2.66 Ln mm

Dry weight-length regressions are:

P. libellula Ln mg = -4.64 + 2.49 Ln mm

P. pacifica Ln mg = -4.65 + 2.79 Ln mm

11. Molting, which accommodates growth, is a period of critical physiological stress. Mortality during molting of winter animals in the laboratory was 55% for Parathemisto libellula and 82% for P. pacifica. Intermolt periods of 22-71 days were observed for P. libellula and up to 42 days for P. pacifica.

12. Feeding appears to occur mostly during the evening vertical migration. From laboratory observations, the Parathemisto do not appear to actively locate and pursue prey, rather capture seems to result from accidental contact with prey. Failure to capture prey upon first contact results in a circling behavior suited to contacting prey which may occur in small dense patches.

13. Small prey may be consumed nearly intact, but larger prey, especially large copepods, euphausiids, and amphipods are dismembered for extraction of body tissues. Exoskeletons of amphipods and euphausiids are generally not ingested.

14. Diets of Parathemisto libellula and P. pacifica were very similar and not separable statistically. Calanoid copepods were the most frequently observed foods, with compound-eyed crustacenas (mostly euphausiids and amphipods) the second ranking foods. Combined, these foods account for about 80% of the food items recorded from Parathemisto crops and stomachs. Cannibalism was less frequent in P. libellula than in P. pacifica.

15. Starvation tolerances of Parathemisto libellula and P. pacifica

differ greatly. At 6° C to 7° C in the laboratory, P. libellula survived 56 days but P. pacifica survived only 35 days before becoming moribund.

16. Respiratory metabolism rates of Parathemisto at various temperatures were obtained with a differential respirometer. Oxygen uptake rates (microliters per hour) were obtained for P. libellula over the temperature range -1.6° C to 17.0° C. A multiple regression technique was used to relate the respiratory rates to weight, temperature, and salinity. Sex, time of day, acclimation time, time in captivity, proximity to molting, proximity to death, and variations of observational technique had no statistically significant effects upon respiratory rates. Nine determinations of respiratory rates for P. pacifica were obtained within the -1.6° C to 5.0° C temperature range.

17. Parathemisto libellula appears to have two responses to temperature changes. From -1.6° C to 5.0° C the relationships of oxygen consumed per hour to weight, temperature, and salinity were:

$$\text{Log } (\mu l \, O_2/hr.) = -1.4166 + 0.4141 \text{ Log (mg dry weight)}$$
$$+ 0.0576 \, (°C) + 0.0617 \, (°/_{oo} \, S).$$

and

$$\text{Log } (\mu l \, O_2/hr.) = -2.4723 + 0.4414 \text{ Log (mg wet weight)}$$
$$+ 0.0556 \, (°C) + 0.0747 \, (°/_{oo} \, S).$$

with the respiratory Q_{10}'s in the range of 3 to 5. From 10.0° C to 17.0° C the observed relationships were:

$$\text{Log } (\mu l \, O_2/hr.) = -1.4995 + 0.7387 \text{ Log (mg dry weight)}$$
$$+ 0.0368 \, (°C) + 0.0423 \, (°/_{oo} \, S).$$

and

$$\text{Log } (\mu l \, O_2/hr.) = -4.2842 + 0.6126 \text{ Log (mg wet weight)}$$
$$+ 0.0289 \, (°C) + 0.1225 \, (°/_{oo} \, S)$$

with a Q_{10} of 1.9 to 2.3. At 7.5° C the respiratory rates had a bimodal distribution, which was interpreted to be an overlap of the two responses as the experimental populations adjusted to rising or falling temperatures.

18. Weight-respiration relationships did not change with temperature.

19. Salinity had a small but statistically significant relationship to respiration rates. Within the range of experimental salinities (30.70 to 32.40 °/$_{oo}$), low salinities correlated with lower respiration rates. If this relationship is true, it may have some significance to maintaining a constant metabolic rate during vertical migration. Low temperatures and higher salinities occur at the depth of daytime residence. The salinity and temperature responses may counteract and balance metabolic rates during vertical migration.

20. Respiration data obtained for Parathemisto pacifica were inadequate for rigorous statistical treatment. The limited data available have a Q_{10} of 1.9 to 2.3 for the temperature range of -1.6° C to 5.0° C.

21. Both Parathemisto libellula and P. pacifica tolerate temperatures as low as -1.6° C for extended periods of time. Parathemisto libellula appears to have an upper ecological and physiological limit near 7-8° C and a lethal limit near 17° C. Parathemisto pacifica has an ecological limit near 18° C, but its upper lethal limit remains unknown.

22. Coexistence of Parathemisto libellula and P. pacifica in Alaska coastal waters appears more dependent upon environmental control of populations, than upon habitat and niche differences. Habitats and

niches are broadly overlapping. Where waters are deep enough some vertical segregation during the day does occur. Niche segregation by means of feeding on different sized prey is possible, but was not evident.

23. Both species can tolerate the full range of seasonal temperatures expected in Alaskan coastal waters. However, their metabolic responses to temperature and starvation tolerance may interact to prevent either species from fully occupying their common habitat and niche. Parathemisto libellula is able to lower metabolic requirements sufficiently to tolerate longer periods of winter semistarvation then P. pacifica. At temperatures above 7° C to 8° C, P. libellula appears unable to acclimate and lower its metabolic requirements enough to adequately utilize available food supplies. Although individuals of either species are able to survive winter or summer stress, the overall population survivals are lowered to the point that neither species is seriously competing for the common habitat and niche.

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