

AN ABSTRACT OF THE THESIS OF

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Title: THE DYNAMICS OF AN ISOLATED POPULATION OF  
ACARTIA TONSA DANA (COPEPODA) IN YAQUINA BAY,  
OREGON

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Charles B. Miller

In the upper estuary of Yaquina Bay, Oregon, there is an annual population explosion of Acartia tonsa, (Dana) a calanoid copepod, during the months of July, August and September, followed by a rapid decline to virtual extinction in November. The restricted estuarine distribution affords an excellent opportunity to study the factors governing the population dynamics of A. tonsa without the disadvantage of potential mixing with other populations on different schedules of development. Field densities of A. tonsa during the 1972 summer were determined by twice weekly sampling with Clarke-Bumpus plankton samplers. In addition, explanation of the production of A. tonsa in the field was attempted by measuring the rates of egg production and development in the laboratory under temperature (21°C) and salinity (25 ‰) conditions comparable to those in the upper estuary.

Daily egg production was found to be  $30.5 \text{ eggs} \cdot \text{day}^{-1} \cdot \text{female}^{-1}$ . The median rate of development from egg to adult required 11.5-11.6 days at  $21^{\circ}\text{C}$  in conditions of either laboratory cultured or wild food organisms. Mortality rates were substantial during the experiments as only 20 - 30% of the original populations survived to adulthood. The cause of mortality is not known but may relate to the molting process.

In the field, six successive generations of A. tonsa were observed during the population explosion. The mean generation time ranged from 16 days in August to 19 days in October. A maximum density of  $16,800 \text{ adults} \cdot \text{m}^{-3}$  in late August was followed by a crash to  $2,100 \text{ adults} \cdot \text{m}^{-3}$  10 days later. Predation and over exploitation of food resources are two possible causes of the crash. However, temperature appears to be the major factor for the subsequent decline and disappearance of A. tonsa in the fall. This thesis presents the first results of ongoing research into the population dynamics of A. tonsa.

The Dynamics of an Isolated Population of Acartia fonsa  
Dana (Copepoda) in Yaquina Bay, Oregon

by

John Kenneth Johnson

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THE DYNAMICS OF AN ISOLATED POPULATION OF ACARTIA  
TONSA DANA (COPEPODA) IN YAQUINA BAY, OREGON

INTRODUCTION

The distribution of copepod species in estuaries can be restricted to short, particularly suitable zones. Cronin et al. (1962), for example, described a distinct and persistent change in species composition related to salinity gradients along the length of the Delaware River estuary. The upper reaches (salinities less than 5 ‰) were dominated by Cyclops viridis while the middle reaches (salinities of 18 ‰ - 30 ‰) was characterized by Temora longicornis, Labidocera aestiva and Centropages sp. These "confined" populations can be of considerable importance as food sources for the commercial fisheries and wildlife of an estuary. However, they are potentially vulnerable to changes in estuary circulation, salinity, temperature, etc., that might result from man's engineering activities in the estuary such as dredging or outfalls of sewage, industrial or thermal waste. With this perspective and significance in mind, a study has been initiated of the population dynamics of Acartia tonsa (Dana, 1848), an important species restricted to the upper estuary of the Yaquina River, Oregon.

The general zooplanktology of Yaquina Bay is well known from the work of Frolander (1964), Zimmerman (1972) and Frolander et al.

(1973). The lower estuary is dominated by two species groups which are shared with the nearshore oceanic water (Miller, 1972; Frolander et al., 1973). Alternations between cold north to south currents along the Oregon coast during the summer and the warm south to north Davidson Current during the winter result in a 'summer-northern' assemblage and a 'winter-southern' assemblage of copepods. The summer population is typified by the copepods Acartia clausi (Giesbrecht, 1889), Acartia longiremis (Lilljeborg, 1853) and Pseudocalanus cf. gracilis (Sars, 1903). These species are present in the lower estuary year around but are dominant during the summer. During the winter, A. clausi becomes co-dominant with several species of southern and offshore affinities, the most important being Paracalanus parvus (Claus, 1863), Ctenocalanus vanus (Giesbrecht, 1888) and Corycaeus anglicus (Lubbock, 1857). These latter three species are generally absent from the estuary during most summers.

The seasonal cycle of the zooplankton inhabiting the brackish water of the upper estuary has been shown to be quite different from that of the lower estuary (Zimmerman, 1972). The upper estuary is characterized by an annual population explosion of Acartia tonsa (Dana, 1848) during the months of July, August and September, followed by a rapid decline to virtual extinction by the end of November. A. clausi is numerically dominant throughout the spring and early summer but is incompletely replaced by the A. tonsa bloom

in August and September. A. clausi becomes the dominant zooplankton again with the decline and disappearance of A. tonsa in October and November, but is significantly displaced downstream by the heavy winter runoff (Zimmerman, 1972).

Acartia tonsa is a species of southern affinities along the Pacific coast (Miller, 1972) and is generally a minor component of the nearshore zooplankton in the northerly Davidson Current off Oregon in the winter. During the summer, A. tonsa is rarely present offshore. The source of the summer repopulation of the upper estuary is not clearly understood but may derive from the low oceanic winter population or from the possible but unverified presence of winter "resting" eggs which have recently been demonstrated for A. tonsa on the Atlantic coast (Zillioux and Gonzalez, 1972).

The zooplankton populations of middle Atlantic and New England estuaries are similarly dominated throughout much of the year by either A. clausi or A. tonsa. A. clausi is typically dominant during the winter-spring season and is followed in succession by A. tonsa, a summer fall form (Jeffries, 1962). A comparable cycle of succession exists in Long Island Sound (Conover, 1956).

The actual existence and the basis of the interaction between the two congeneric species, that is, what they are competing for, is not understood. However, the seasonal reversal in relative numbers of A. clausi and A. tonsa is related to a difference in tolerance to higher

temperature and lower salinity extremes between the species. A. tonsa is less affected by low salinity (Lance, 1962, 1963) and high temperatures and consequently, becomes much more abundant than A. clausi in the summer when water temperatures are maximal (Jeffries, 1962, 1967). During such conditions A. tonsa becomes extremely abundant. Densities greater than 100,000 individuals (all stages) per cubic meter were reported in certain areas of the Patuxent River estuary (Chesapeake Bay) by Heinle (1966).

## STATEMENT OF THE PROBLEM

The annual population explosion of Acartia tonsa in Yaquina Bay provides an excellent opportunity to study the factors governing the population dynamics of copepods in a restricted, relatively closed system. Other population studies of zooplankton such as Mullin and Brook's (1970) work on the production of Calanus off La Jolla, California, suffer from the disadvantage of unknown but potential mixing with other populations on different schedules of development. In contrast, the A. tonsa population of Yaquina Bay is protected from mixing with other populations. As noted above, there are essentially no A. tonsa offshore in the summer. However, the population is not completely contained; there are some losses to the lower bay by flushing and by tidal diffusion to the upper bay. Losses to the lower bay appear to be very small (Zimmerman, 1972; see also Figure 24 and Table 3).

Explanation of the production of A. tonsa in the field can be attempted by measuring the rates of fecundity and development under controlled conditions in the laboratory and extrapolating to the natural population (Heinle, 1966; Mullins, 1969). In addition, the rates of production can be corrected for age specific mortality by frequently sampling all life stages of the natural population and estimating the absolute abundance of each. This thesis, then, presents the first

results of ongoing research into the population dynamics of Acartia  
tonsa, an important zooplankter in the upper reaches of Yaquina Bay,  
Oregon.

## PHYSICAL DESCRIPTION OF YAQUINA BAY ESTUARY

### Location and General Description

The Yaquina Bay estuary is located about 185 kilometers south of the mouth of the Columbia River on the central Oregon coast at  $44^{\circ} 35'$  N Latitude and  $124^{\circ} 04'$  W Longitude (Figure 1). The small community of Newport (1970 population: 5,188) is located near the entrance to the estuary and serves as a port for ocean-going vessels and a commercial-sport fishing fleet. The deep-draft ocean vessels generally take aboard cargoes of logs and lumber for Oriental ports. Toledo (1970 population: 2,818), the only other major community, is located 20 kilometers upstream and is the site of the large Georgia-Pacific Corporation Kraft process pulp mill (Percy *et al.*, 1973).

The estuary is dredged regularly to maintain a channel depth of 8 meters in the lower estuary to accommodate the deep-draft ocean-going vessels. A channel depth of approximately 4 meters is maintained by rather infrequent dredging from Buoy 21 to Toledo to permit the passage of fishing vessels and tugboats with lografts.

The Yaquina River is the major tributary of the estuary and has its zero kilometer at the seaward entrance to the estuary. The head of tidewater for the estuary is at Elk City, 35.4 kilometers upstream, where the Yaquina River is joined by Elk Creek. Elk

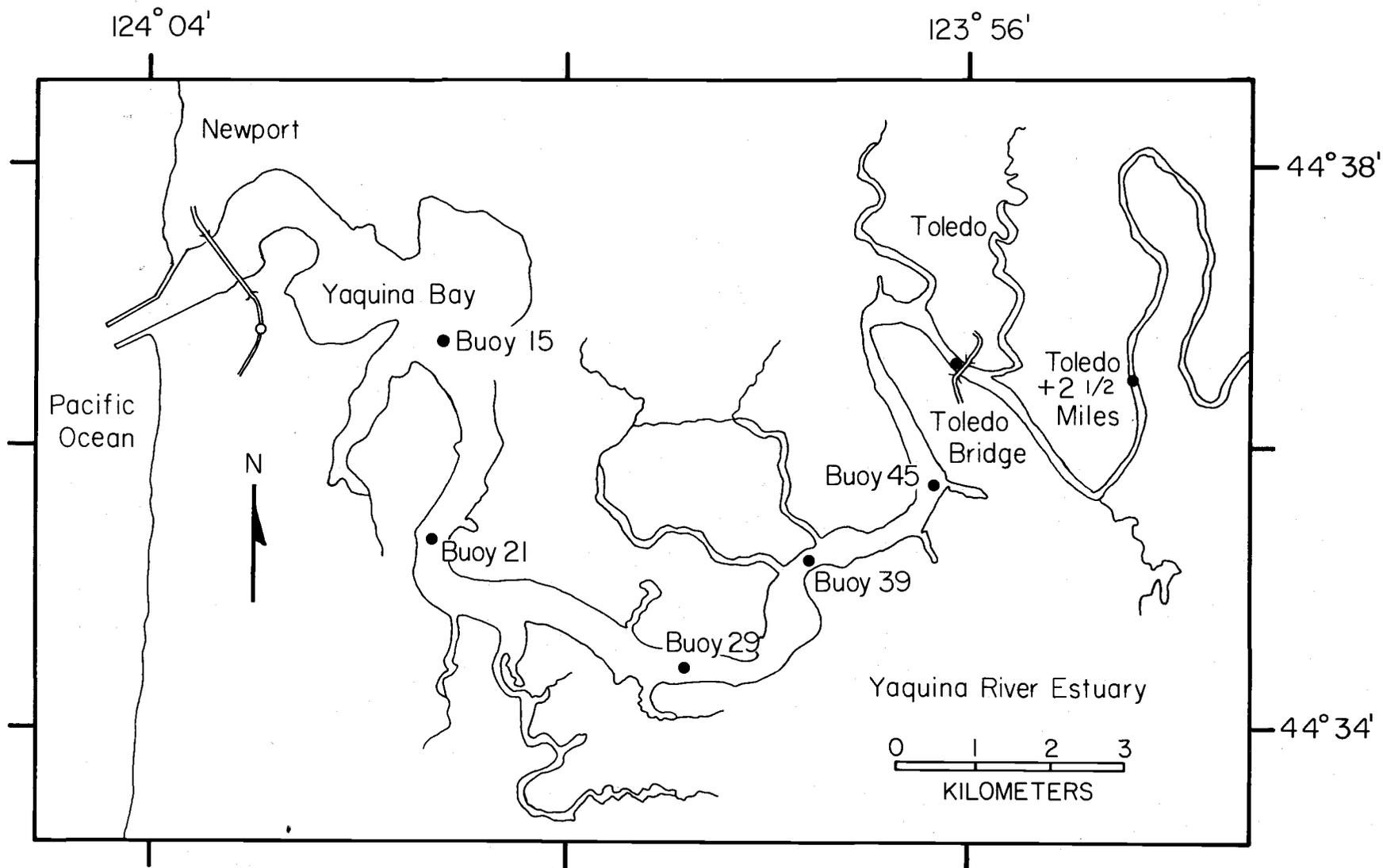


Figure 1. Map of Yaquina Bay estuary showing sampling locations at navigational buoys B-21, B-29, B-39, B-45, Toledo Bridge and 2 1/2 miles above Toledo Bridge.

Creek is the only other important tributary for the estuary (Kulm and Byrne, 1967). The total drainage system is relatively small, consisting of approximately 632 square kilometers of the western slope of the coast range (Goodwin et al., 1970). Elevations range from sea level to about 460 meters (Kulm, 1965).

### Climatic Conditions

The climate of the coastal drainage system alternates between relatively cool dry summers and mild rainy winters. Mean annual air temperatures at Newport, averaged from 1937 to 1969, ranged from  $14.2^{\circ}\text{C}$  in August to  $6.4^{\circ}\text{C}$  in January (Holbrook, 1970).

Temperatures have a wider annual range inland. Mean monthly air temperatures in 1972 at Toledo, 20 kilometers inland, ranged from  $18.5^{\circ}\text{C}$  in August to  $6.4^{\circ}\text{C}$  in December (Figure 2). Only the 1972 temperature data for Toledo are plotted in Figure 2 as long term temperature data, comparable to that recorded at the Newport Weather Station, are not available. The 95% confidence limits are also plotted to provide an idea of variability about the mean values.

Annual rainfall for Newport averaged from 1938 to 1969 (Figure 3) is  $173.7 \pm 12.3$  cm (mean  $\pm$  2 std. errors) (Holbrook, 1970) and increases to 254 - 305 cm in the eastern portion of the drainage basin (Oregon State Water Research Board, 1965). The heavy winter

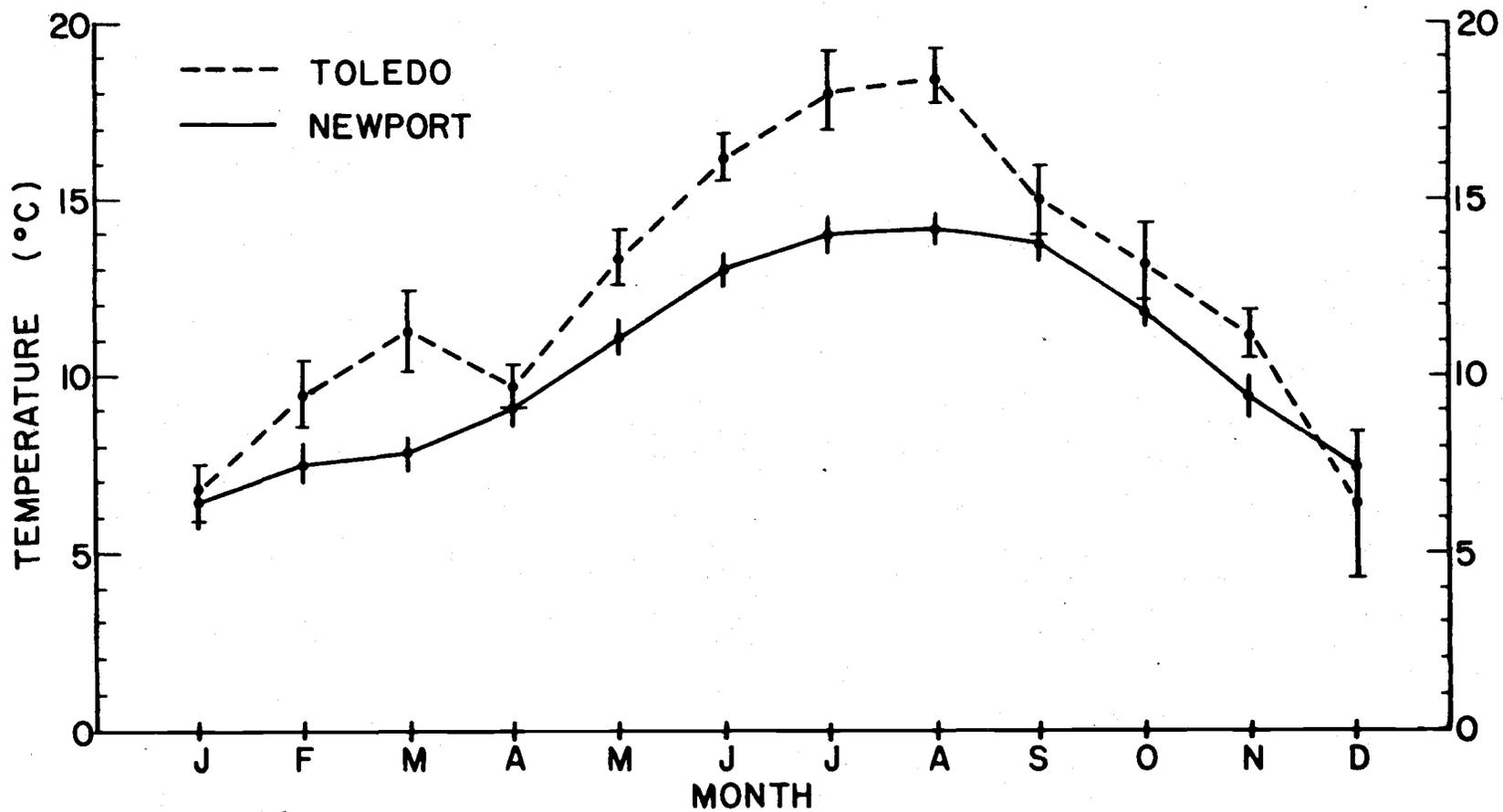


Figure 2. Mean monthly air temperatures ( $^{\circ}\text{C}$ ) at Newport (1937-1969) and Toledo (1972 only) with 95% confidence limits. Data from Holbrook, 1970.

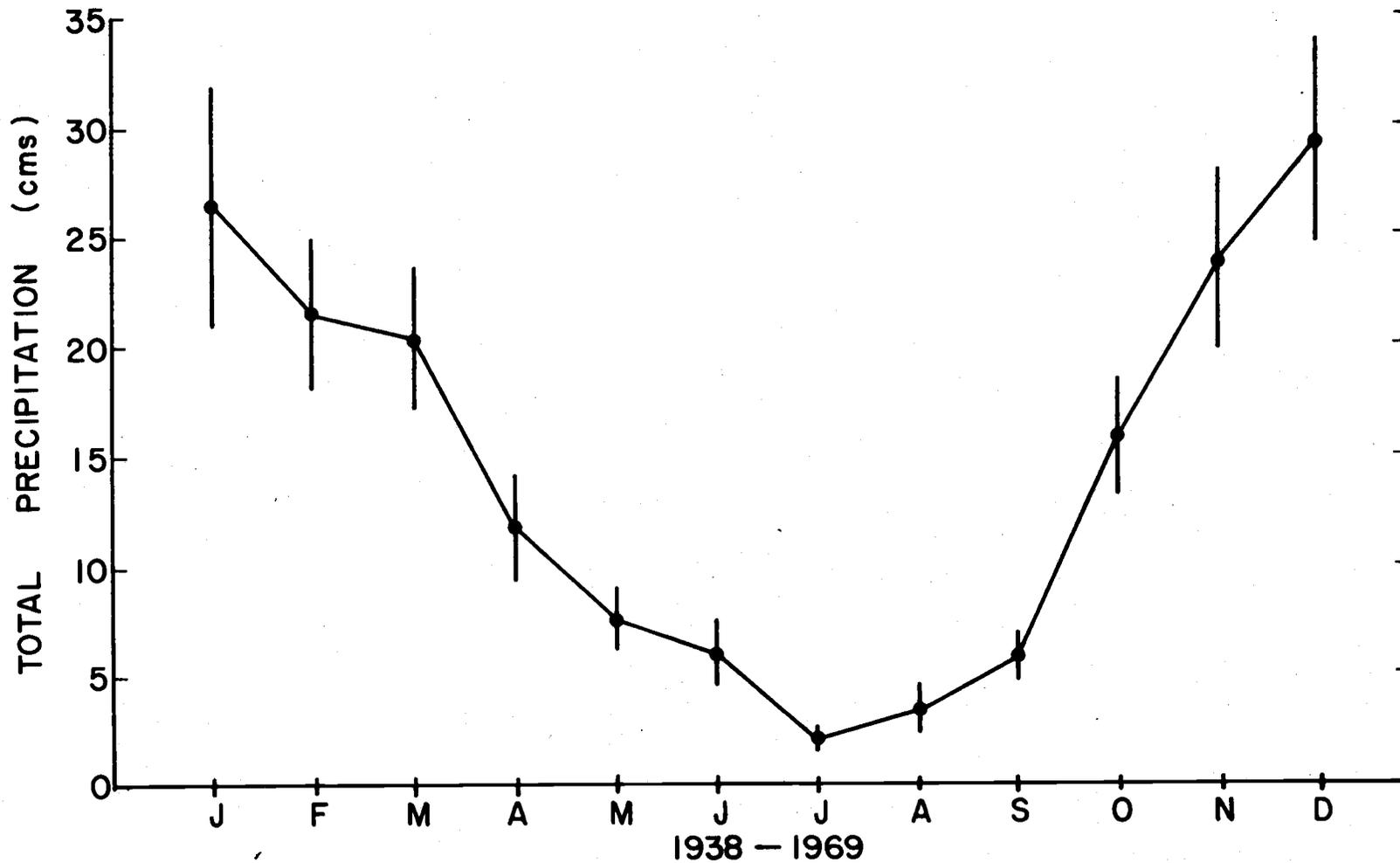


Figure 3. Mean monthly precipitation (cms) at the Newport Weather Station (1938-1969) with 95% confidence limits. Data from Holbrook, 1970.

precipitation is produced by the general eastward movement of cyclonic low-pressure weather systems. Rains commence in November, are heaviest in December (29.2 cm) and January (26.2 cm) and gradually terminate by early May. Minimum precipitation falls in July (1.7 cm) and August (2.6 cm) (Holbrook, 1970).

Winds are seasonal in direction and velocity in the Yaquina Bay region. During the winter low velocity winds are generally offshore, with less frequent high velocity storm winds blowing from the south-southwest. The summer wind regime is characterized by mild to strong onshore winds from the north-northwest (Kulm and Byrne, 1966). These summer winds are responsible for the cold upwelled water and high biological productivity along the Oregon coast in the summer. Wind stress of the north-northwest winds coupled with the right-deflecting Coriolis force (northern hemisphere) causes a westerly offshore movement of warmer coastal surface waters and the subsequent upwelling of cold, nutrient rich, high density water from deeper layers to preserve mass continuity. Upwelled water is often flushed into the estuary by tidal action, and causes large fluctuations in temperature and salinity in the middle and upper reaches of the estuary (Buoy 21 to Toledo).

### Tidal Conditions

Tides in Yaquina Bay are the mixed, semidiurnal type. The mean tidal range at Newport is 1.8 meters with a diurnal range of 2.4 meters and a mean tidal level of 1.3 meters. Extreme spring tides in 1972 had a maximum range of 3.8 meters (Tide Tables West Coast of North and South America, 1972).

A tidal study of the Yaquina Bay estuary (Goodwin et al., 1970) revealed that amplification of the tidal range occurs with increasing distance upstream. The relative importance of upstream amplification also increases with decreasing tidal ranges at the entrance of the estuary. As an example, Goodwin et al. (1970) note a tidal range of 2.75 meters at Newport corresponds to 2.93 meters at Elk City, while a tidal range of 0.61 meters at Newport is equivalent to 0.85 meters at Elk City. The ratios between the selected tidal range examples are 1: 1.07 and 1: 1.39, respectively.

A phase difference of 90 to 100 degrees (time lag of approximately 0 - 20 minutes) was also found to exist between tidal elevation and currents in Yaquina Bay. Amplification of the tidal range and phase differences of  $90^{\circ}$  indicate the presence of reflected waves and/or resonance conditions (Goodwin et al., 1970).

### Tidal Currents

Tidal currents are highly variable, varying with the phase of the moon, stage of tide, distance upstream and streamflow. Maximum tides (spring tides) and tidal currents occur when the moon, sun and earth are in conjunction. Conversely, minimum tides (neap tides) and tidal currents historically occur when the two celestial bodies are  $90^{\circ}$  out of alignment. Tidal currents are also greatest at the mid-stage of the flood or ebb tides and decrease to zero at slack water. Maximum velocities, however, decrease somewhat with increasing distance upstream. Measurements collected over 24 hours at various depths at five stations in Yaquina Bay during a period of minimal river flow in July (Table 1) reveal that maximum flood currents which occurred near the entrance to the estuary had decreased 77 percent in the vicinity of Buoy 45. Upstream of Buoy 45, the tidal flood currents were of the same general strength (Goodwin et al., 1970). An increase in freshwater streamflow will also decrease the upstream extension and velocities of flood tidal currents.

### Tidal Volumes

The volume of the Yaquina Bay estuary is estimated to be  $55.2 \times 10^6 \text{ m}^3$  at MHHW and  $26.3 \times 10^6 \text{ m}^3$  at MLLW (after Zimmerman, 1972). The surface area of the estuary ranges between  $17.1 \text{ km}^2$  at

Table 1. Mean tidal current flux in Yaquina Bay Estuary, July 21, 1969. Currents are averaged over several depths (after Goodwin et al., 1970).

Recording Station	Distance Upstream (km)	Maximum Floodtide ( $m^3 \cdot s^{-1}$ )	Maximum Ebbtide ( $m^3 \cdot s^{-1}$ )	Water Depth** (m)
Newport	3.1	0.062	0.022	5.4
*River Bend ("Buoy 21")	8.8	0.042	0.031	3.9
*Georgia-Pacific Dock ("Buoy 45")	17.2	0.014	0.017	2.9
Mill Creek (4.3 km above Toledo)	24.4	0.017	0.034	4.9
Head of Tidewater	41.9	0.020	0.037	3.1

\* Buoys 21 and 45 are in the near vicinity and are considered equivalent to the sampling stations of Goodwin et al. (1970).

\*\* Water depths are not representative of main channel depths.

MHW and  $9.1 \text{ km}^2$  at MLW (Johnson, 1972). The large difference in volume and surface area at high and low water is caused by the filling and emptying of a large embayment located 3.2 km from the mouth of the estuary (Figure 1). The tidal prism at Buoy 15 (located approximately in the center of the embayment) is  $21.4 \times 10^6 \text{ m}^3$  with a cross-sectional area at MHHW that is 72% greater than that at MLLW (Goodwin et al., 1970). Buoy 21, located 8.8 km upstream in the constricted river channel proper, has a much smaller tidal prism of  $13.3 \times 10^6 \text{ m}^3$ . Consequently the planktology in the thesis study area upstream of Buoy 21 reflects the increasing influence of the fluvial regime while the planktology below Buoy 21 is more similar to nearshore coastal waters (Frolander et al., 1973).

Using Ketchum's (1951, 1954) modified tidal prism method, Zimmerman (1972) calculated the exchange ratio and flushing time for the Yaquina estuary to be 52% and 13.3 cycles, respectively, during the month of August. Zimmerman assumed a stream flow of  $0.9 \text{ m}^3 \cdot \text{s}^{-1}$  (33.5 cfs) based on data from Burt and Marriage (1957). Incomplete stream flow records near Elk City during the period 1937 to 1963 (Figure 4) indicate the average minimal, maximal and annual stream flow to be  $1.2 \text{ m}^3 \cdot \text{s}^{-1}$  (August),  $34.8 \text{ m}^3 \cdot \text{s}^{-1}$  (February) and  $14.3 \text{ m}^3 \cdot \text{s}^{-1}$  respectively (Oregon State Water Resources Board, 1965). Thus Zimmerman's (1970) calculation of a flushing period of

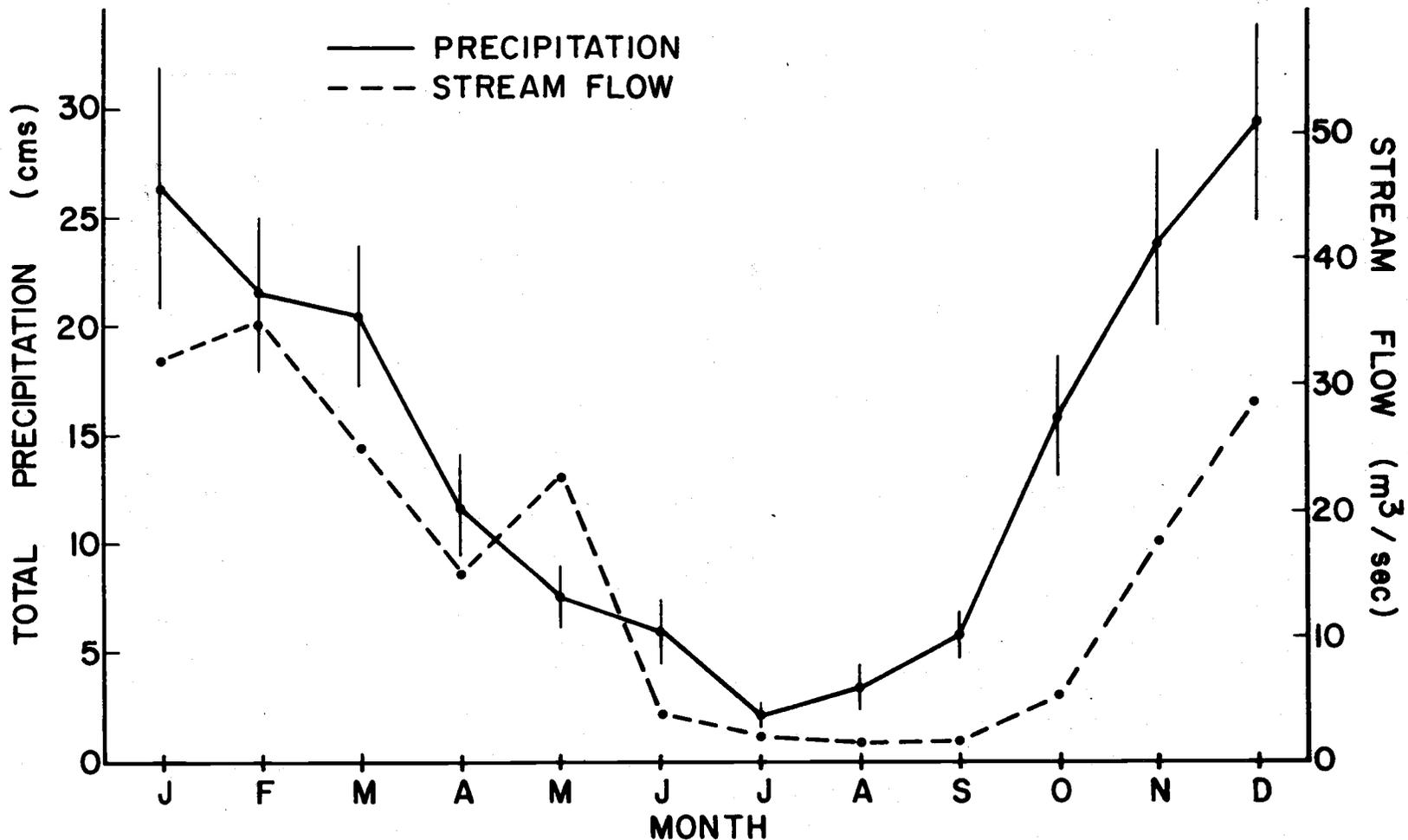


Figure 4. A comparison of mean monthly precipitation (cms) at Newport (1938-1969) and stream flow ( $m^3 \cdot s^{-1}$ ) of the Yaquina River recorded near Elk City (incomplete record from 1937-1963). 95% confidence limits included for the precipitation data. Precipitation and stream-flow data from Holbrook (1970) and the Oregon State Water Resources Board (1965), respectively.

13.3 tidal cycles is more representative of the flushing of Yaquina Bay during slightly drier than normal summers. The seasonal stream flow of Yaquina River is highly correlated with the seasonal precipitation throughout the entire year (Figure 4). The one exception in May is likely incorrect and may reflect the very incomplete nature of the stream flow data for Yaquina River. The published value for May could also be a misprint or miscalculation. This could not be determined, however, as the monthly means or standard deviations for each year's data were not published by the Oregon State Water Resources Board (1965).

#### Salinity Structure

The Yaquina estuary alternates between a partly mixed (type B) and well-mixed (type D) estuary (Burt and McAlister, 1959). The classification is based on vertical salinity gradients and follows the system of Pritchard (1955). High freshwater runoff during the rainy winter months (Figure 4) causes the development of a partly-mixed stratified system with a well developed salt wedge. The vertical salinity gradient varies between 4 ‰ and 19 ‰. During this period, however, the heavy freshwater runoff restricts the intrusion of the salt wedge to approximately Toledo (20 km) at high tides (Walker, 1974). As the freshwater flow decreases during the months

of June to October, the estuary becomes vertically well mixed with a maximum vertical salinity gradient of 3 ‰. The head of the salt water wedge extends inland approximately 42 km. Tidal induced variations in the salinity structure increase in magnitude upstream and are most extreme at the head of the estuary.

### Water Temperature

The small volume and shallowness of estuaries precludes the seasonal storage of the vast quantity of solar energy typical of the open ocean. As a result, estuaries reflect the local seasonal climate and are characterized as warmer than the oceans in the summer and colder in the winter. Annual seasonal temperature variations become progressively greater inland from the mouth of the estuary. Tidal mixing of nearshore neritic water with freshwater runoff produces wide spatial and temporal variations of temperature which are superimposed on the seasonal cycles. Like salinity, tidally induced variations in temperature increase upstream (Frolander, 1964). However, tidal variations of temperatures are normally less pronounced than salinity and usually reach a maximum at the middle of the estuary (see Figures 9 and 12).

Mean monthly water temperatures at Buoy 15 and Buoy 39 can be used to illustrate the increasing importance of seasonal atmospheric temperature upstream (Figure 5). The relatively small seasonal

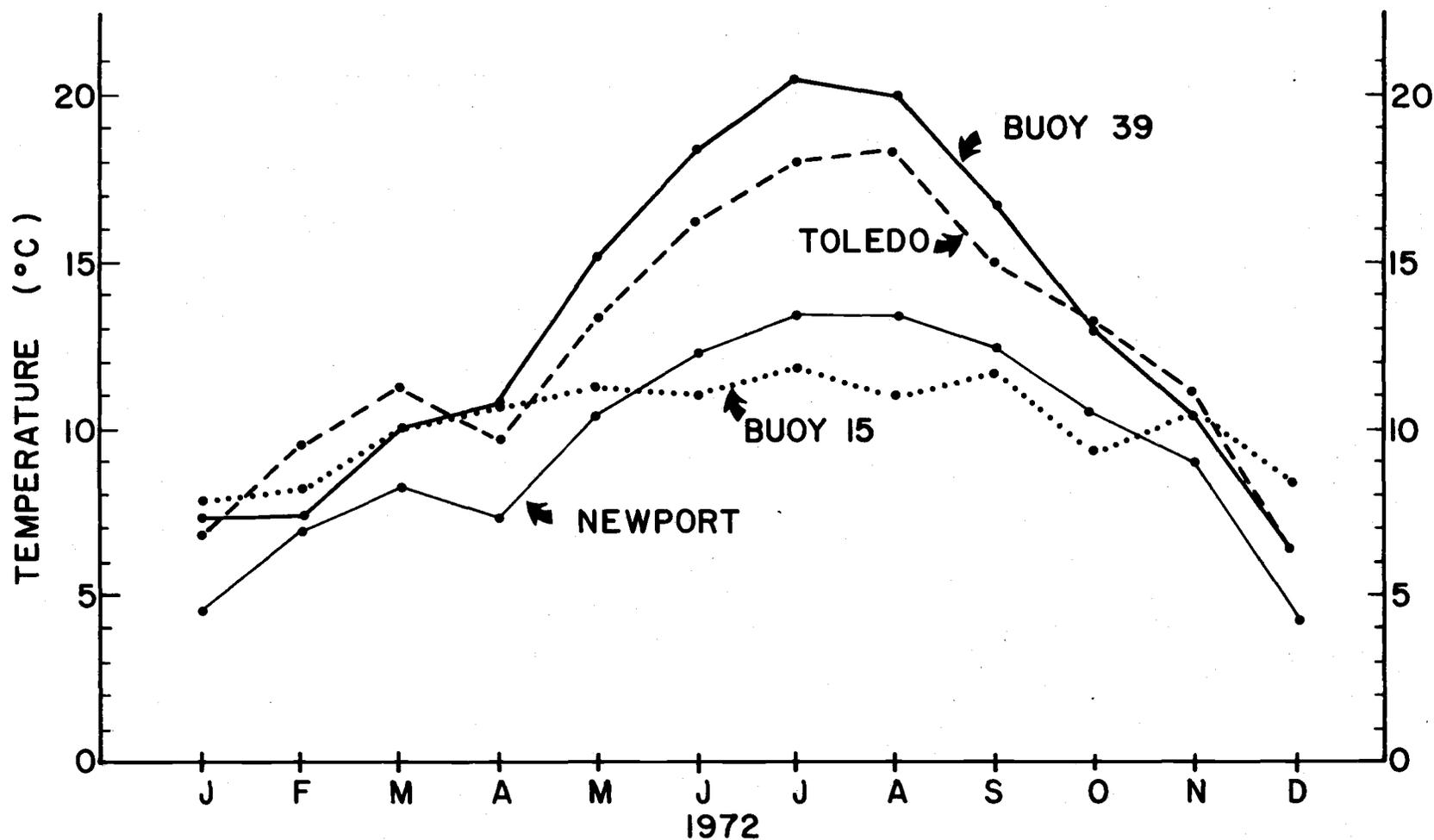


Figure 5. A comparison of mean monthly water temperatures ( $^{\circ}\text{C}$ ) at Buoy 15 and 39 with mean monthly air temperatures ( $^{\circ}\text{C}$ ) at Newport and Toledo. (Buoy 15 - solid dots; Buoy 39 - upper solid line; Newport - lower solid line; Toledo - broken line).

variability at Buoy 15 (3.2 km) reflects the moderate to strong influences of cold neritic waters in the large embayment throughout the year. Mean water temperatures ranged from  $7.8^{\circ}\text{C}$  in January to  $11.9^{\circ}\text{C}$  in July. Cold upwelled water was often present in the lower estuary during the summer months and helped maintain the low temperatures. Seasonal air temperatures at Newport were quite similar to water temperatures at Buoy 15 because the cold, relatively stable ocean nearby cools the local atmosphere. The influence of the cold oceanic water decreases rapidly upstream. At Buoy 39 (15.2 km) the mean temperatures of the shallow waters (4 m) closely correlated with seasonal air temperatures which were recorded just upstream at Toledo (20 km). Mean water temperatures ranged from  $6.5^{\circ}\text{C}$  in December to  $20.4^{\circ}\text{C}$  in July. Mean air temperatures at Toledo for the same two months were  $6.5^{\circ}\text{C}$  and  $18.7^{\circ}\text{C}$ , respectively. Water temperatures were actually higher than air temperatures throughout the summer because of the high specific heat of water. Because of this property, water can absorb large quantities of energy relative to either the atmosphere or land and retain it for a much longer period.

## MATERIALS AND METHODS

### Field Methods

Zooplankton samples were collected in the upper Yaquina Bay twice weekly (Monday and Thursday) from May 15 to November 20, 1972. The 35 foot research vessel Paiute was used to make all plankton tows. Because of scheduling problems, the samples were collected during daylight hours (normally between 0900 and 1700 hours) without regard to the stage of the tide. The five stations sampled twice weekly in the upper reaches of the estuary are referred to in Figure 1 as Buoy 21, Buoy 29, Buoy 39, Buoy 45 and Toledo Bridge. The first four stations correspond with navigation buoys in the immediate vicinity. An additional station 2 1/2 miles above the Toledo Bridge was sampled weekly during the months of August, September and October to establish the upper extension of the A. tonsa population.

Three zooplankton samples were simultaneously collected at each station by using three modified Clarke-Bumpus samplers of 12.5 cm diameter (Clarke and Bumpus, 1950; Paquette and Frolander, 1957), fitted with nylon nets of differing mesh sizes. Mesh sizes of 233  $\mu\text{m}$ , 110  $\mu\text{m}$  and 64  $\mu\text{m}$  were used to sample the water column for adult A. tonsa, copepodite stages and naupliar stages, respectively.

The 233  $\mu\text{m}$  and 110  $\mu\text{m}$  mesh Clarke-Bumpus samplers were modified to fit into a frame to tow side-by-side, while the 64  $\mu\text{m}$  mesh Clarke-Bumpus sampler was mounted just above the pair on the towing wire. The two coarser mesh samplers were towed for six minutes with the opening-closing door tied open. The 64  $\mu\text{m}$  mesh sampler was closed with the messenger after one minute to prevent clogging of the very fine mesh by silt and plankton.

All tows were oblique in a step-wise fashion from a depth of approximately four meters in mid-channel to the surface. The nets were rapidly lowered to within one meter of the bottom and towed for three minutes, then rapidly raised to the surface layer for the remaining three minutes in the tow. Three equally spaced two minute steps were used at Buoy 21, however, because the depth of water averaged eight meters. A calibrated propellor flow meter in the mouth of the two coarser nets generally indicated four to six cubic meters of water had been filtered. Meters were calibrated at the middle and end of the sampling period and varied less than 8 percent. Immediately after recovery of the nets, the plankton samples were preserved in 5% formaldehyde for later laboratory analysis.

Physical data were also collected at each station. An N. I. O. (National Institute of Oceanography) bottle equipped with a reversing thermometer was used to collect salinity and temperature data just

above the river bottom. Surface salinity samples were obtained with a bucket, and surface temperature was determined with a bucket thermometer. Salinity was determined with an inductive salinometer in the laboratory.

The numerical abundance of A. tonsa adult females, adult males and copepodite stages V, IV and III were determined by subsampling the plankton samples with a 1 ml Stempel pipette. All 233  $\mu\text{m}$  mesh and 110  $\mu\text{m}$  mesh samples were counted. Each zooplankton sample was diluted 5 to 15 times the settled volume of plankton. After stirring, successive 1 ml subsamples were removed from the diluted sample and counted until either a minimum of 50 specimens of each stage of A. tonsa had been counted or a total of 5 ml had been examined under 250 X magnification. An attempt was made to count a minimum of 2 ml even when the number in the first ml exceeded 50 specimens for each stage. The counts, subsample fraction, meter revolutions and calibration factor were then punched on computer cards for calculation of population densities per cubic meter.

#### Fecundity Experiments

To measure egg production in the laboratory, an adult male and a female A. tonsa were placed in seawater of 25 parts per thousand salinity in each of twenty-five 250 ml beakers and maintained at  $21 \pm 0.1^{\circ}\text{C}$  in a circulating water bath. The experimental salinity and

temperature approximated the average physical conditions at Buoy 39 at the beginning of August when the natural population was experiencing exponential growth. The experimental light regime followed the diurnal cycle of light and darkness. Interior illumination (400 lux) provided by fluorescent lighting supplemented natural light from a window during the daylight hours. At night the culture room was dark. A mixture consisting of equal parts of Isochrysis galbana (flagellate - Class Chrysophyceae), Rhodomonas sp. (flagellate - Class Cryptophyceae) and Thalassiosira sp. (centric diatom - Class Chrysophyceae) was provided as food at an initial concentration of 50,000 to 70,000 cells·ml<sup>-1</sup>. A hemocytometer was used to determine food density every second day and losses due to grazing and sinking were replaced with fresh food. New water and food were provided every fourth day.

The adult A. tonsa were collected in the vicinity of Buoy 39 and transferred to the experimental beakers within a few hours after capture. Eggs and stage I nauplii were counted and removed from the beakers with a pipette on every second day. Females that died during the first two weeks were replaced and a new experiment started. The replacement of males did not necessitate the start of a new experiment. After the first two weeks, females were not replaced and the experiments gradually terminated at the end of 39 days.

### Development Rate Experiments

Experiments to determine the rate of development from egg to adult under dissimilar food conditions were also performed at  $21 \pm 0.1^{\circ}\text{C}$  in a circulating water bath. The natural diurnal cycle of light and darkness was followed as in the fecundity experiments. Eggs and stage I nauplii were obtained by placing numerous male and female adults in several 1000 ml beakers with ample food for 48 hours. After removal of the adults with a  $110\ \mu\text{m}$  mesh filter, the eggs and stage I nauplii from all beakers were mixed together. Equal portions of the mixture were then used to inoculate sixty 600 ml beakers. Development rates were determined under conditions of both laboratory cultured and natural food organisms. Half of the beakers contained sand filtered ultraviolet sterilized seawater ( $27\ \text{‰}$ ) to which was added an algal concentration of  $50,000 - 70,000\ \text{cells}\cdot\text{ml}^{-1}$  consisting of equal parts of Isochrysis galbana, Rhodomonas sp. and Thalassiosira sp. Grazing and sinking losses were estimated with a hemocytometer and replaced with fresh food every second day. New water and fresh food were provided every fourth day. The remaining 30 beakers contained estuary water ( $25\ \text{‰}$ ) collected in the vicinity of Buoy 39 from which the largest phytoplankton and all zooplankton had been removed with a  $64\ \mu\text{m}$  mesh filter. The initial phytoplankton density was not determined. Food was not added nor the water

changed in the beakers containing the estuary water. Once a day, the contents of two beakers of each experiment (referred to hereafter as LAB I and BAY I) were concentrated with a 64  $\mu\text{m}$  mesh filter and preserved in 5% formaldehyde. Total counts were later made to determine the percentage of the population at each of the 13 stages in the life cycle of A. tonsa.

Two additional developmental rate experiments were performed two weeks later at a continuous interior; illumination of 860 lux at the beaker level, with Vita-lite (R) fluorescent lamps (Duro-Test Corp.). All other parameters, with the exception of the unknown density of the estuarine phytoplankton, were identical. Therefore these latter two experiments, known as LAB II and BAY II, were not replicates of LAB I and BAY I in the strictest sense.

## RESULTS

Physical Properties of the Yaquina  
Estuary, Summer, 1972

Salinity data collected during the present study (Figures 6, 7, 8) show the estuary was well-mixed (type D, salinity gradient  $< 3$  ‰) from late June through October, 1972. This is in agreement with previous results (Burt and McAlister, 1959) described above. The vertical salinity gradient was greater than 3 ‰ only in isolated exceptions at all stations. The weak partial mixing at Toledo on several occasions (Figure 8) was probably caused by waters of higher salinity, and therefore density, collecting in a localized depression in the river bottom at the Toledo bridge sampling station.

Mean salinities at Buoy 21 (Figure 6), fluctuated the least during the study period, ranging from 27.1 ‰ to 33.8 ‰. The relatively stable high salinity profile from July through October indicates water at Buoy 21 is under strong oceanic influence during summer months. Buoy 39 is representative of truly estuarine conditions, ranging from 15.6 ‰ to 30.1 ‰ (Figure 7). The range at Toledo, a station under moderate to strong fluvial influence in the summer, was 5.6 ‰ to 24.3 ‰ (Figure 8).

Mean salinity values were highest at all stations during the months of August and September, reflecting the annual minima in

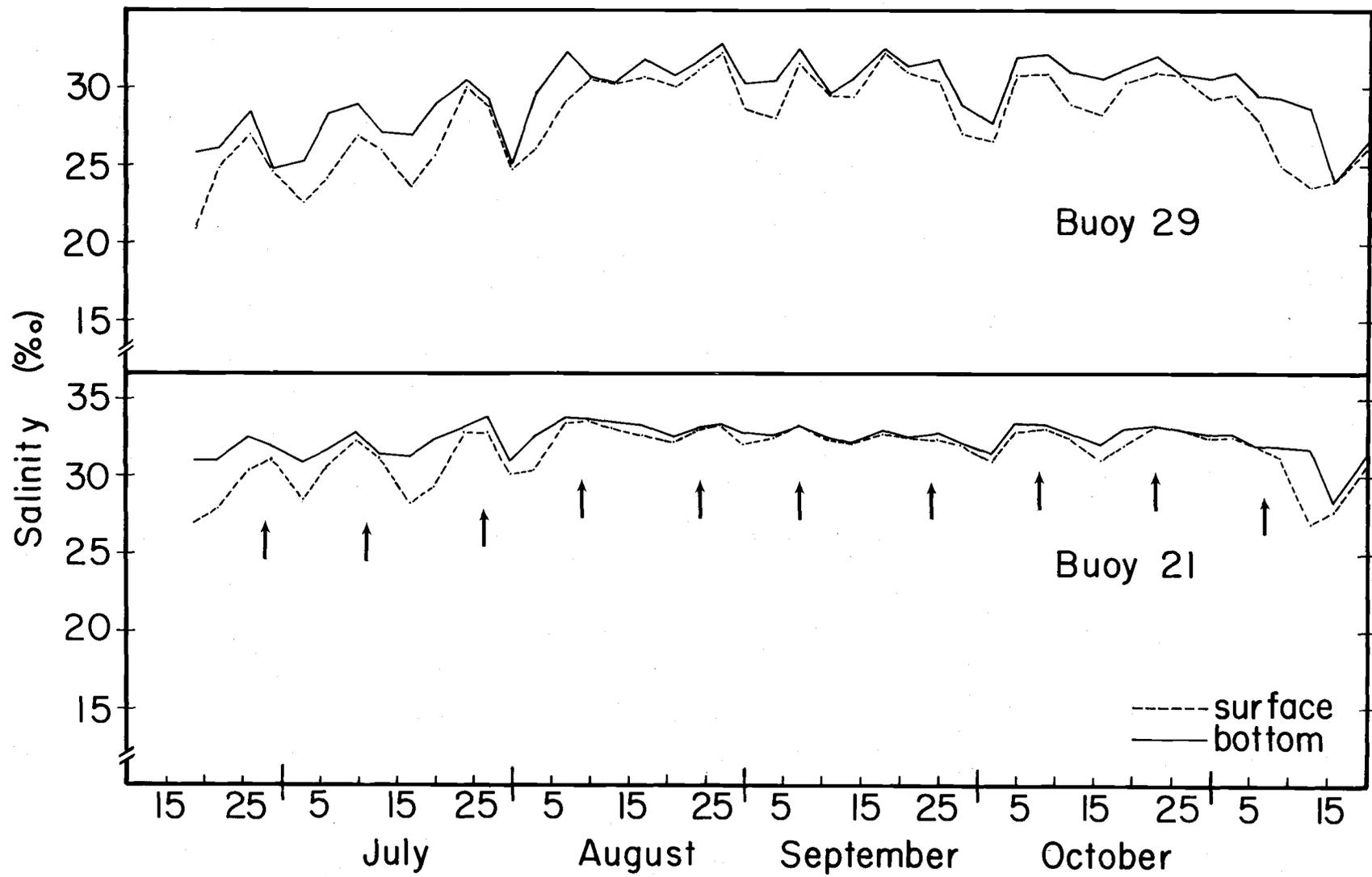


Figure 6. Salinity ( $^{\circ}/_{\infty}$ ) (surface and bottom) at Buoys 21 and 29 during the summer and fall of 1972. Arrows indicate occurrence of maximum spring tides.

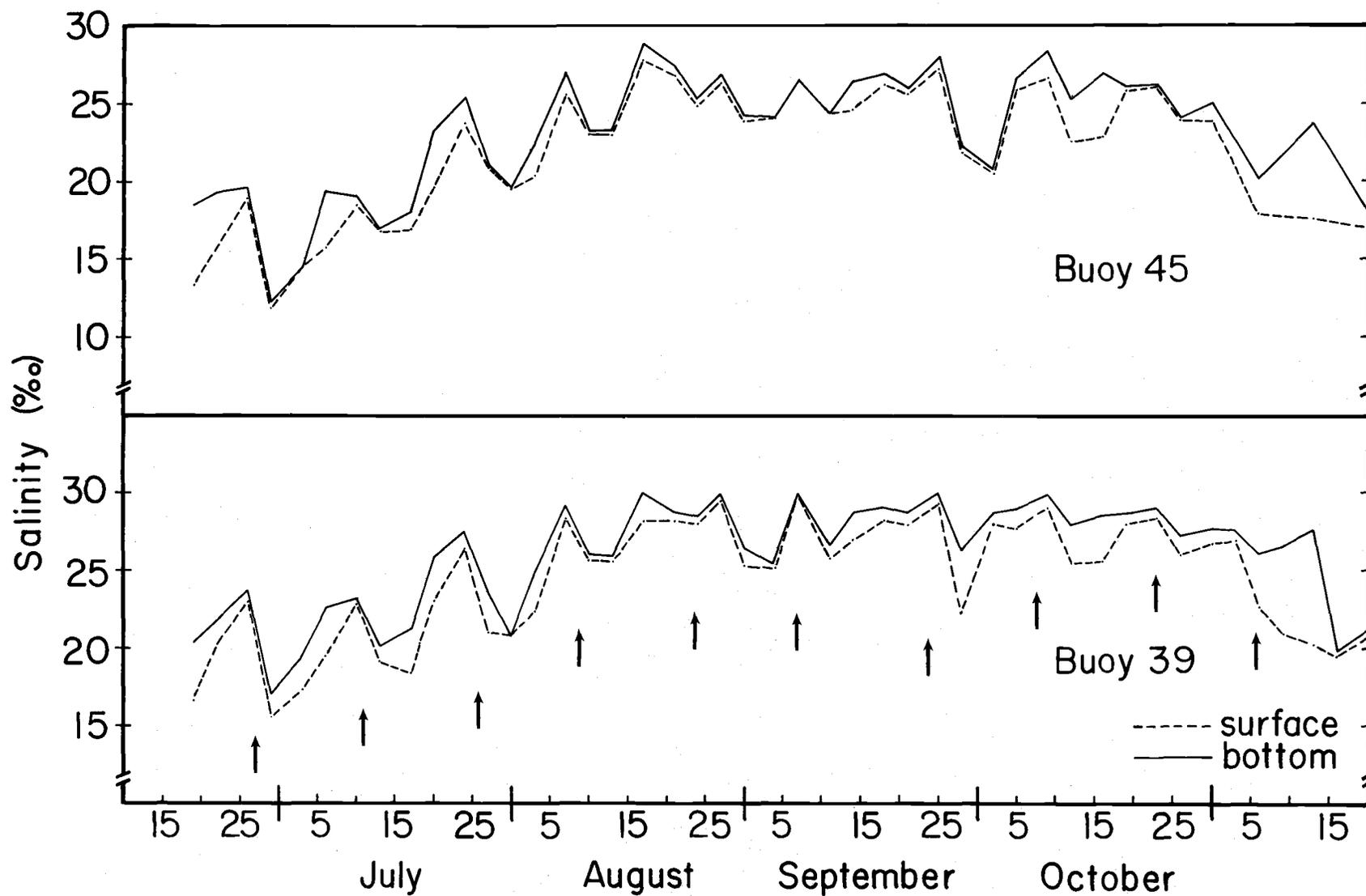


Figure 7. Salinity (‰) (surface and bottom) at Buoys 39 and 45 during summer and fall of 1972. Arrows indicate occurrence of maximum spring tides.

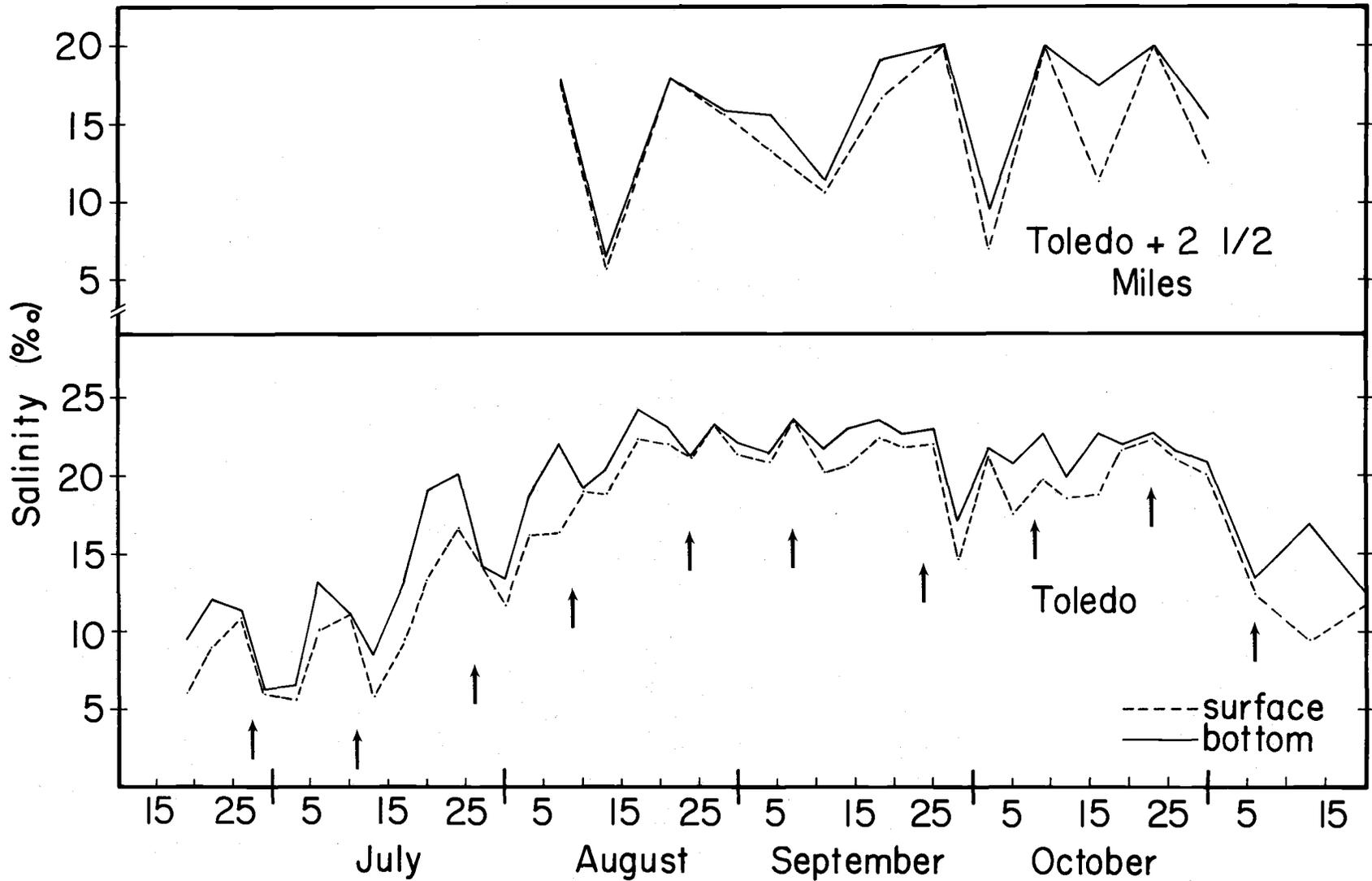


Figure 8. Salinity (‰) (surface and bottom) at Toledo Bridge and 2 1/2 miles above Toledo Bridge during summer and fall of 1972. Arrows indicate occurrence of maximum spring tides.

precipitation and river runoff (Figure 9). The large fluctuations in salinity observed on successive sampling days were primarily caused by the necessity to sample without regard to the stage of the mixed semidiurnal tides. The variability introduced by the tides became progressively more important upstream. The most pronounced fluctuations occurred in August and September at the upper-most station, Toledo + 2 1/2 miles, and alternately represented salinity under fluvial conditions (low water) and estuarine conditions (high water).

Temperatures at all stations (Figures 10, 11) increased during early June and July, peaked in late July, gradually declined in August and then fell rapidly throughout September and October. The station at Toledo had the greatest seasonal extremes of temperature recorded at the five stations sampled twice weekly during the study period, varying from  $23.6^{\circ}\text{C}$  in July to  $10.3^{\circ}\text{C}$  in November. Buoy 21, however, had the most extreme variations in temperature on a two week cycle. For example, temperatures dropped from  $17.1^{\circ}\text{C}$  on August 1 to  $10.3^{\circ}\text{C}$  on August 10 and then rose steadily again to  $16.3^{\circ}\text{C}$  on August 21. This cyclic variation was caused by the fortnightly spring tides which alternately introduced cold oceanic water far up into the estuary or allowed the warmer upper bay water to flow much farther down into the lower bay than normal. In addition, cold,

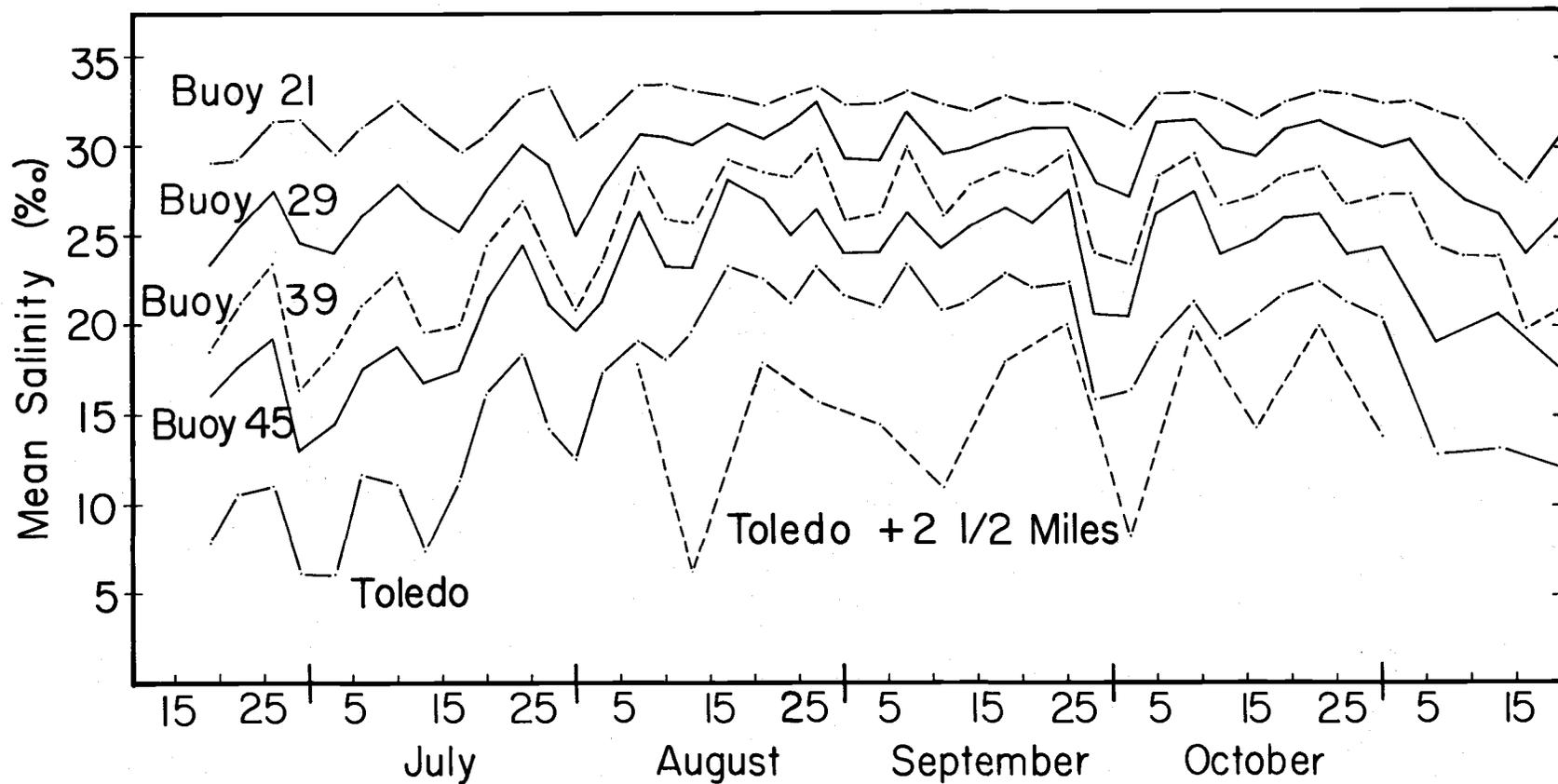


Figure 9. Average of surface and bottom salinity (‰) at all stations during summer and fall of 1972.

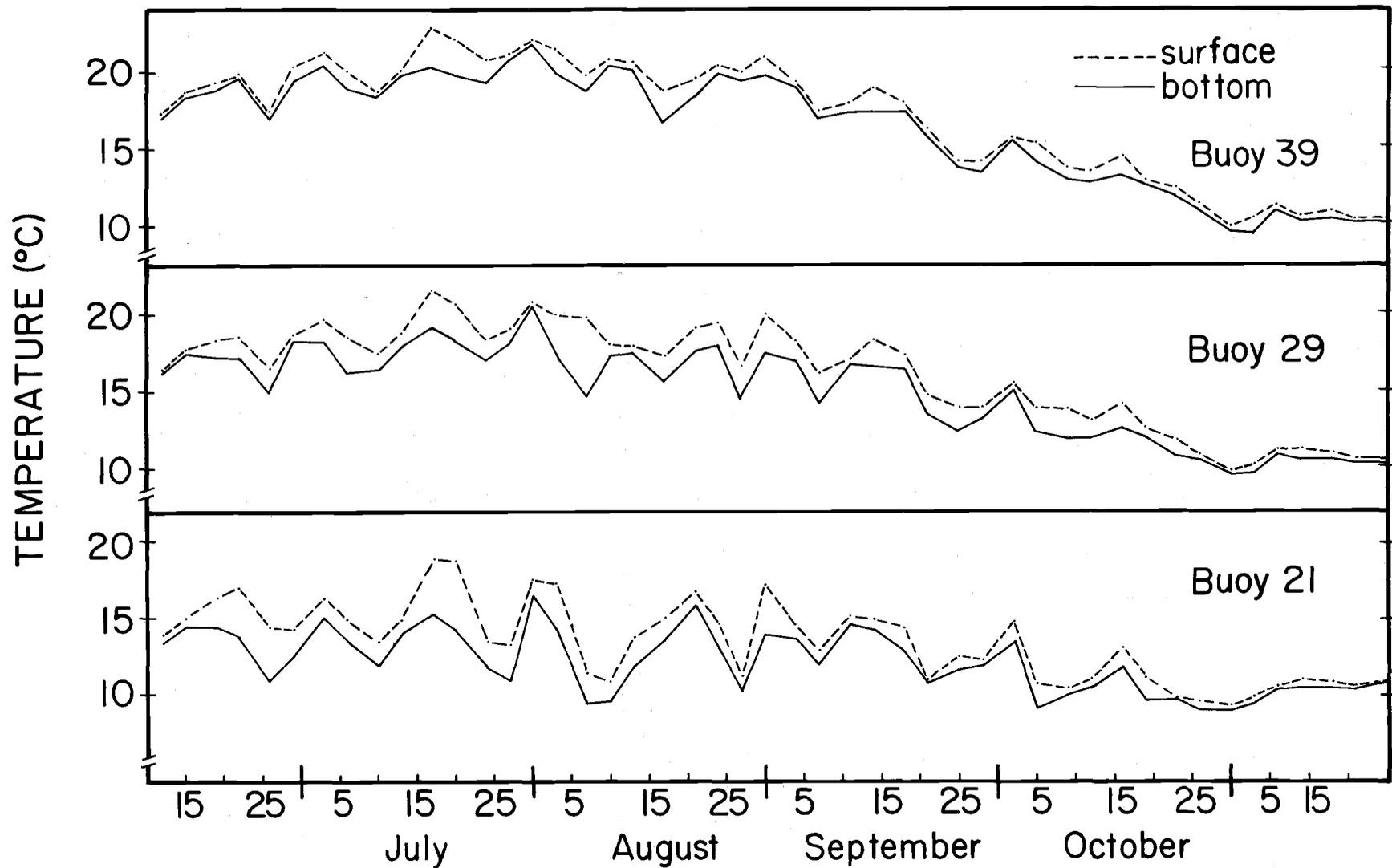


Figure 10. Temperature ( $^{\circ}\text{C}$ ) (surface and bottom) at Buoys 21, 29 and 39 during summer and fall of 1972.

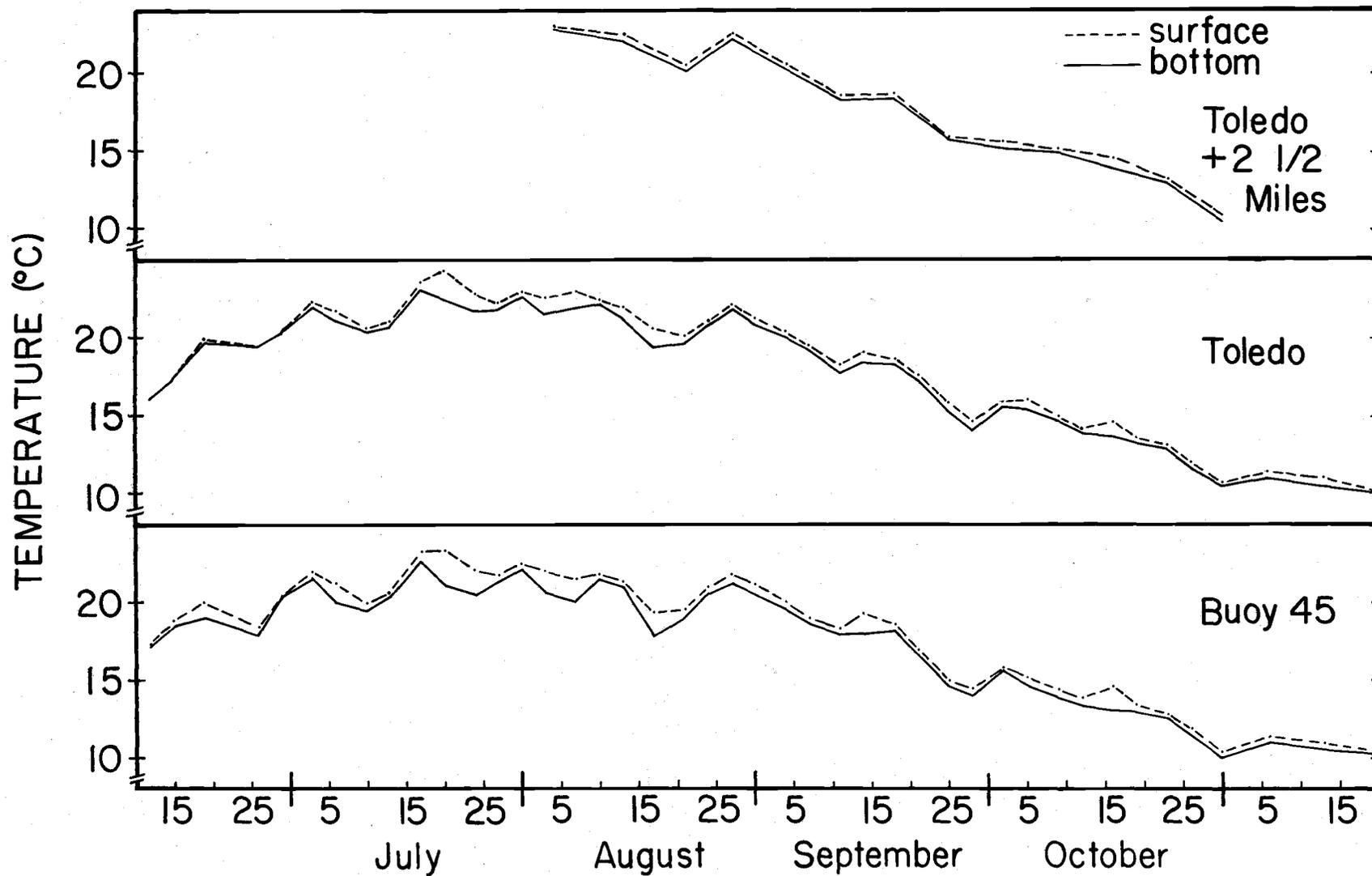


Figure 11. Temperature ( $^{\circ}\text{C}$ ) (surface and bottom) at Buoy 45, Toledo Bridge and 2 1/2 miles above Toledo Bridge during summer and fall of 1972.

high salinity upwelled coastal waters were introduced into the estuary by tidal influx, depending on local coastal wind conditions during the summer.

Water temperatures at Buoy 39, the center of the study area, were much less influenced by the cyclic tidal events so important at Buoy 21. The range of temperature variability at Buoy 39 during August was  $4.1^{\circ}\text{C}$  as compared to  $6.8^{\circ}\text{C}$  at Buoy 21. Mean water temperatures at Buoy 39 for July, August and September were  $20.4^{\circ}\text{C}$ ,  $20.1^{\circ}\text{C}$  and  $16.9^{\circ}\text{C}$ , respectively (Figure 12). Seasonal extremes at Buoy 39 during the course of the study ranged from  $22.0^{\circ}\text{C}$  on July 30 to  $10.5^{\circ}\text{C}$  on November 20. November was a period of transition in the seasonal temperature structure of the upper estuary (Figure 12). After mid-November, the water of the upper estuary was colder than the more oceanic water at Buoy 21 because of the falling atmospheric temperatures (Figure 5).

Seasonal temperature variations were even more pronounced at the Toledo and Toledo + 2 1/2 miles stations because of the atmospheric regulation of water temperatures. Mean monthly water temperatures at Toledo for July, August and September were  $22.1^{\circ}\text{C}$ ,  $21.4^{\circ}\text{C}$  and  $17.8^{\circ}\text{C}$ , respectively with seasonal extremes ranging from  $22.9^{\circ}\text{C}$  on July 30 to  $10.2^{\circ}\text{C}$  on November 20.

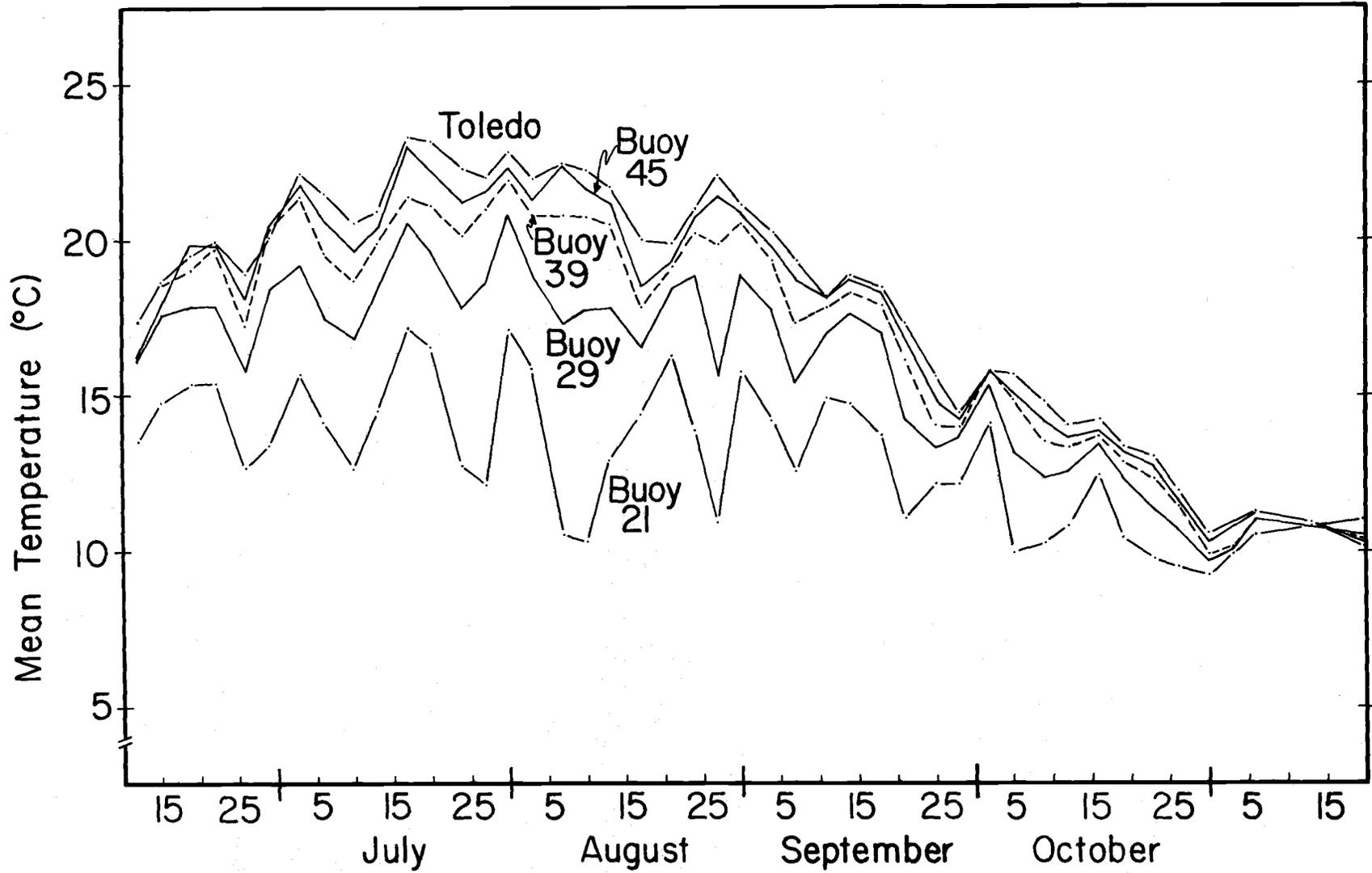


Figure 12. Average of surface and bottom temperatures ( $^{\circ}\text{C}$ ) at all stations during summer and fall of 1972.

### Fecundity of *Acartia tonsa*

In order to estimate the rate of egg production of *A. tonsa* in Yaquina Bay, numerous adult females were captured in the vicinity of Buoy 39 in early September and their subsequent reproductive output followed in the laboratory. The culture conditions of 21°C temperature and 22 ‰ salinity approximated field conditions associated with the center of the field population of *A. tonsa* during the peak of the population explosion.

The daily egg production of 8 adult female *A. tonsa* is shown in Figures 13 and 14. Rates were determined as the average number of eggs·day<sup>-1</sup>·female<sup>-1</sup>. Daily production was quite variable. Female A-9 (Figure 13), for example, had a daily rate which fluctuated from 14 to 50 eggs while female A-31 varied from 20 to 58 eggs. Variability between females was much lower. Mean egg production for 34 females was 30.5 (± 3.0) eggs·day<sup>-1</sup> with a range of 10.4 to 47.2 eggs·day<sup>-1</sup>. The value in parentheses above (and hereafter) refers to the 95% confidence limits (± 2 standard errors) about the mean.

Females were maintained from 4 days to a maximum of 31 days in the laboratory cultures. Estimates of total lifetime egg production, unfortunately, were not possible as the reproductive time span prior to capture was not known. However, an approximation of total egg production can be inferred from recent work on the Atlantic *A. tonsa*

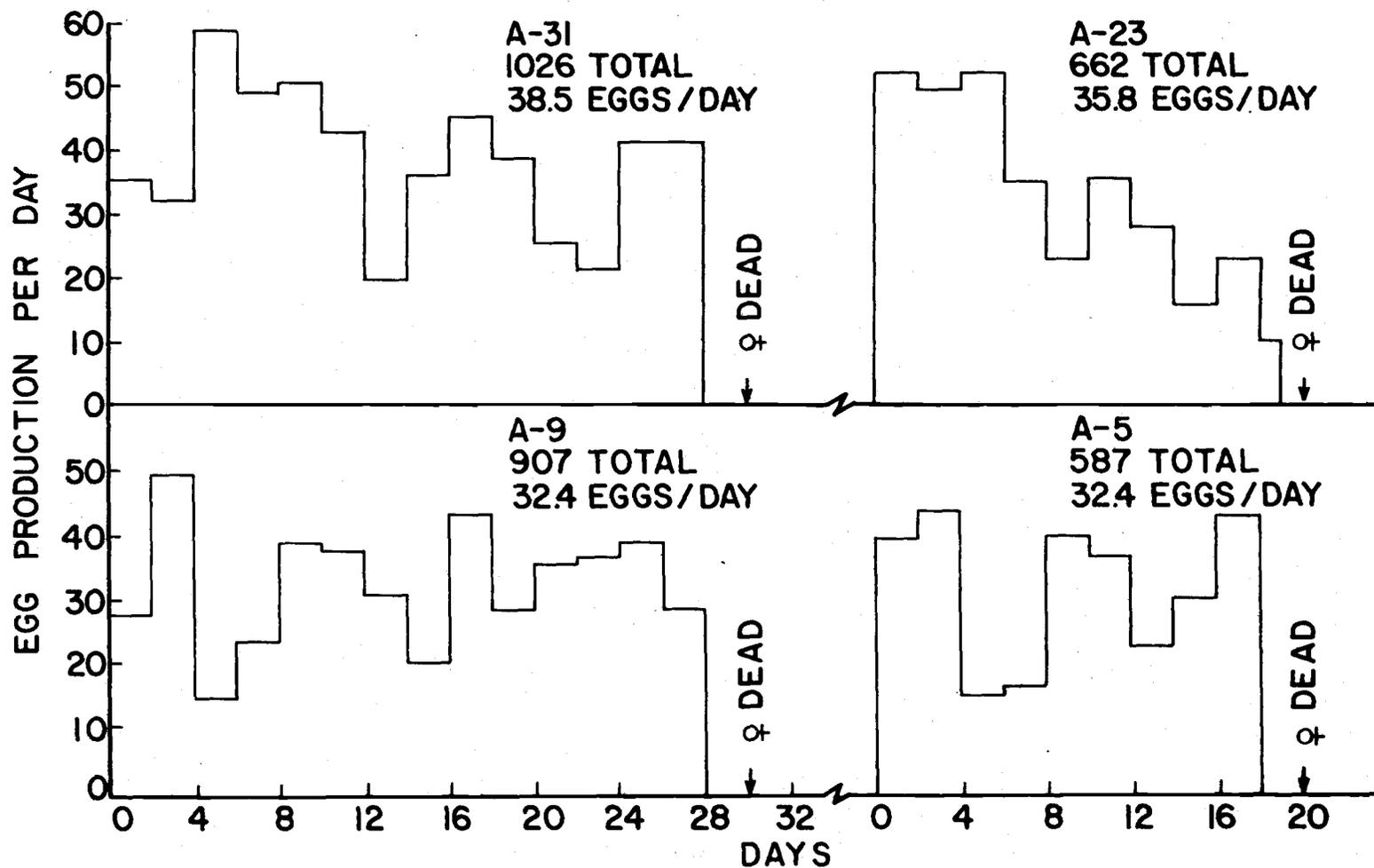


Figure 13. Daily egg production of individual adult female *Acartia tonsa* in beakers at 21°C and 22 ‰ salinity. The laboratory assigned number, total egg production and daily rate are included for each female. Algal cultures were used for food.

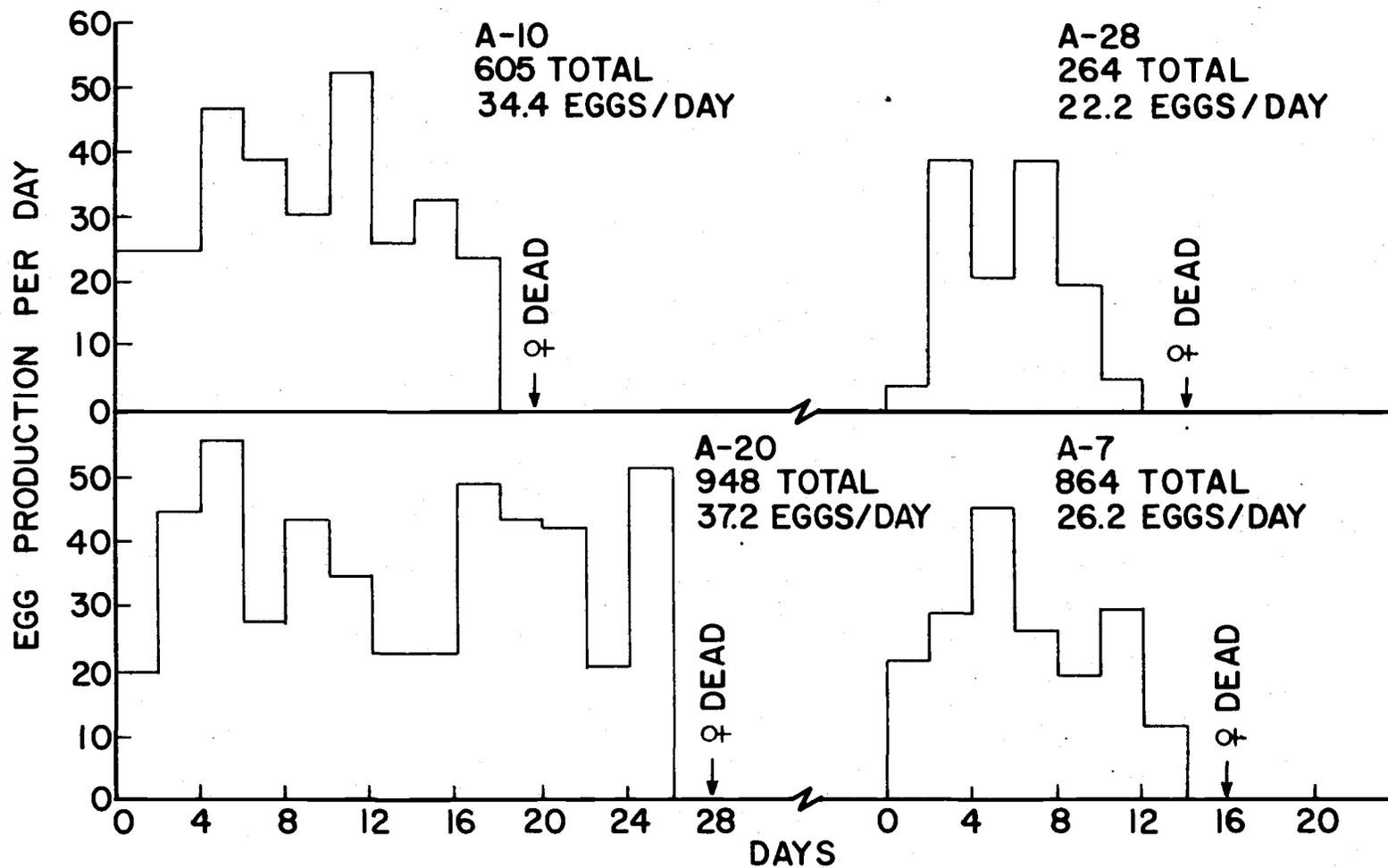


Figure 14. Daily egg production of individual adult female *Acartia tonsa* in beakers at 21°C and 22 ‰ salinity. The laboratory assigned number, total egg production and daily rate are included for each female. Algal cultures were used for food.

by Wilson and Parrish (1971). Using adult females which had just molted from copepodite stage V, A. tonsa was found to have an average life span in the laboratory of 37.7 ( $\pm$  2.5) days with a mean total egg production of 1256.2 ( $\pm$  184.9) eggs. The average is 33.3 eggs  $\cdot$  day<sup>-1</sup> female<sup>-1</sup> (n = 6 females). Thus comparable data verify that A. tonsa is capable of sustaining high egg production over a period of more than one month. It must be noted, however, that continued presence of males was essential. A single mating was found to be inadequate to achieve the total reproductive potential of A. tonsa females (Wilson and Parrish, 1971). Females of Eurytemora affinis Pope, another estuarine copepod, must also be mated several times during their reproductive span (Heinle, 1970).

#### Development Rate of Acartia tonsa

Adult A. tonsa were successfully reared in the laboratory from eggs through the eleven instar stages at 21°C and 25 ‰ salinity, using laboratory cultures or natural populations of phytoplankton as food. The two experiments were each performed twice and are referred to as LAB I, LAB II (Figures 15, 16), BAY I, and BAY II (Figures 20, 21). To facilitate graphing, Acartia tonsa stages were grouped as follows: eggs, nauplii I-II, nauplii III-IV, nauplii V-VI, copepodites I-II, copepodites III-IV, copepodite V and adults. The

abundance of each stage during an experiment is expressed as a percentage of the total count of two combined replicate samples. Therefore the average stage of development was calculated as the median of each group of stages represented on a given day. For example, on the eighth day the LAB I population (Figure 15a) consisted of 33% copepodites I-II, 52% copepodites III-IV and 15% copepodite V. Thus the copepodite stage III-IV represented the median stage of development at that time.

The results of the four experiments indicate a wide and increasing range of time was required for each successive instar stage. This is evidenced by the increasing slope of the stage division lines. Part of the variation in molting frequency was experimentally introduced because the experiments could not be started with eggs of uniform age. As noted previously, adult females were allowed to lay eggs for 48 hours before being removed from the experimental beakers. Consequently many eggs had already hatched into nauplii before the last eggs were released. This "artificial" variation persists throughout the results plotted in Figures 15, 16, 20 and 21. The change in slope of the instar lines with increasing time, however, is not experimental error but is a function of intrinsic differences in individual growth rates.

In order to remove the variability introduced by the experimental design, the data for each stage were fitted to a best fit line by

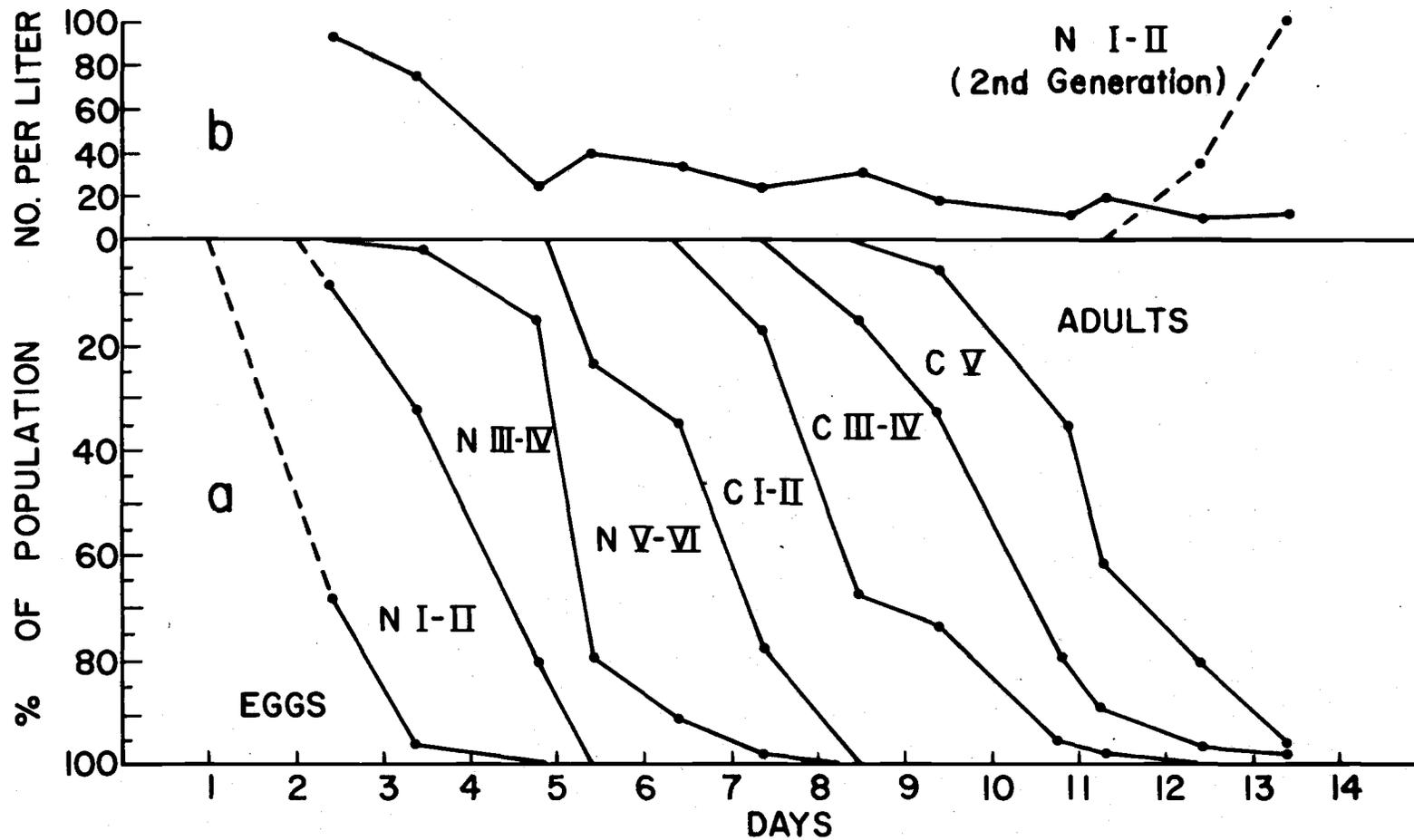


Figure 15a. LAB I Development Rate Experiment. Percentage of individuals in different life cycle stages at progressively greater ages in beakers at 21°C and 25 ‰ salinity. Algal cultures were used as food.

b Survival during the rearing period.

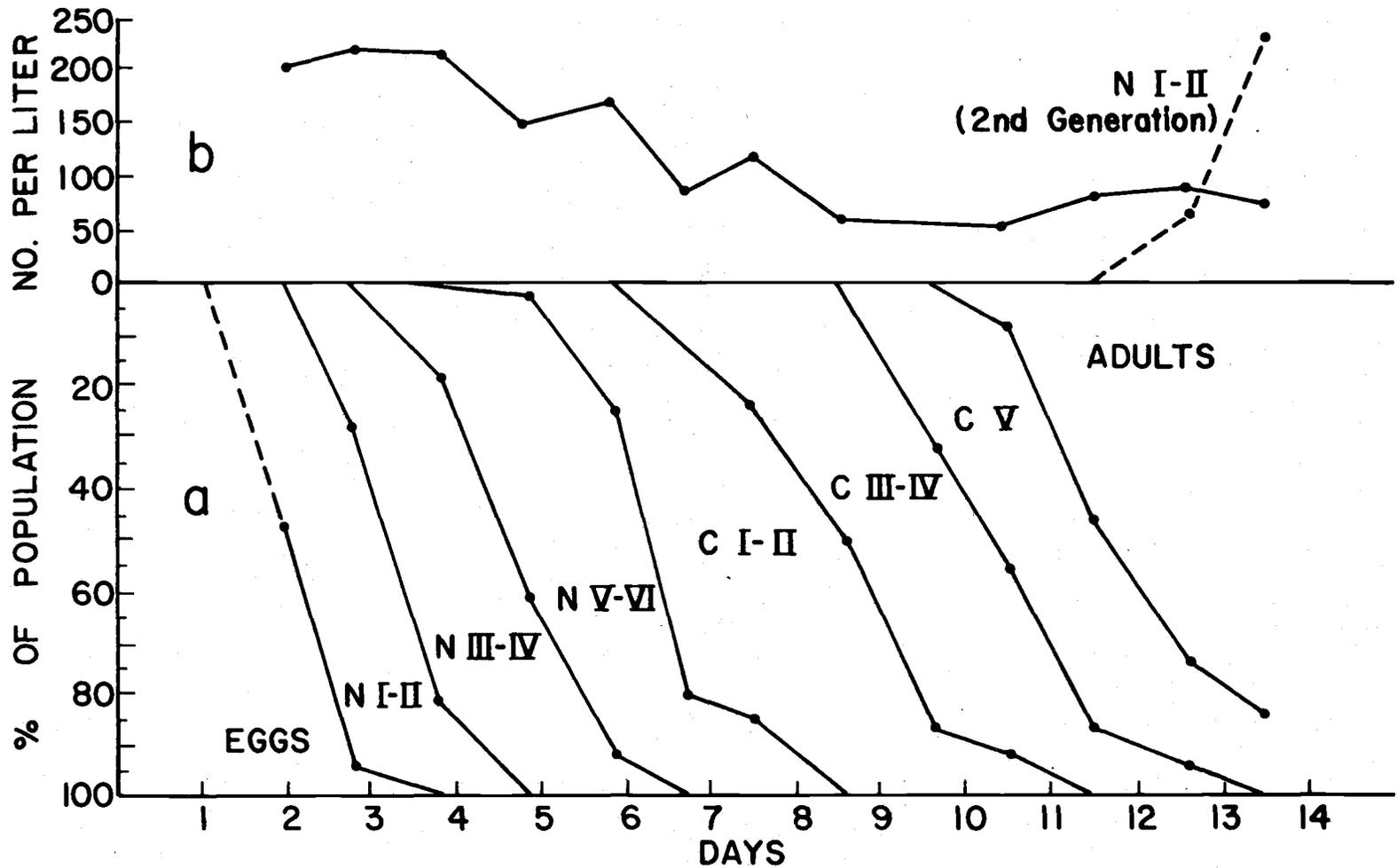


Figure 16a. LAB II Development Rate Experiment. Percentage of individuals in different life cycle stages at progressively greater ages in beakers at 21°C and 25 ‰ salinity. Algal cultures were used as food.

b. Survival during the rearing period.

linear regression. Regression lines for the LAB II experiment are provided as an example of the method (Figure 17). This technique provided a much better estimate of when individuals first entered a given stage and when 100% had molted from the previous stage. The assumption was then made that 90% of the nauplii I-II line slope was caused by the introduced experimental error. The remaining 10% was attributed to variation in egg hatching time. This is only a first order approximation but quite reasonable because the slopes of the first few stages are very similar in all experiments. Therefore 90% of the nauplii I-II slope was subtracted from all slopes as a correction term. The results for LAB II are seen in Figure 18. As the remaining variability was largely caused by intrinsic development rate differences, maximum, median and minimum development rates were determined by calculating linear regression equations for the 0%, 50% and 100% levels of presence for all stages (Figures 19 and 22).

Development from egg to adult in the LAB I experiment required a median of 11.5 days at 21<sup>o</sup>C with a range of 10.0 to 13.0 days (Figure 19). Individuals in the LAB II experiment were not significantly different, requiring a median time of 11.6 days with a range from 10.4 to 13.2 days. The development rates of individual nauplii and copepodites were quite varied but comparable in the two experiments. The range of days required to molt into a given instar

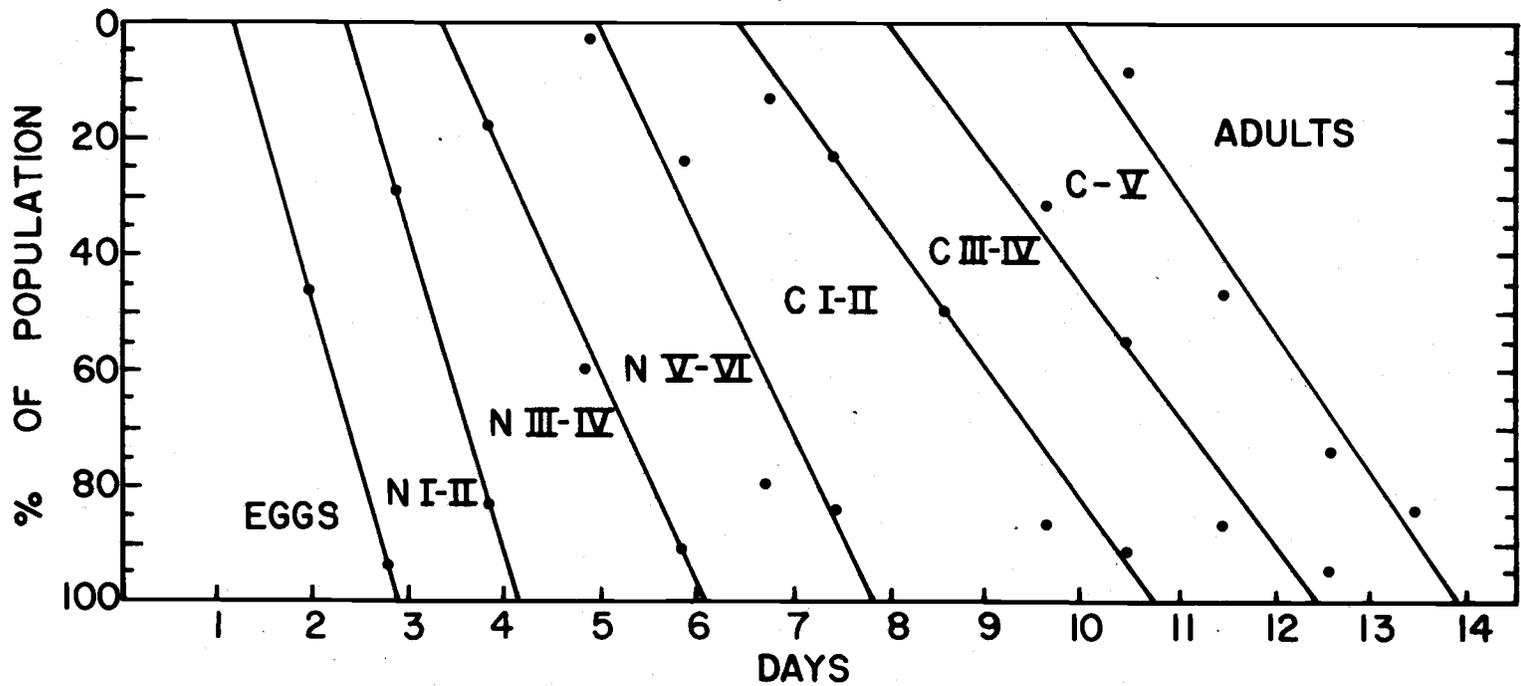


Figure 17. LAB II Development Rate Experiment. Development rates of *Acartia tonsa* expressed as best fit linear regression lines. The increasing variability with time is attributed to introduced experimental error and intrinsic differences in development rates. See text for details.

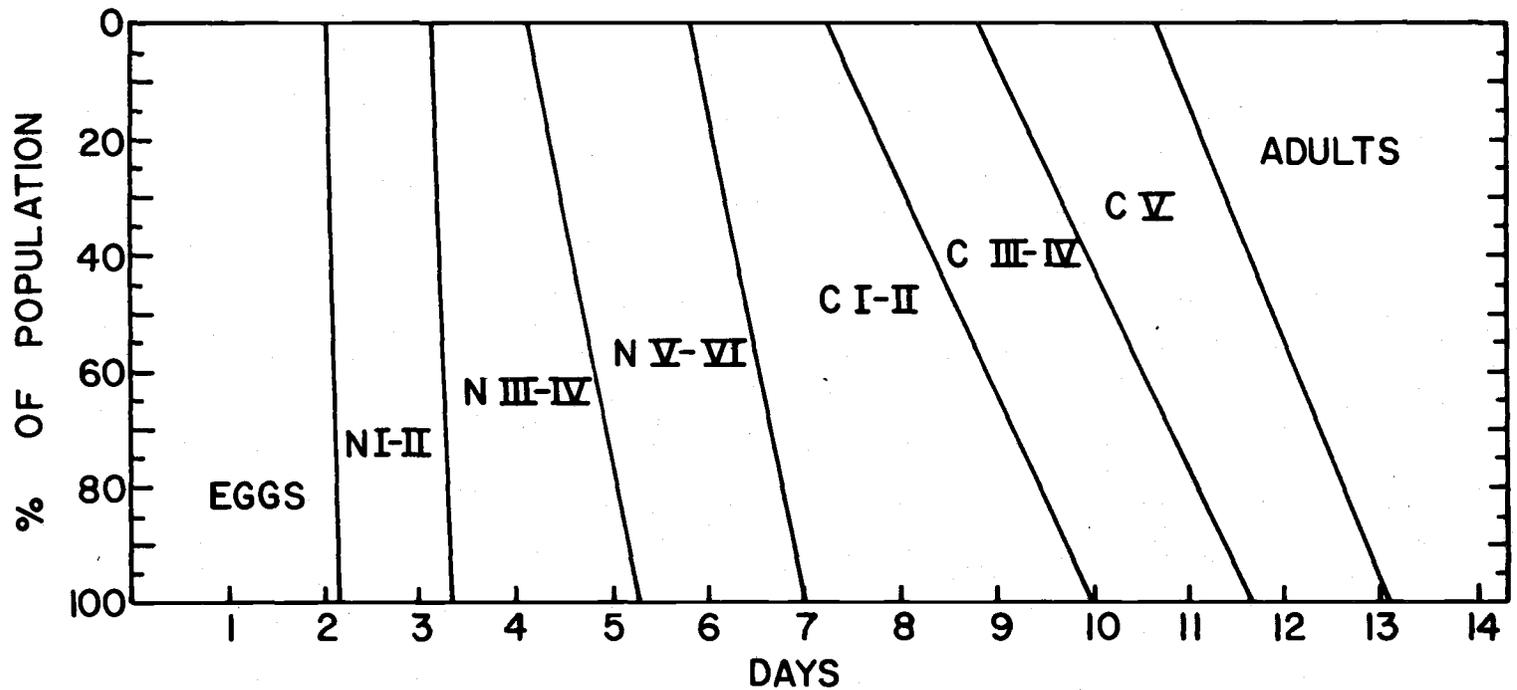


Figure 18. LAB II Development Rate Experiment. First order approximation of *Acartia tonsa* development rate after correction for introduced experimental error. The increase in variability with time is primarily a function of intrinsic differences in development rates.

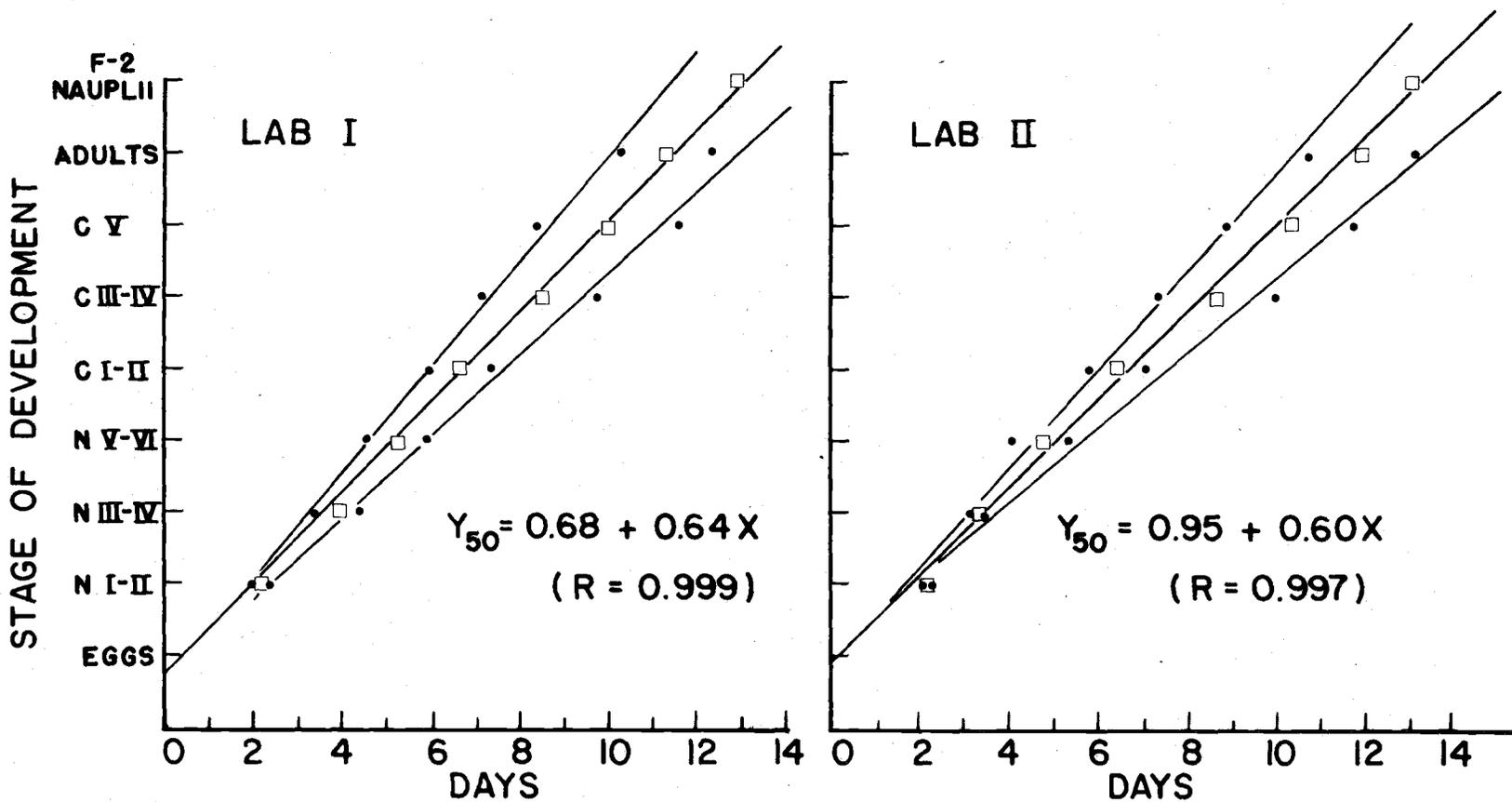


Figure 19. LAB I and II Development Rate Experiments. Linear regression best fit slopes for the maximum (upper slope), median ( $Y_{50}$ ) and minimum (lower slope) development rates of *Acartia tonsa* at 21°C and 25 ‰ salinity. Algal cultures provided as food.

stage became progressively greater with increasing maturity. Copepodites in the 5th stage, for example, molted into adults over a full three day span while the nauplii III-IV stage required only 1.4 days to molt into the nauplii V-VI stage.

In spite of the significant variability of individual development rates, the median stage of development plotted against time yields a straight line (Figure 19), indicating a constant rate of stage change from egg to adult. This is in agreement with Heinle's (1969) work on the development rate of A. tonsa from the Patuxent estuary on the Atlantic coast. The least squares regression equation for the development rate in the LAB I experiment is:

$$Y_{50} = 0.68 + 0.64 X. \quad (1)$$

when  $Y_{50}$  equals the estimated median stage of development at  $21^{\circ}\text{C}$  and  $X$  equals days. The slope of the regression equation for the LAB II experiment is nearly identical:

$$Y_{50} = 0.95 + 0.60 X. \quad (2)$$

Linear correlation coefficients for the LAB I and LAB II regression equations are 0.999 and 0.997, respectively. The two sets of data were not treated by an analysis of covariance because the increase in variance with time violates a basic assumption of the test.

Maximum and minimum development rates are also highly linear. Regression lines for the "0%" and "100%" levels are plotted

in Figure 19 to demonstrate the rate and amount of divergence in development with increasing time. The two extreme growth rates are analogous to a confidence limit for the median development rate.

Mortality rates (Figures 15b, 16b) were much higher during the late naupliar stages than during the copepodite stages in both the LAB I and LAB II experiments. Approximately 50% of the nauplii had died by the time the median individual reached copepodite stage 1-2. Another 25 to 30% died as copepodites. While only 20 to 25% of the original populations survived to adulthood, reproduction was very successful. Second generation nauplii appeared in large numbers 12 1/2 days after the first generation eggs hatched, indicating second generation egg production probably commenced during the 11th day when the medial copepodite V reached adulthood.

Development rates of A. tonsa at 21°C in raw estuary water appeared to vary as a function of the amount of phytoplankton available for grazing. During the latter part of the BAY I experiment (Figures 20a, 22), for example, the mean development rate slowed and became anomalous following the near total depletion of the natural phytoplankton population. Naupliar development rates (or molting frequency) was relatively uniform and similar to that observed in the LAB I experiment, indicating an adequate food supply was available for the first six or seven days. Development slowed, however, as the

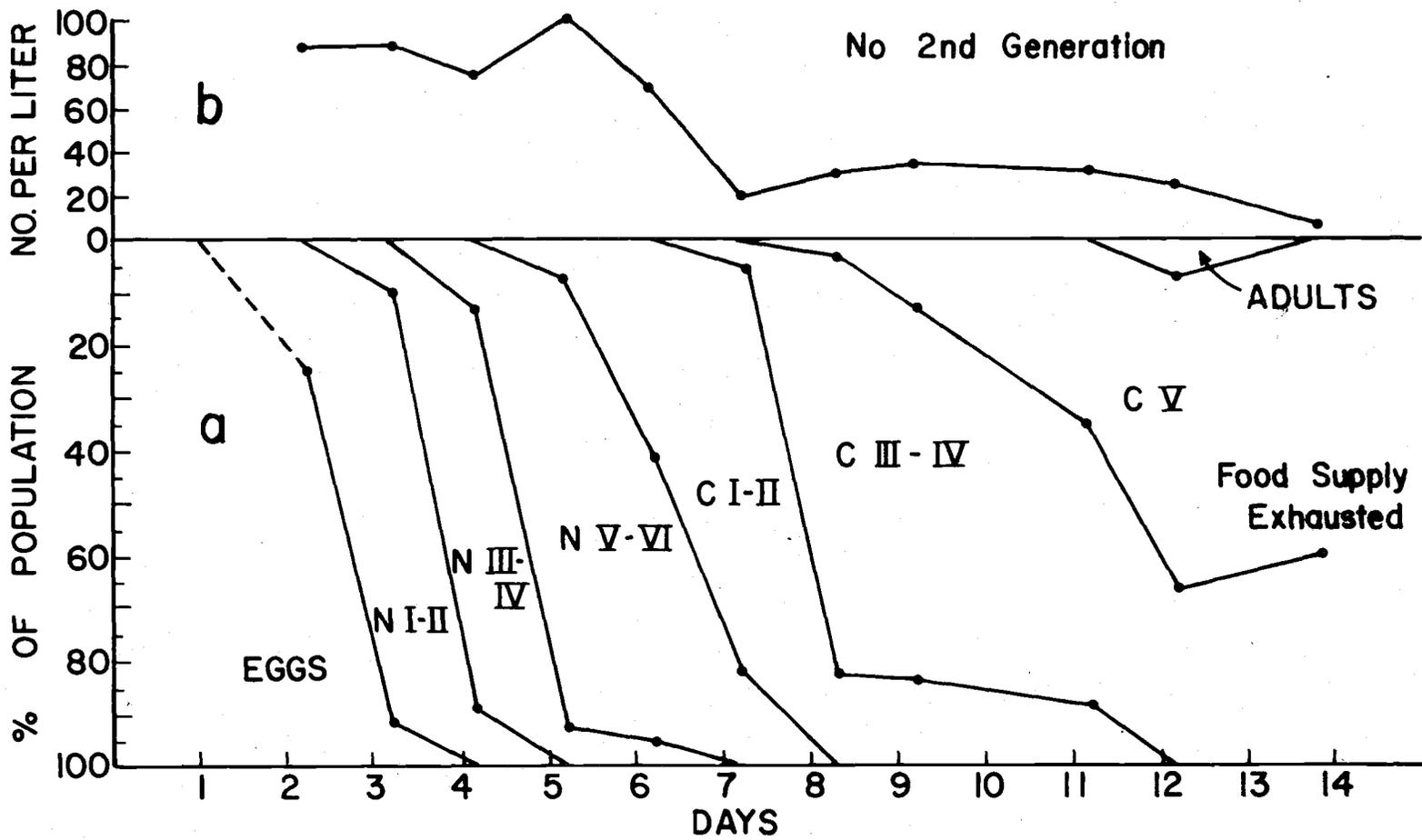


Figure 20a. BAY I Development Rate Experiment. Percentages of individuals in different life cycle stages at progressively greater ages in beakers at 21°C and 25 ‰ salinity. Estuary water filtered through a 64 μm screen was used as food.

b. Survival during the rearing period.

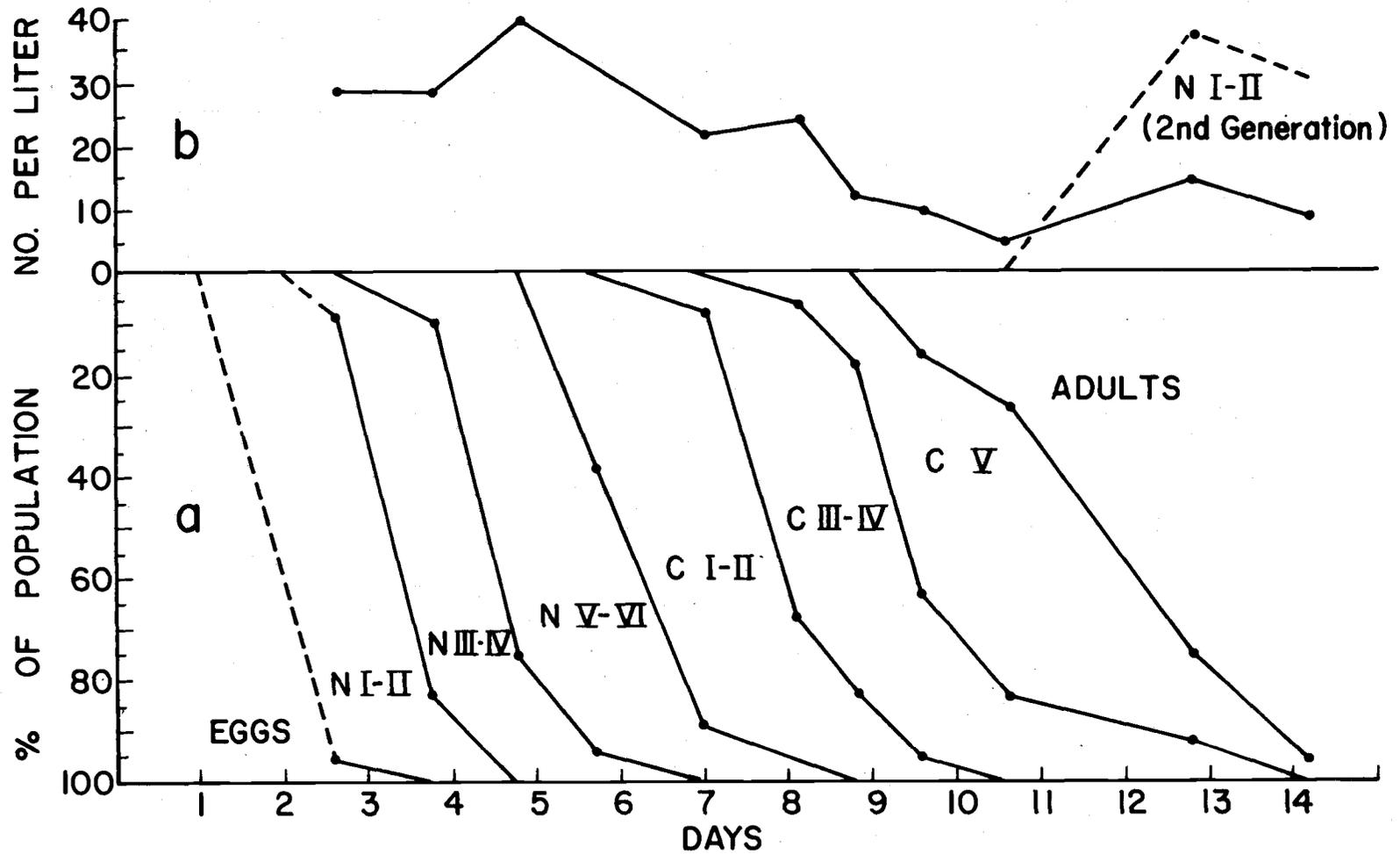


Figure 21a. BAY II Development Rate Experiment. Percentages of individuals in different life cycle stages at progressively greater ages in beakers at 21°C and 25‰ salinity. Estuary water filtered through a 64 μm screen was used as food.

b. Survival during the rearing period.

nauplii molted to the copepodite III-IV-V stages. The two copepods which did successfully molt into the adult stage were both males. Data for the BAY I experiment are included in Figure 22 to demonstrate the possible effect of starvation on copepodite development.

Development rates of A. tonsa during the BAY II experiment were nearly identical to those rates observed during the laboratory-cultured algal diet LAB experiments (Figure 19). Approximately 11.6 days were required for half of the surviving population to reach adulthood, suggesting food resources were adequate for normal growth to the adult stage. The mean stage of development plotted against time (Figure 22) yields a linear regression equation having a slope most similar to the LAB II regression equation (Figure 19). For the BAY II growth experiment:

$$Y_{50} = 1.29 + 0.58 X. \quad (3)$$

The linear correlation coefficient is 0.997. Food supplies, however, did appear to run out. An examination of the water with a hemocytometer revealed few phytoplankters remained at the end of the thirteen days. The low number of second generation nauplii produced (Figure 21b) by the BAY II females was probably caused by the depletion of the natural food supply.

Mortality rates of juvenile A. tonsa in raw estuary water (Figures 20b, 21b) were quite similar to those rates seen in the LAB

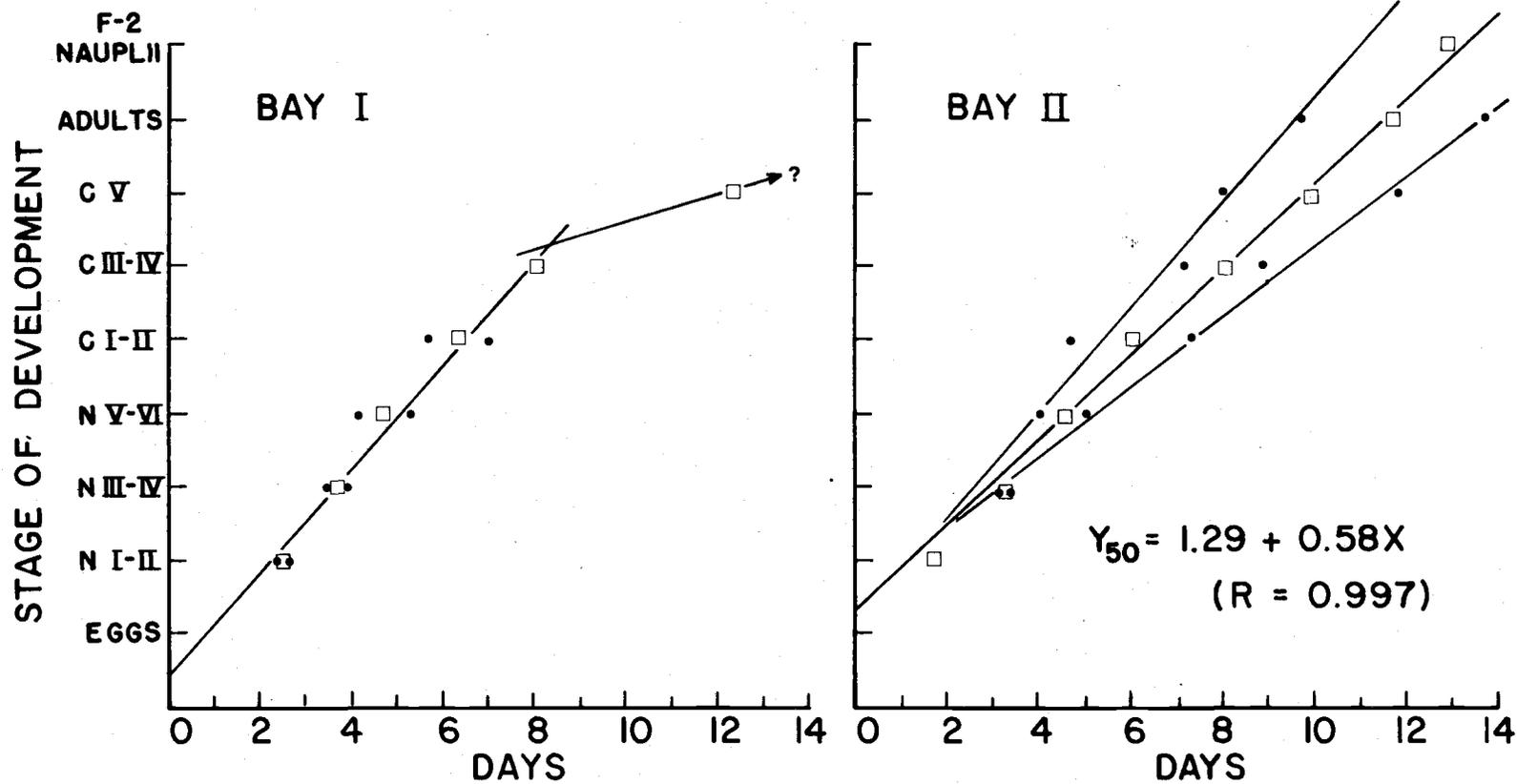


Figure 22. BAY I and II Development Rate Experiments. Linear regression best fit slopes for maximum (upper slope), median ( $Y_{50}$ ) and minimum (lower slope) development rates of *Acartia tonsa* at 21°C and 25 ‰ salinity. Estuary water filtered through a 64 µm screen used as food.

experiments. In general, the early nauplii (stages I-IV) and late copepodites (stages III-V) were very successful in molting while the late nauplii (stages V-VI) and early copepodites (stages I-II) had a high mortality rate. The transition from the naupliar to copepodite stage is apparently a critical period in the life cycle of A. tonsa.

#### Abundance and Distribution of *Acartia tonsa* in Yaquina Estuary

Density estimates for the adult and copepodite stages III, IV and V were completed for the 110  $\mu\text{m}$  net samples. Estimates of adult densities were also completed for the 233  $\mu\text{m}$  net samples. However, the 233  $\mu\text{m}$  net estimates were rejected as too low when a comparison of simultaneous catches with the 110  $\mu\text{m}$  net revealed a significant loss (12 - 32%) of adult A. tonsa males through the 233  $\mu\text{m}$  mesh during the months of July, August and September (Table 2). The larger females were retained equally well by the two mesh sizes throughout the entire summer months. These conclusions are based on the non-parametric Signed Rank Test (Tate and Clelland, 1957).

The seasonal variation of escapement of adult male A. tonsa from the 233  $\mu\text{m}$  net was caused by a gradual reduction of overall body size resulting from high rates of metabolism and more frequent molting induced by high water temperatures (Deevy, 1960). This phenomenon is illustrated in Figure 23. The mean cephalothorax

Table 2. Analysis of adult male and female *Acartia tonsa* escapement losses from the 233  $\mu\text{m}$  net as determined from simultaneous 110  $\mu\text{m}$  net tows at the population center during the summer and early fall of 1972.

Date	Field Temperature (°C)	Adult Males $\cdot \text{m}^{-3}$		Adult Females $\cdot \text{m}^{-3}$	
		233 $\mu\text{m}$	110 $\mu\text{m}$	233 $\mu\text{m}$	110 $\mu\text{m}$
Jun 19	19.1	6	7	31	35
22	20.0	2	0	9	7
26	17.2	0	0	2	0
29	18.4	19	16	19	23
Mean	18.68°C	6.75	5.75	15.25	16.25
Signed Rank Test		Not Significant		Not Significant	
Jul 6	20.7	3	6	25	16
13	18.4	13	33	22	33
17	23.0	5	19	34	35
20	22.2	3	8	21	13
24	21.3	104	190	135	196
31	20.8	1331	1410	541	692
Mean	21.07°C	243.17	277.67	129.67	164.17
Signed Rank Test		P $\leq$ 0.05		Not Significant	
Aug 3	21.3	339	405	927	700
7	20.8	953	2391	1879	1992
10	20.7	3163	3477	3694	4226
17	18.6	2534	4420	2557	2684
24	20.3	5213	6115	3995	4892
31	20.9	2310	3193	6929	6353
Mean	20.43°C	2418.67	3333.50	3330.17	3474.50
Signed Rank Test		P $\leq$ 0.05		Not Significant	

Table 2. Continued.

Date	Field Temperature (°C)	Adult Males · m <sup>-3</sup>		Adult Females · m <sup>-3</sup>	
		233 μm	110 μm	233 μm	110 μm
Sept 4	17.7	2842	3541	3402	2940
11	17.8	1320	1992	2602	2235
18	17.9	690	1041	1178	989
21	16.1	1001	1726	1647	1538
25	14.8	552	965	922	1050
28	13.6	1110	1790	1457	1691
Mean	16.32°C	1252.50	1842.50	1868.00	1740.50
Signed Rank Test		P ≤ 0.05		Not Significant	
Oct 9	14.2	403	689	1042	1018
16	13.7	360	383	724	793
19	13.2	557	574	585	548
23	12.7	526	471	550	593
26	11.4	340	296	436	305
30	9.9	88	107	250	164
Mean	12.52°C	379.00	420.00	597.83	570.17
Signed Rank Test		Not Significant		Not Significant	

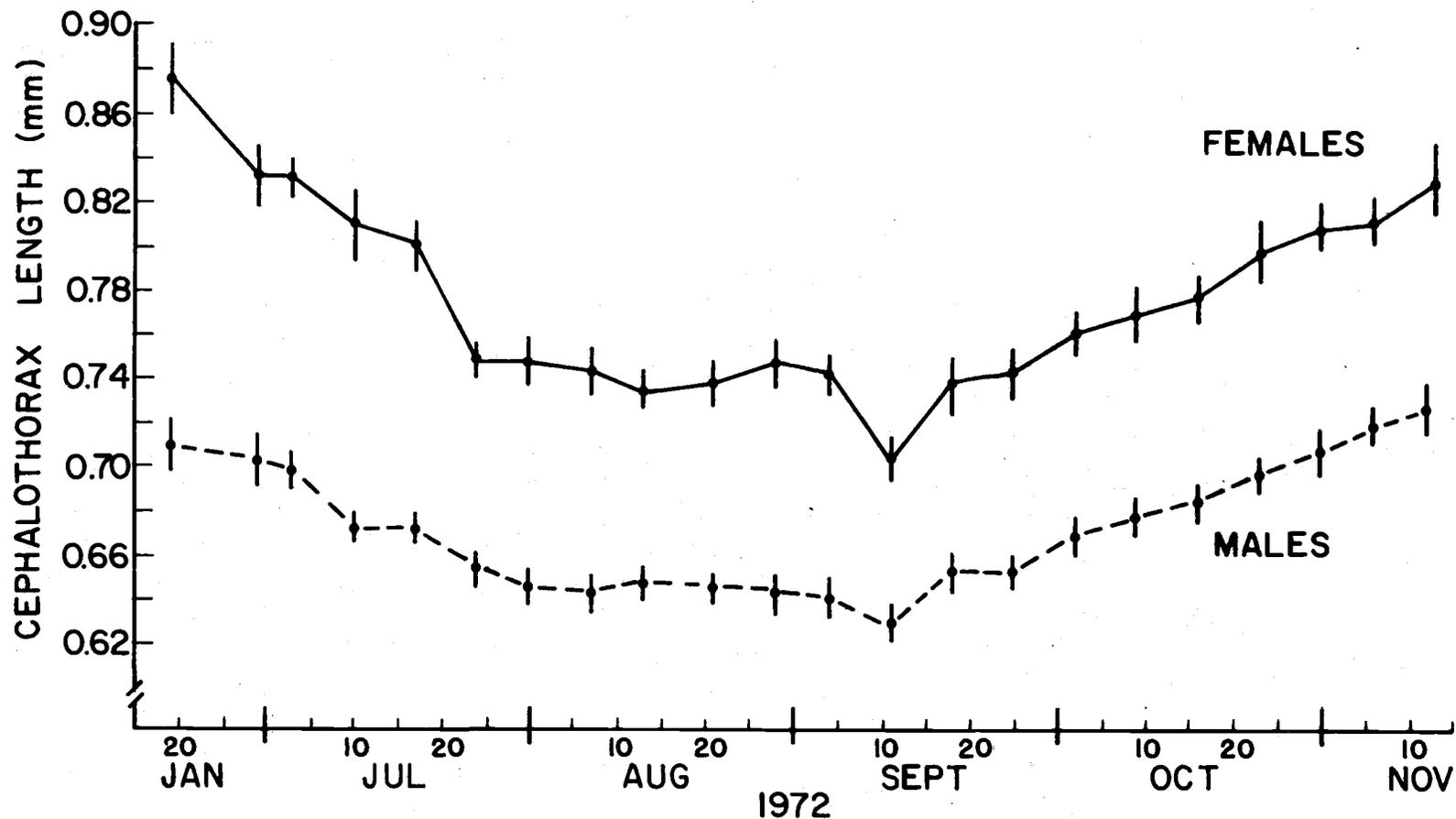


Figure 23. Mean cephalothorax length of male and female *Acartia tonsa* during the summer and early fall of 1972. All measurements were made on individuals captured at the population center. N = 25 for each sex. 95% confidence limits included.

length ( $n = 25$ ) is plotted for both males and females from June to November. Male escapement losses through the 233  $\mu\text{m}$  mesh occurred when the mean cephalothorax length fell below 0.68 mm (680  $\mu\text{m}$ ). The females never reached this level and consequently were retained by the 233  $\mu\text{m}$  net throughout the warmest months. It should be noted that the diameter of the cephalothorax, not the length, determines whether or not escapement can occur. However, the cephalothorax length is used as the index of body size because of the much greater ease and accuracy in making measurements.

Since the 1960's, all plankton samples from Yaquina Bay with the exception of this study, have been collected with a 233  $\mu\text{m}$  net. Therefore, the seasonal loss of male A. tonsa from the 233  $\mu\text{m}$  net has an important implication concerning the general planktology of the congeneric associate, A. clausi, in Yaquina Bay as reported by Frolander (1964), Zimmerman (1972) and Frolander et al. (1973). Acartia clausi has a bi-modal population (Zimmerman, 1972) which consists of a large "race" (females: 0.82 - 0.90 mm) in the lower estuary and a small "race" (females: 0.56 - 0.77 mm) in the upper estuary (measurements refer to mean cephalothorax length only). The upper bay A. clausi males and females are consistently smaller than A. tonsa males (0.63 - 0.73 mm). Consequently, during the summer period of rapid growth and smaller body size, A. clausi must have even higher rates of escapement than A. tonsa from the 233  $\mu\text{m}$

net. Although no numerical data have been compiled for escapement losses of A. clausi, it appears the reported densities of A. clausi in the upper Yaquina estuary must be underestimated during the summer months. Thus, A. clausi and A. tonsa are even more numerically important components of the upper estuary zooplankton than previously realized.

The calculation of age specific mortality rates of A. tonsa will not be attempted until estimates are available for the absolute density of the copepodite I-III and naupliar I-VI stages. At that time, other parameters of the population dynamics will be calculated and published in the expanded Ph.D. thesis work now in progress. These parameters will include the components of the intrinsic rate of increase ( $r$ ) such as the instantaneous birth ( $b$ ) and death ( $d$ ) rates as well as finite survivorship ( $s$ ) and finite death rate ( $D$ ).

The maximum range of the population of A. tonsa in the Yaquina estuary occurred during August and September and extended from Buoy 21 to Toledo + 2 1/2 miles upstream (Figure 1). These two stations represent the general limits of the population distribution as few adults and only rare copepodites were ever present. The bulk of the population was restricted to the region of the estuary between Buoy 29 and Toledo with an approximate center in the vicinity of Buoy 39. The copepodites generally exhibited an even more restricted distribution than the adults, indicating reproduction and

survival of the immature stages were highest between Buoy 29 and Buoy 45. These population characteristics can be seen in Table 3 which contains the mean monthly density (number  $\cdot$  m<sup>-3</sup>) of A. tonsa adults and copepodite stages III, IV and V at the six sampling stations during the summer and fall of 1972.

The center of the population was not static around the general vicinity of Buoy 39 because of diurnal tidal movement. Frolander (1964) demonstrated that horizontal transport of zooplankton population centers in Yaquina Bay can be on the order of several kilometers over a twenty-eight hour span. Sampling without regard to the stage of the tides in this study occasionally showed the population center to be located at Buoy 45, 1.9 kilometers upstream from Buoy 39, or more rarely at Buoy 29, 2.6 kilometers downstream from Buoy 39 (Figures 24, 25, 26).

On a given sampling day, the location of the population center for the copepodite stages III, IV and V generally coincided with that of the adult population. However, during half of the July sampling tows and infrequently during the remainder of the summer, the copepodite population center was found displaced one station downstream from the adult center. The downstream displacement was found to occur only during the periods of neap tides. This phenomenon can be best demonstrated in Figure 27 which represents mean temperature and salinity values associated with the population centers.

Table 3. Mean monthly density (number  $\cdot$  m<sup>-3</sup>) of Acartia tonsa adults and copepodite stages III, IV and V at six stations in the upper Yaquina Bay estuary. Samples were collected twice weekly from June to November, 1972.

Month	Stage	Stations					Toledo	Toledo + 2 1/2 miles
		B-21	B-29	B-39	B-45			
Jun	Adults	0	10	13	9	0		
	Copepodites	0	10	32	19	0		
	Total	0	20	45	28	0		
Jul	Adults	1	257	385	201	10		
	Copepodites	0	363	583	466	28		
	Total	1	620	968	667	38		
Aug	Adults	10	2511	6225	5226	926	114	
	Copepodites	19	1619	7236	5244	207	5	
	Total	29	4130	13,412	10,471	1133	119	
Sept	Adults	14	2074	2787	2290	622	31	
	Copepodites	5	3415	2873	2392	163	5	
	Total	19	5489	5660	4682	785	36	
Oct	Adults	7	833	1418	2130	244	6	
	Copepodites	7	1466	643	841	41	1	
	Total	14	2299	2061	2971	285	7	
Nov	Adults	0	16	120	83	3	0	
	Copepodites	0	1	18	14	1	0	
	Total	0	17	138	97	4	0	

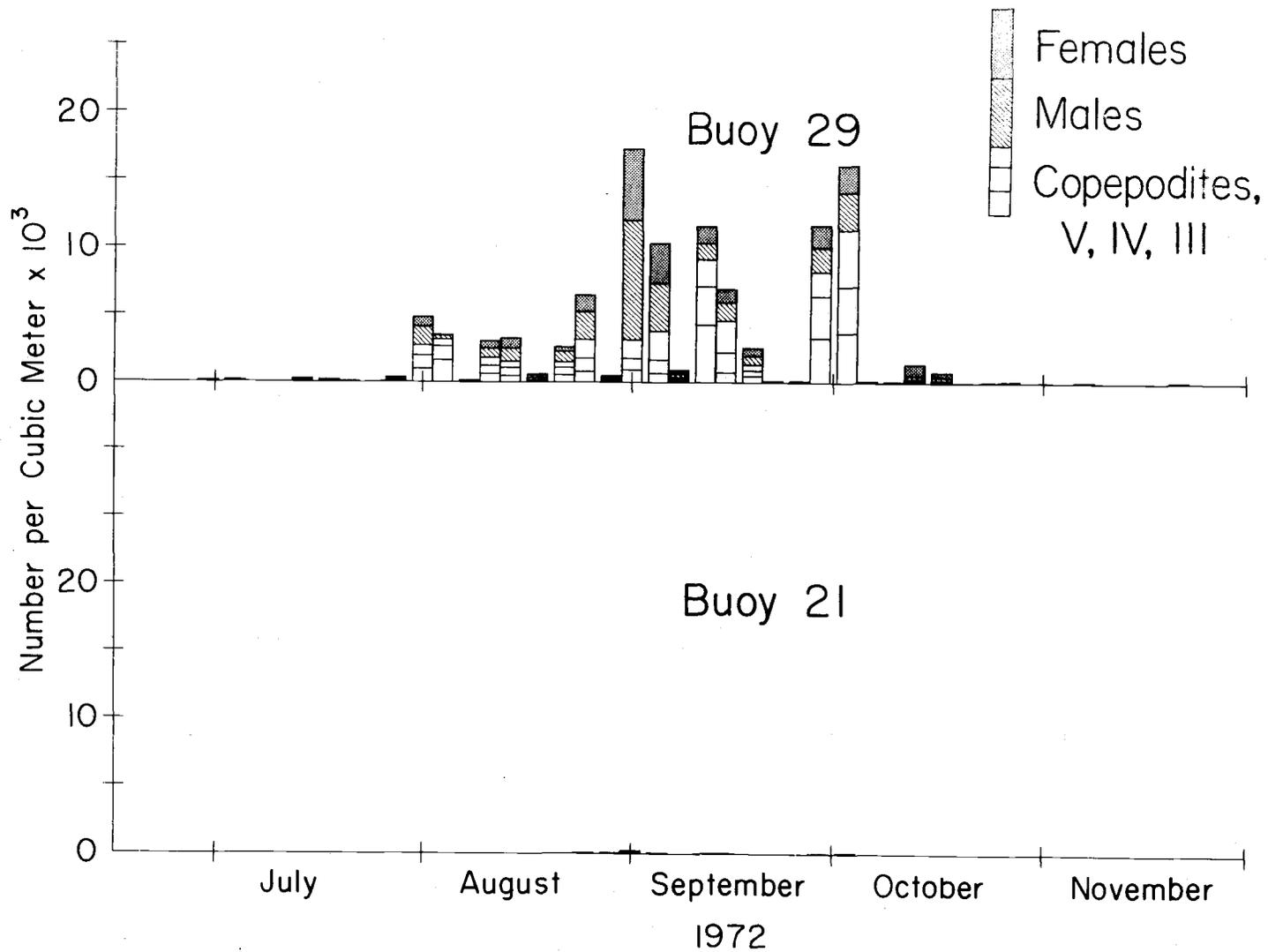


Figure 24. Abundance of *Acartia tonsa* females, males and copepodite stages (V, IV and III) at buoys 21 and 29 during the summer and fall of 1972.

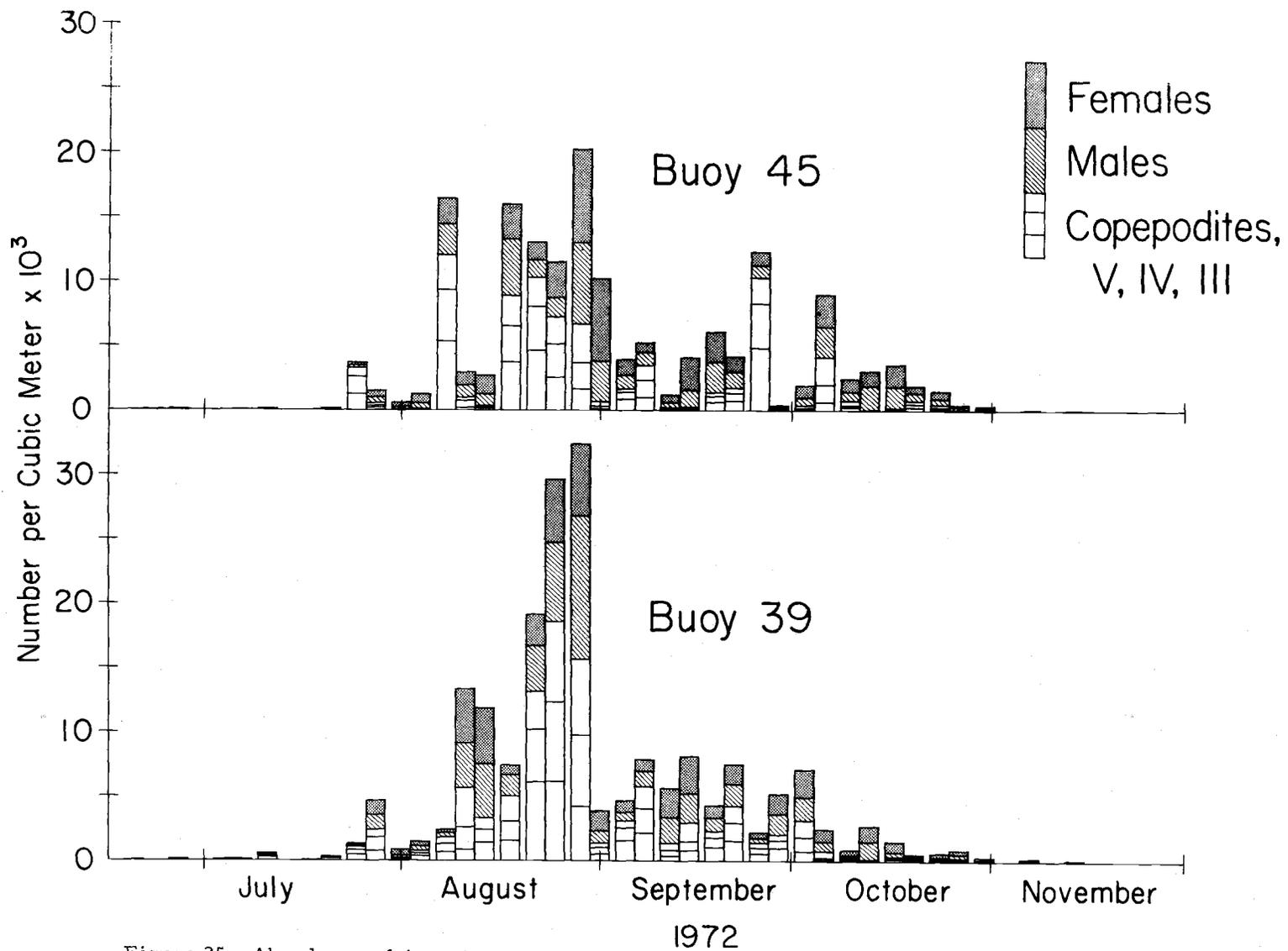


Figure 25. Abundance of *Acartia tonsa* females, males and copepodite stages (V, IV and III) at buoys 39 and 45 during the summer and fall of 1972.

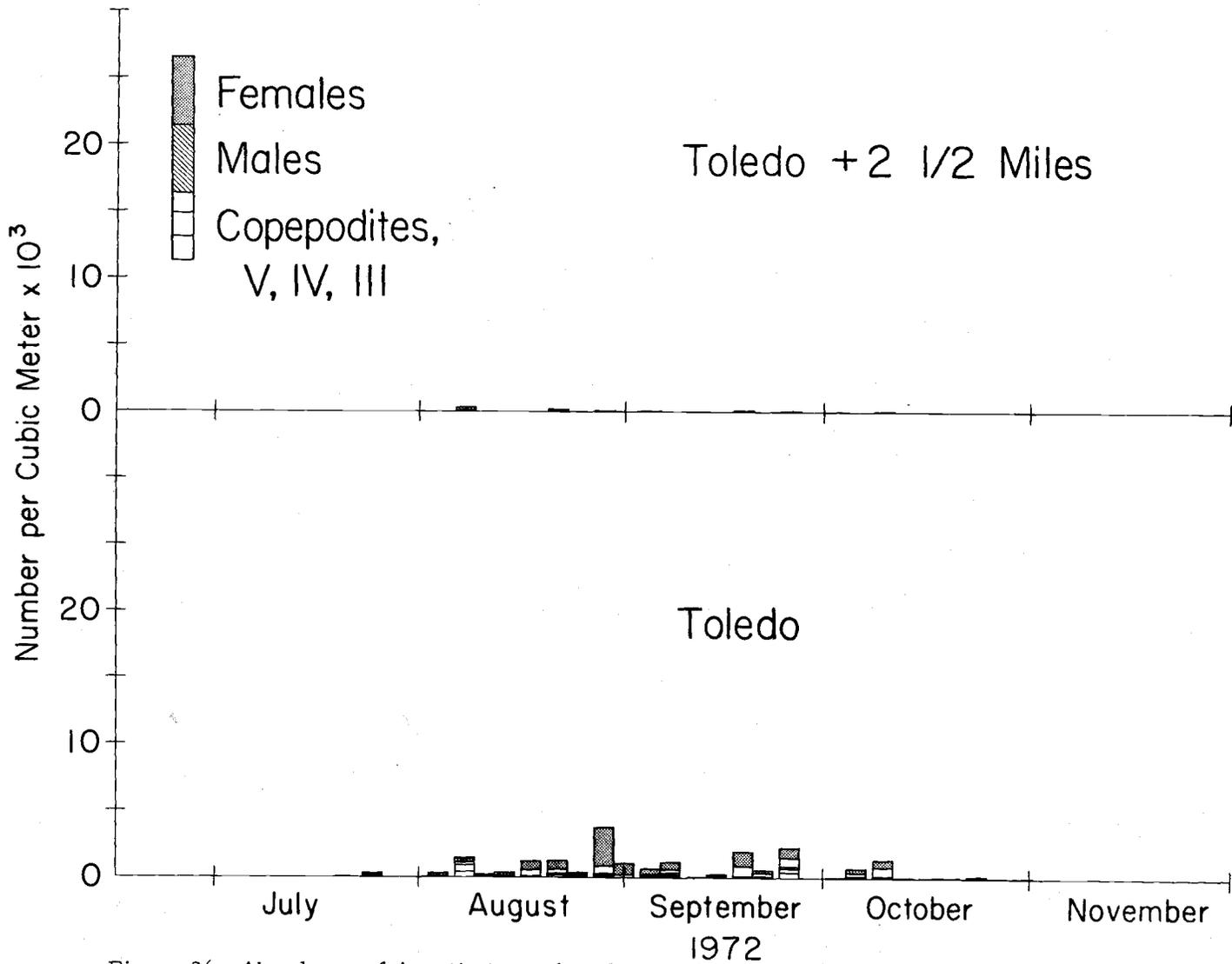


Figure 26. Abundance of *Acartia tonsa* females, males and copepodite stages (V, IV and III) at Toledo and 2 1/2 miles above Toledo during summer and fall of 1972.

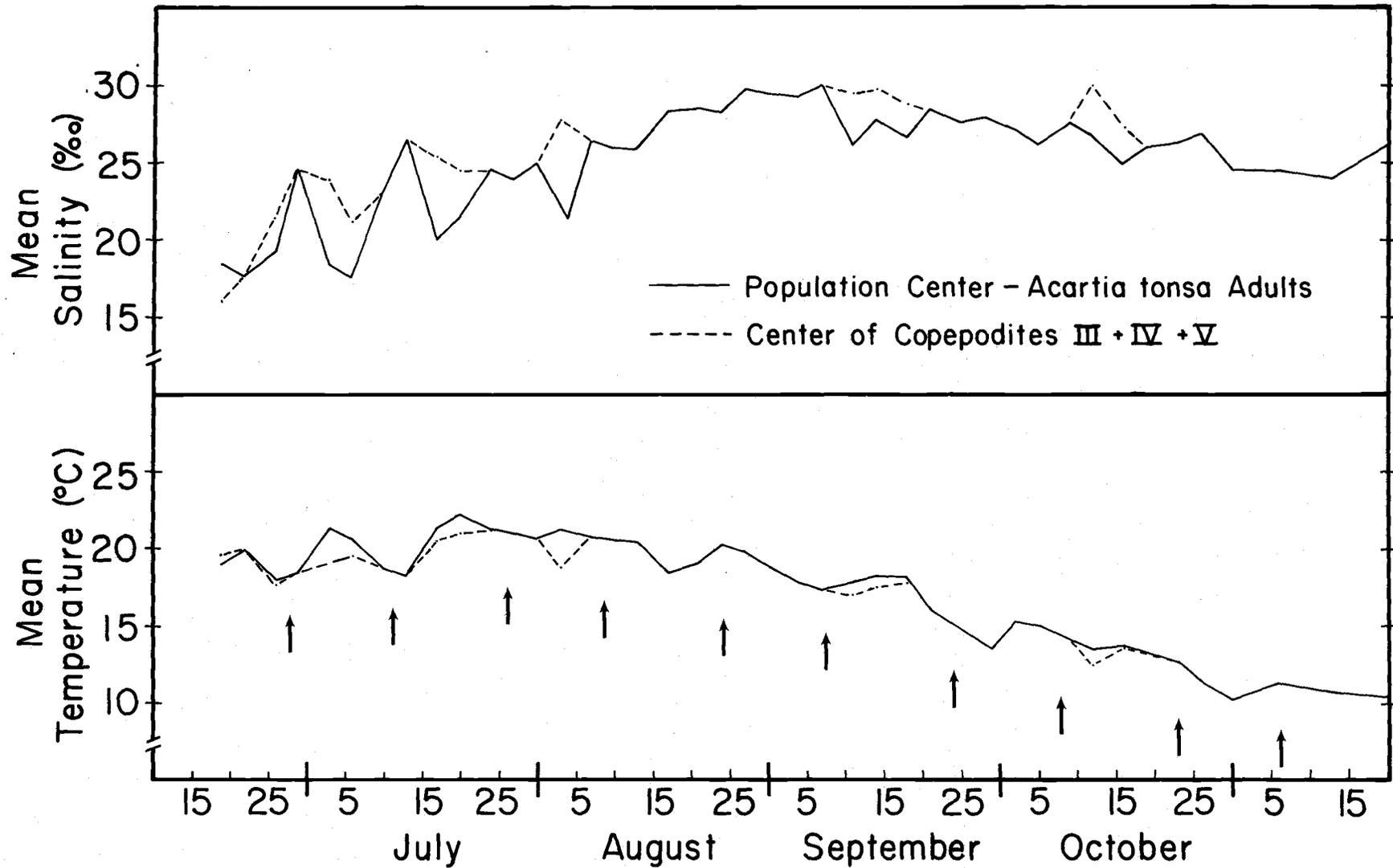


Figure 27. Mean of surface and bottom temperature and salinity at the stations with highest adult and highest copepodite abundance at each semi-weekly sampling during summer and fall of 1972. The adult and copepodite populations are represented by solid and dash lines, respectively. Arrows indicate the occurrence of spring tide maxima.

The occasional dashed lines correspond to the copepodite center when it was found downstream from the adult population center. Arrows at the base of the figure indicate the occurrence of the maximum spring tides. The downstream displacement can not be attributed to field sampling variability because of the general persistence of the phenomenon in July. More likely, the horizontal distribution patterns of A. tonsa are determined by behavioral patterns which tend to displace the immature stages downstream from the adult population under existing tidal and fluvial conditions.

Acartia tonsa adults and copepodites are known to undergo a relatively weak diurnal vertical migration which tends to concentrate them in the deeper layers during daylight hours (Schallek, 1942; Barlow, 1955). The nauplii, according to Barlow (1955) are rather uniform in their vertical distribution. Heinle (1972) however reported them to be somewhat more abundant near the surface during daylight hours.

Estuarine circulation is typified by a net upstream flow of more saline bottom waters and a net downstream flow of fresher surface layers (Pritchard, 1952; Frolander, 1964). Consequently, the adult A. tonsa and late copepodite stages which frequent the bottom layers during daylight hours will experience a net displacement upstream. Maximum upstream displacement should occur during the early summer when daylight hours are maximal. On the other hand, the

nauplii in the surface layer should undergo a net displacement downstream from the adult population as they hatch from eggs and begin to develop. As they molt into the early copepodite stages, they would spend more time in the bottom layers and would eventually be recruited into the adult population by the net upstream bottom currents.

The occasional existence of the copepodite population center downstream from the adult population center therefore indicates significant variations occur in the rate of horizontal displacement between the net surface downstream and net bottom upstream currents. As the displacement was observed only during the period of neap tides, the irregular and yet periodical phenomenon must primarily be a function of the alternating spring and neap tides. The importance of the fresh water runoff is minimal because the streamflow is very low and relatively constant during the dry summer months (Figure 4). Possibly the lower tidal exchange during neap tides reduces mixing and permits the surface downstream current to increase in relative magnitude. This is evidenced by a greater vertical salinity gradient in the upper estuary during periods of neap tides. Conversely, the greater tidal volume during spring tides increases mixing and decreases vertical salinity stratification (Figures 6, 7, 8). The net result is horizontal downstream displacement of a majority of the A. tonsa juveniles from the adults during periods of neap tides and

reconvergence of the two population centers by increased tidal mixing during the spring tides.

The cyclic tidal movements are superimposed on a very slow net seaward drift at all levels of the estuary during the late summer and early fall (Burt and McAlister, 1959). Thus the maintenance of the population center of A. tonsa in the general region of Buoy 39 must be accomplished by high rates of reproduction in order to offset net downstream displacement losses. Even so, little evidence is present to substantiate large losses to the lower estuary by flushing, for few A. tonsa were ever collected at Buoy 21 regardless of the time of the tows (Figure 24).

The complexities involved in analyzing a moving population of zooplankton were circumvented by considering the mass of water inhabited by A. tonsa as a closed system. This is reasonable because of the low diffusive losses of A. tonsa to the lower bay (Figure 24). Therefore the maximum density per cubic meter observed on a given sampling day was considered to be at the approximate population center, regardless of location in the river. Plotting the maximum density values observed at any station for both copepodites and adults on successive sampling days generated an unsophisticated but workable presentation of the population dynamics (Figure 28). The density of adult A. tonsa was less than  $50 \text{ animals} \cdot \text{m}^{-3}$  from June 19 to July 6. During the period of July 10 to July 13, adults reached a

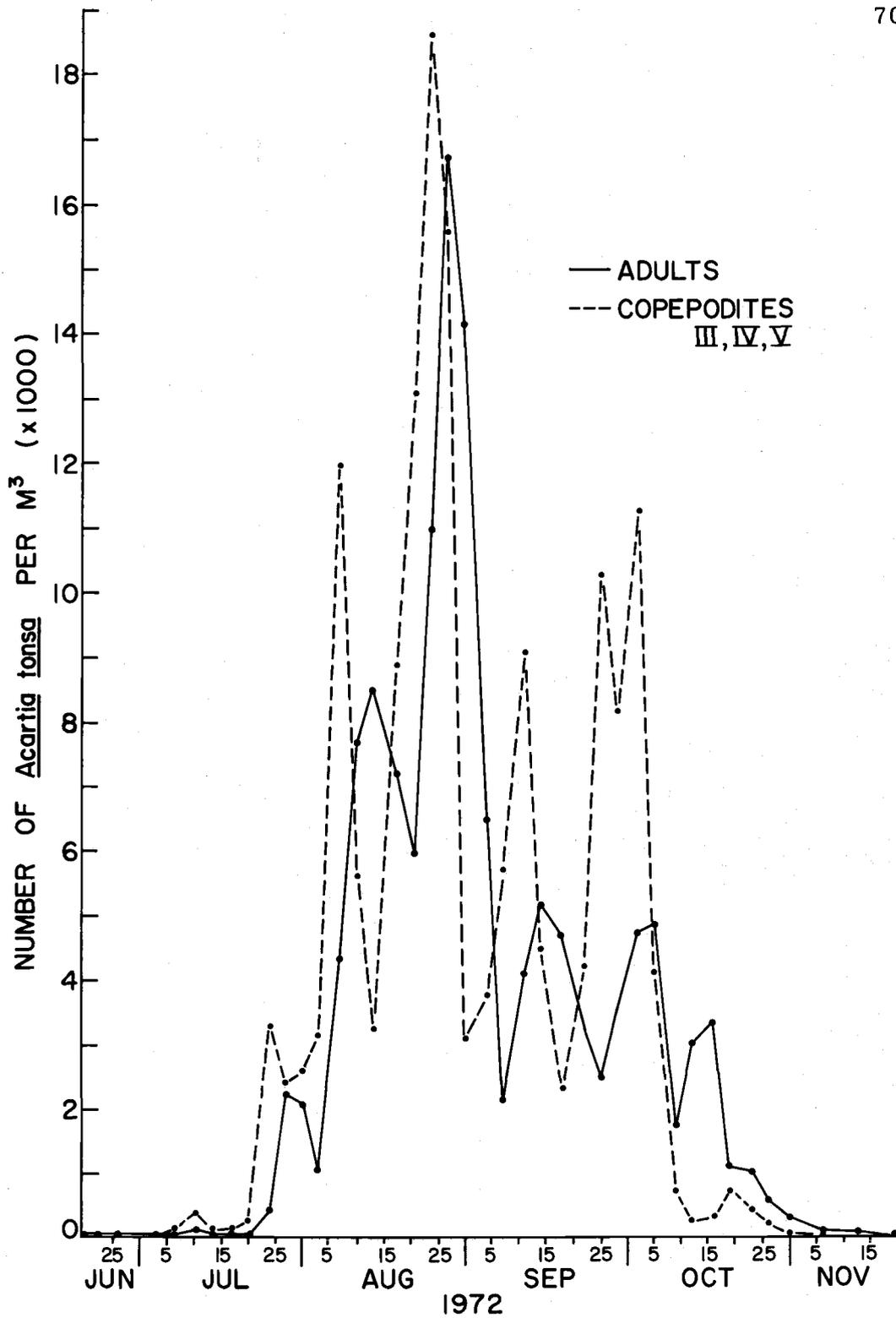


Figure 28. Abundance of *Acartia tonsa* copepodites (V, IV and III) and adults at the station with highest abundance at each semi-weekly sampling during summer and fall of 1972.

minor peak of 128 animals·m<sup>-3</sup>. Seventeen days later, on July 17, the adults peaked at a new maximum of an estimated 2263 animals·m<sup>-3</sup> and the annual population explosion was underway. The population explosion reached its peak on August 28 when a maximum density of 16,760 adults·m<sup>-3</sup> were estimated to be in the upper Yaquina estuary. By September 7, ten days later, the adult population had crashed to a density of 2140 animals·m<sup>-3</sup>. The adult population never fully recovered and oscillated between 5000 animals·m<sup>-3</sup> and 2000 animals·m<sup>-3</sup> throughout the remainder of September and early October. From mid-October onward, the total population decreased rapidly and essentially disappeared by the latter part of November.

During the course of collecting zooplankton data, dense schools of herring (Clupea harengus) and anchovy (Engraulis mordax) fingerlings, approximately two to four inches in length, were commonly observed feeding in the surface waters at Buoy 29, 39 and 45. The schools, with seagulls frequently seen feeding on them, were most prevalent during the months of August and September. Preliminary gut analysis studies revealed that A. tonsa was the major prey of the fishes at that time.

The estimated total density of the copepodite stages III, IV and V exhibits a remarkably good correlation with the total adult densities three to six days later throughout most of the sampling period

(Figure 28). With the exception of the month of October, every adult peak was preceded by a larger copepodite peak. Maturation of the copepodites associated with a given copepodite peak caused a sharp decrease in copepodite densities and a corresponding increase in adult densities. The total egg production was probably great when the adults attained a peak of density. Thus there must have been periodic pulses of high egg production. A given pulse of eggs hatched and eventually produced another peak of copepodite and then of adult abundance. The fact that these cyclic pulses can be followed throughout the summer indicates the field sampling variability must be quite low. The statistical analysis of field variance could not be attempted, however, as replicate tows were not taken.

The periods between the six adult peaks were used to infer development rates from egg to egg under fluctuating field conditions. The average time interval between adult peaks in July and August was 16 days at an approximate water temperature of  $20^{\circ}\text{C}$ . During September, October and November, development rates decreased presumably because of the falling water temperatures (Figures 12 and 27). Starting with the August 28 adult peak, 17 and 19 days were required for eggs to reach maturity at estimated field temperatures of  $18^{\circ}$  and  $16^{\circ}\text{C}$ , respectively.

## DISCUSSION

Acartia tonsa produces approximately 1200 - 1300 viable eggs during a relatively brief adult life span of less than 40 days in the laboratory, a rate of approximately 30 eggs per day. The biological significance of this high fecundity may be demonstrated by comparing A. tonsa with other calanoid copepods. Paracalanus crassirostris, an estuarine and neritic species, produces between 10 to 20 eggs·day<sup>-1</sup> in the laboratory (Lawson and Grice, 1973). Calanus finmarchicus, an oceanic species, produces between 200 - 300 total eggs at a rate of 8 - 15 eggs·day<sup>-1</sup> (Marshall and Orr, 1955). Another oceanic species, Calanus hyperboreus, produces approximately 1300 - 1400 total eggs in a life span, comparable to that of A. tonsa, but differs greatly in the daily rate of egg production as well as life span. Adult C. hyperboreus have been maintained in the laboratory at 5°C for over one year with spawning mainly confined to a six month period (Conover, 1967). The daily rate of egg production was 5 - 8 eggs·day<sup>-1</sup> with only 58% egg viability. In spite of the low egg viability, Conover (1967) felt a single mating was adequate for C. hyperboreus. In contrast, A. tonsa produces 30 - 33 eggs·day<sup>-1</sup> with approximately 100% viability. The much greater egg production rate and egg viability of A. tonsa would appear to be traits of great adaptive value, allowing the species to respond quickly to short term favorable

environmental conditions in an estuary. It would also be an important mechanism for establishing and maintaining a dominant population in an estuary in spite of heavy losses from predation by juvenile fishes and other predators or from flushing.

Mortality rates were substantial during the present A. tonsa development experiments as only 20 - 30% of the original population survived to adulthood. Heinle (1966, 1969) performed similar development rate experiments with A. tonsa but found essentially no mortality. The cause for the high mortality in the present studies is not known but may be related to the molting process. On the basis of mortality rates, the most critical period for molting occurred during the transition from the late naupliar stages to the early copepodite stages.

Additional evidence for mortality associated with molting is presented by Raymont and Miller (1962). They estimated A. tonsa population densities in large fertilized seawater tanks and reported high rates of mortality. Less than 10 - 15% of the eggs produced were believed to reach adulthood. As fish and jellyfish predators had been excluded from the tanks, Raymont and Miller attributed the mortality to the intra-molt periods (ecdysis) when crustaceans are more vulnerable because of physiological stress and soft exoskeletons. Their evidence for intra-molt mortality is weakened somewhat by the presence of other copepods in the tanks. Paracalanus crassirostris, Eurytemora hirundoides and Oithona sp. were also present in low

numbers. It is generally acknowledged that copepods are herbivores, but some information suggests that copepods may actually be omnivores in many cases (Anraku and Omori, 1963). Therefore the mortality rates of A. tonsa juveniles in the fertilized tanks may have been partly caused by predation from other copepods.

In spite of the low survival in the laboratory experiments, reproduction was highly successful when food supplies were adequate (Figures 15b, 16b). Mortality rates must be much greater in the field populations because of fluctuating food supplies and significant losses to predators. The fact that A. tonsa is so successful in Yaquina Bay during August and September attests to the fact that egg production rates are indeed high and more than adequate to compensate for postulated population losses to predation and other natural causes such as intra-molt mortality.

The egg to egg generation time of 11.5 - 12.0 days for Acartia tonsa at 21°C with either laboratory diets (50,000 to 70,000 cells/ml) or natural food agrees fairly well with Heinle's (1966, 1969) results on the Atlantic coast. He found development of A. tonsa from egg to egg in estuary water required 4, 7, 9 and 13 days at 30.7°C, 25.5°C, 22.4°C and 15.5°C, respectively. A mean generation time of 25 days at 17.5°C was reported for A. tonsa by Zillioux and Wilson (1966). However their experimental animals were maintained on what they described as a suboptimal algal diet (10,000 to 30,000 cells/ml)

consisting of equal parts of Isochrysis galbana, Rhodomonas sp. and an unidentified (5 - 6  $\mu$ m) diatom. Food quantity and perhaps quality can therefore modify the temperature regulation of growth rate.

This effect was also seen in the BAY I experiment when development rates were greatly reduced because of food depletion.

On the basis of successive adult population peaks, the mean generation time for A. tonsa in Yaquina Bay was estimated to be 16 days at a mean temperature of 20°C in July and August, four days longer than in the laboratory. The longer field generation time can be explained in part by slightly lower temperatures. Using Heinle's (1966, 1969) results for A. tonsa development at different temperatures, a 1°C drop in temperature should increase the mean generation time by one day or more. Another factor, abundance of A. tonsa, may also be important. As the large pulses of eggs hatched and eventually molted into the late copepodite stages, the food resources in the estuary may have actually become limiting and thus slowed the overall rate of population growth. In addition, the individual variation in intrinsic development rates observed in the laboratory experiments would tend to smear the timing of successive generations in the field. This is further complicated by the fact that A. tonsa females are iteroparous spawners and may persist in the population through one or more full generations. For these reasons,

the correlation of the field and laboratory generation times was felt to be quite good.

Much longer generation times have also been estimated for A. tonsa elsewhere on the basis of successive peaks in the field population density. Conover (1956), for example, estimated that 3 - 4 weeks were required for a brood in Long Island Sound at 20 - 25°C while Woodmansee (1958) reported 11 generations per year at 21.6 - 31.0°C in Biscayne Bay, Florida. Raymont and Miller (1962) found a comparable period of 24 to 32 days at 20.5 to 21.5°C in their fertilized tanks. An even longer period of 6 - 7 weeks at 20 - 25°C was reported for two successive major adult maxima in Tisbury Great Pond, Massachusetts (Deevy, 1948). However Deevy noted that two secondary adult maxima were also produced. This could also be interpreted as a 3 - 4 week generation period.

All of these latter generation time estimates are approximately equivalent for field temperatures above 20°C and are based on weekly sampling. An examination of Zimmerman's (1972) data for A. tonsa in Yaquina Bay, also based on weekly sampling, likewise does not reveal the 16 - 17 day generation periods in July to September which were detected by the present twice weekly sampling plan. It is therefore apparent that a weekly sampling frequency is too long to detect successive population peaks of a population that can turn over in less than two weeks at temperatures above 20°C unless it is

exactly in phase with the population. It is also interesting to note that Conover (1956) did observe a two week generation period in September which he could not interpret on the basis of a postulated three - four week generation period for A. tonsa in Long Island Sound.

The annual population explosion and subsequent crash of the A. tonsa population constitutes a major feature of the planktology of the upper Yaquina estuary from June to November. It is therefore of interest to examine the possible causes for this seasonal pattern. The triggering mechanism for the cyclic pulses during the population explosion is not understood at this time. Temperature and salinity, two potential factors in triggering the population explosion, seemed to be of minor importance as values associated with the population center of A. tonsa were relatively similar through June and July (Figure 27).

The population crash in early September is partly attributable to the cyclic nature of A. tonsa production. Based on the preceding cycles, a sharp decline was expected following the maximum density of  $16,760 \text{ adults} \cdot \text{m}^{-3}$  on August 28, but not to the extreme low density of  $2140 \text{ adults} \cdot \text{m}^{-3}$  (Figure 28). Likewise a successive adult peak of even higher densities would have been anticipated assuming maximum egg production also occurred during the August 28 period. As the population never fully recovered from the crash, it is evident that the

population growth was checked by some factor, or factors, of the environment which became limiting and decreased the birth rate, increased the mortality rate, or did both.

Environmental control in the form of flushing or dilution by short term influxes of fresh water from rainstorms can not be successfully argued as a causative factor in the population crash of A. tonsa in the upper estuary. Very little rain fell during the 1972 summer and early fall, with the exception of one prolonged rainy period from September 18 to September 24, when a total of 7.19 centimeters of precipitation was recorded at the Marine Science Center at Newport, Oregon (Figure 29). Heavy rainfall occurred two weeks after the crash during a period when adult A. tonsa densities were again declining and copepodite densities were increasing. Neither group appeared to be adversely affected (Figure 28). A graph of the mean salinities associated with the population center(s) (Figure 27) also indicated no significant dilution occurred as a result of the rainfall. This is not surprising since most of the early fall precipitation is soaked up by the undersaturated soil of the Yaquina River drainage basin (Kulm and Byrne, 1966). It should be noted that once the soil has been saturated, the river runoff quickly increases (Figure 4). Consequently, the October and November increase in river runoff or flushing rate possibly accelerates the final



disappearance of the A. tonsa population from the upper estuary in November.

In contrast to salinity, water temperatures must play a major role in the decline and eventual extinction of the A. tonsa population in the upper bay. An examination of the temperatures associated with the population center (Figure 27) revealed a gradual and fairly consistent rate of decline occurred throughout August, September and October with only two periods of possible significance. Temperatures fell from 20.4°C to 17.5°C between August 24 and September 7, the general period of the population crash. Another major drop from 18.0°C to 13.5°C occurred between September 18 and 29 during the period of the heavy rainfall. Neither of these two temperature decreases would normally be considered as constituting thermal shock for the changes were less than 5°C and occurred over a span of many days. This range is well within the tolerance extremes of 5°C to 30 - 35°C reported by Heinle (1969) for A. tonsa. He found that juvenile stages of A. tonsa have a low temperature tolerance limit comparable to that of the adults. At 5°C hatching eggs required two months to reach adulthood. As field temperature in Yaquina Bay had only dropped to 10°C by November, the decline of the wild population could not have been caused by catastrophic mortality from low temperatures.

Development rates of zooplankton, however, are clearly controlled by temperature. Experiments by Heinle (1966), noted above, have demonstrated that even a  $1^{\circ}\text{C}$  or  $2^{\circ}\text{C}$  decrease in water temperature results in a pronounced increase in the time A. tonsa required for development from egg to adult. The average development time for a generation in Yaquina Bay was 16 days in July and August when water temperatures approximated  $20^{\circ}\text{C}$ , 17 days in September at  $18^{\circ}\text{C}$  and 19 days in October at  $16^{\circ}\text{C}$ . The falling water temperatures, therefore, caused a decrease in the development rate which in turn, caused a decrease in the population's intrinsic rate of increase. This also increased the interval of time each successive generation was exposed to predation or other mortality causing factors prior to spawning. Consequently, fewer individuals reached adulthood to reproduce as temperatures decreased. The net result was a continual decline in the standing crop of A. tonsa in the upper estuary. It may also be that egg production per day per female decreased with falling temperatures. This has not yet been verified in the laboratory.

The existence of temperature-dependent egg dormancy in the egg of A. tonsa has been recently demonstrated by Zillioux and Gonzalez (1972). Their laboratory studies indicate egg dormancy commences when water temperatures decrease to  $14,5^{\circ}\text{C}$ . Production in the field, however, continues as laying of nondormant eggs

occurs concurrently with dormant eggs between  $9^{\circ}$  -  $14.5^{\circ}\text{C}$ . At  $5^{\circ}\text{C}$  they found all eggs to be dormant. This phenomenon was proposed as the mechanism responsible for the reappearance of A. tonsa in the spring months following the winter disappearance in the Atlantic coastal area north of  $40^{\circ}$  latitude.

Egg dormancy has not been demonstrated for the Pacific A. tonsa but probably occurs. It is one plausible explanation for the repopulation of the upper Yaquina Bay in the early summer months. As temperatures fall below  $15^{\circ}\text{C}$  during late September and early October, the production of the wild population would be decreased in proportion to the percentage of eggs that enter the resting stage. The importance of this phenomenon would increase as temperature continues to fall in late October and November, thus helping to accelerate the decline and subsequent disappearance of the field population. It must be noted that the Yaquina Bay population had disappeared by the time water temperatures averaged  $10^{\circ}\text{C}$ . Therefore, egg dormancy may not be totally responsible for the population's disappearance. Other factors, such as increased exposure to predation as discussed above, are probably also important.

The nature of predation on A. tonsa and other members of the zooplankton in Yaquina Bay has not yet been completely determined, but the small pelagic fishes such as the clupeids are significant predators. In the lower estuary, Russell (1964) found that one to

four year old herring prey heavily on A. clausi and Pseudocalanus sp. During the present study, dense schools of herring and anchovy fingerlings were commonly observed feeding in the surface waters at Buoy 29, 39 and 45 during August and September. A. tonsa was found to be the major prey taken. Hydrozoan medusae are also minor predators of zooplankton (McCormick, 1958). Phialidium gregarium, for example, attained its maximum summer (1972) density of  $13.6 \cdot m^{-3}$  at Buoy 39 coincident with the population crash of A. tonsa in early September (personal observations).

Alternate hypotheses for the causation of the population crash and subsequent decline have not, of course, been eliminated. Depletion of the phytoplankton food supply is an outstanding possibility. Quantitative data are not available to test this hypothesis at this writing. However, current research is being concentrated on the correlation between A. tonsa population dynamics and the standing phytoplankton crop and primary productivity in Yaquina Bay.

## CONCLUSIONS

The zooplankton of the upper Yaquina estuary is dominated by Acartia clausi throughout much of the year. However, as water temperatures become maximal in the summer, Acartia tonsa is able to replace A. clausi because of lower sensitivity to low salinity and high temperatures. As a result, A. tonsa becomes the dominant herbivore in the plankton and accounts for the bulk of the total secondary production during the warmest summer months. A. tonsa is an important prey organism for the pelagic fishes such as the commercially important herring (Clupea harengus) and anchovy (Engraulis mordax) in the estuary. Adult Clupea and Engraulis, in turn, are important prey of the salmonid fishes of the nearshore oceanic waters. Only a restricted section of the estuary provides a suitable habitat for the population explosion and high productivity of A. tonsa. Industrial pollution or other changes in the upper estuary could conceivably cause serious repercussions in the whole food chain by removal of the localized A. tonsa link. These considerations strongly suggest that the consequences to planktonic life must be seriously considered before any major modification of Yaquina Bay is contemplated.

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APPENDIX

## APPENDIX

ESTIMATED DENSITIES OF ACARTIA TONSA IN  
YAQUINA BAY, OREGON, DURING THE  
SUMMER OF 1972

ESTIMATES FOR 06/19		MALES	5TH COP.	4TH COP.	3RD COP.	TOTAL
BUOY 21	FEMALES 0	0	0	0	0	0
BUOY 29	0	1.8416	0	0	0	1.8416
BUOY 39	35.0118	7.0024	7.0024	0	0	49.0165
BUOY 45	12.0143	1.7163	0	0	0	13.7386
TOLEDO	0	0	0	0	0	0
ESTIMATES FOR 06/22		MALES	5TH COP.	4TH COP.	3RD COP.	TOTAL
BUOY 21	FEMALES 0	0	0	0	0	0
BUOY 29	0	0	0	0	0	0
BUOY 39	0	6.5364	3.2682	6.5364	9.8045	26.1455
BUOY 45	6.8717	1.7179	0	0	0	8.5896
TOLEDO	0	0	0	0	0	0
ESTIMATES FOR 06/26		MALES	5TH COP.	4TH COP.	3RD COP.	TOTAL
BUOY 21	FEMALES 0	0	0	0	0	0
BUOY 29	0	0	0	0	0	0
BUOY 39	1.5204	.1901	31.7390	31.7390	39.5312	104.7196
BUOY 45	15.0405	0	25.0674	33.4232	16.7116	90.2428
TOLEDO	0	0	0	0	0	0
ESTIMATES FOR 06/29		MALES	5TH COP.	4TH COP.	3RD COP.	TOTAL
BUOY 21	FEMALES 0	0	0	0	0	0
BUOY 29	23.4601	15.6401	0	7.8200	31.2002	78.2805
BUOY 39	0	1.7742	0	0	0	1.7742
BUOY 45	0	0	0	0	0	0
TOLEDO	0	0	0	0	0	0
ESTIMATES FOR 07/03		MALES	5TH COP.	4TH COP.	3RD COP.	TOTAL
BUOY 21	FEMALES 0	0	0	0	0	0
BUOY 29	1.6326	3.5918	10.7754	21.5509	36.2447	73.7954
BUOY 39	47.4237	37.9390	4.7424	0	0	90.1050
BUOY 45	1.5411	0	1.5411	0	0	3.0822
TOLEDO	0	0	0	0	0	0
ESTIMATES FOR 07/06		MALES	5TH COP.	4TH COP.	3RD COP.	TOTAL
BUOY 21	FEMALES 0	0	0	0	0	0
BUOY 29	0	0	0	0	0	0
BUOY 39	9.1623	3.1152	33.5340	27.4869	30.6021	103.9804
BUOY 45	16.1075	6.4430	19.3290	12.8860	3.2215	57.9869
TOLEDO	.1779	0	0	0	0	.1779
ESTIMATES FOR 07/10		MALES	5TH COP.	4TH COP.	3RD COP.	TOTAL
BUOY 21	FEMALES 0	0	0	0	0	0
BUOY 29	1.9845	0	0	0	0	1.9845
BUOY 39	68.7172	60.1963	75.5889	123.6909	219.0950	548.0883
BUOY 45	9.1201	1.2800	16.9602	27.0403	33.7604	88.1610
TOLEDO	0	0	0	0	0	0

ESTIMATES FOR 07/13						
	FEMALES	MALES	5TH COP.	4TH COP.	3RD COP.	TOTAL
BUOY 21	0	0	0	0	0	0
BUOY 29	33.4165	33.4165	31.0031	43.4415	61.8209	203.0981
BUOY 39	0	1.8435	0	2.7652	5.5304	10.1391
BUOY 45	0	0	0	0	0	0
TOLEDO	0	0	0	0	0	0
ESTIMATES FOR 07/17						
	FEMALES	MALES	5TH COP.	4TH COP.	3RD COP.	TOTAL
BUOY 21	.1668	0	0	0	0	.1668
BUOY 29	4.9476	32.9843	29.3193	63.5863	30.6021	161.4396
BUOY 39	18.3995	25.0902	5.0180	6.6907	0	55.1984
BUOY 45	34.7476	19.1112	0	0	0	53.8587
TOLEDO	0	0	0	0	0	0
ESTIMATES FOR 07/20						
	FEMALES	MALES	5TH COP.	4TH COP.	3RD COP.	TOTAL
BUOY 21	0	0	0	0	0	0
BUOY 29	0	1.9284	.3857	19.2840	15.4272	37.0253
BUOY 39	7.7542	1.9385	21.7117	54.9889	143.8403	270.2336
BUOY 45	13.4565	7.6894	9.2273	48.4435	34.6025	113.4192
TOLEDO	17.3589	1.5781	1.5781	0	0	20.5151
ESTIMATES FOR 07/24						
	FEMALES	MALES	5TH COP.	4TH COP.	3RD COP.	TOTAL
BUOY 21	0	0	0	0	0	0
BUOY 29	.1476	0	0	0	0	.1476
BUOY 39	81.0989	148.6813	236.5384	371.7032	+33.2032	1271.2251
BUOY 45	196.2383	190.2002	694.3815	1388.7631	1222.7153	3692.2984
TOLEDO	36.8980	33.6162	56.5769	93.4750	44.2776	264.8457
ESTIMATES FOR 07/27						
	FEMALES	MALES	5TH COP.	4TH COP.	3RD COP.	TOTAL
BUOY 21	0	0	0	0	0	0
BUOY 29	51.2616	39.8701	22.7829	74.0445	108.2189	296.1782
BUOY 39	1101.1004	1161.6004	620.2462	1043.7464	710.9962	4637.6896
BUOY 45	498.9613	435.4571	211.9225	181.4405	83.0997	1410.8810
TOLEDO	0	0	0	0	0	0
ESTIMATES FOR 07/31						
	FEMALES	MALES	5TH COP.	4TH COP.	3RD COP.	TOTAL
BUOY 21	1.7523	8.7613	0	0	0	10.5135
BUOY 29	692.3386	1410.6399	778.8809	969.2740	351.9655	4803.0989
BUOY 39	454.2897	235.8812	66.3962	59.4071	45.4290	861.4032
BUOY 45	360.5735	171.8621	10.1095	23.5889	16.8492	582.9833
TOLEDO	1.6788	.1679	0	1.6788	0	3.5254
ESTIMATES FOR 08/03						
	FEMALES	MALES	5TH COP.	4TH COP.	3RD COP.	TOTAL
BUOY 21	0	0	0	0	0	0
BUOY 29	77.6176	252.2571	509.3653	1083.4119	1568.5218	3491.1737
BUOY 39	334.3250	353.8245	183.8287	236.3274	314.9921	1423.2978
BUOY 45	700.3346	404.6378	70.5522	29.0509	12.4504	1217.0259
TOLEDO	249.7401	50.9674	0	0	0	300.7074

ESTIMATES FOR 08/07							
	FEMALES	MALES	5TH COP.	4TH COP.	3RD COP.	TOTAL	
BUOY 21	0	0	0	0	0	0	
BUOY 29	19.7663	51.3941	15.8136	15.8136	0	102.7881	
BUOY 39	228.6335	354.1578	520.0292	627.6214	636.5875	2367.0294	
BUOY 45	1992.1377	2390.5652	2706.4533	3984.2754	5356.6369	16424.0686	
TOLEDO	462.4948	293.5083	233.7995	496.3743	366.8854	1753.0623	
TOL +2.5	223.5532	37.7078	8.0802	6.0802	2.6934	286.1149	
ESTIMATES FOR 08/10							
	FEMALES	MALES	5TH COP.	4TH COP.	3RD COP.	TOTAL	
BUOY 21	6.2217	6.2217	0	0	0	12.4434	
BUOY 29	574.6901	696.5941	587.7513	631.2884	565.9827	3056.3066	
BUOY 39	4226.3755	3477.0181	3057.3780	1738.5091	359.1832	13358.4638	
BUOY 45	997.6687	943.8040	275.0721	525.8732	216.3493	2952.7672	
TOLEDO	158.3757	40.2346	0	3.2919	3.2919	205.1935	
ESTIMATES FOR 08/13							
	FEMALES	MALES	5TH COP.	4TH COP.	3RD COP.	TOTAL	
BUOY 21	0	0	0	0	0	0	
BUOY 29	767.4048	1044.2146	462.2921	556.6374	+62.2921	3292.8403	
BUOY 39	4363.5414	4191.7484	876.1441	1030.7578	1374.3438	11836.5356	
BUOY 45	1453.5285	918.6306	97.6771	169.3353	123.2592	2702.4002	
TOLEDO	235.5178	95.5336	5.5398	5.5398	5.5398	342.7211	
TOL +2.5	0	0	0	0	0	0	
ESTIMATES FOR 08/17							
	FEMALES	MALES	5TH COP.	4TH COP.	3RD COP.	TOTAL	
BUOY 21	0	0	0	0	0	0	
BUOY 29	38.3671	188.6382	137.4821	75.5369	83.1287	521.1531	
BUOY 39	743.9859	1660.1802	1559.5569	1487.8117	142.2439	7393.6986	
BUOY 45	2663.5043	4419.3895	2367.7979	2762.4319	3762.1679	15955.7906	
TOLEDO	666.6074	430.8730	34.1493	31.7160	26.8316	1190.1713	
ESTIMATES FOR 08/21							
	FEMALES	MALES	5TH COP.	4TH COP.	3RD COP.	TOTAL	
BUOY 21	2.0394	0	0	0	0	2.0394	
BUOY 29	334.2324	783.7885	409.4347	526.4161	509.7044	2568.5761	
BUOY 39	2441.1726	3564.1126	2529.4071	4101.1700	6102.9316	19138.7934	
BUOY 45	1386.2584	1365.2525	2268.4196	3462.6294	4520.8547	13043.4125	
TOLEDO	664.8388	298.9198	77.3068	98.9528	117.5064	1257.5245	
TOL +2.5	129.7424	9.7307	0	0	0	139.4730	
ESTIMATES FOR 08/24							
	FEMALES	MALES	5TH COP.	4TH COP.	3RD COP.	TOTAL	
BUOY 21	19.5917	0	42.4487	0	0	62.0404	
BUOY 29	1219.9245	2081.6677	1372.2655	1014.2835	742.6146	6430.7563	
BUOY 39	4892.0817	6115.1022	6274.6266	6221.4518	6115.1022	29618.3644	
BUOY 45	2758.3017	1519.5435	2114.1474	2576.0172	2543.5836	11512.1935	
TOLEDO	265.2852	66.0835	22.5313	37.5522	12.5174	337.9695	
ESTIMATES FOR 08/28							
	FEMALES	MALES	5TH COP.	4TH COP.	3RD COP.	TOTAL	
BUOY 21	6.4732	9.7098	0	0	0	16.1830	
BUOY 29	171.2283	134.7972	94.7223	25.5022	14.5727	446.8231	
BUOY 39	5466.8315	11178.1686	5892.8389	5528.3334	4191.8132	32197.9855	
BUOY 45	7222.0417	6335.7002	2987.2991	2035.3027	1541.3731	20221.7167	
TOLEDO	2867.3532	581.3990	168.4231	94.2809	70.7107	3742.1668	
TOL +2.5	54.1053	3.3092	0	0	0	57.4145	

ESTIMATES FOR 08/31							
	FEMALES	MALES	5TH COP.	4TH COP.	3RD COP.	TOTAL	
000Y 21	15.5630	21.7882	68.4772	40.4438	18.6756	164.9677	
000Y 29	5275.5595	8878.3807	1376.7924	862.1936	574.9708	17267.8370	
000Y 39	1522.5997	974.7861	368.6464	495.4491	459.1967	3820.6780	
000Y 45	6353.2551	3192.5905	351.1850	166.3147	102.1629	10165.2082	
TOLEDO	351.0884	165.8901	2.6850	2.8850	2.8850	1025.6336	
ESTIMATES FOR 09/04							
	FEMALES	MALES	5TH COP.	4TH COP.	3RD COP.	TOTAL	
000Y 21	15.9448	15.9448	0	16.6830	0	42.5725	
000Y 29	2940.2698	3548.9701	2149.8747	1011.7058	621.8829	10264.7333	
000Y 39	961.9778	654.1817	525.3277	1011.0681	1526.4240	4618.9193	
000Y 45	1247.0817	1073.0703	241.7308	558.2866	341.6551	3661.2245	
TOLEDO	433.8920	101.8204	13.2809	38.3671	59.0263	643.3867	
TOL +2.5	11.5372	2.8843	0	0	0	14.4215	
ESTIMATES FOR 09/07							
	FEMALES	MALES	5TH COP.	4TH COP.	3RD COP.	TOTAL	
000Y 21	0	0	0	0	0	0	
000Y 29	302.0904	223.9023	159.9302	117.2822	67.5261	870.7312	
000Y 39	935.2644	1207.3413	1700.4807	1887.5336	2125.6009	7856.2210	
000Y 45	767.9694	993.8427	1163.2477	1321.3590	393.8427	5240.2615	
TOLEDO	287.7038	151.7559	69.5548	69.5548	41.1005	619.6698	
ESTIMATES FOR 09/11							
	FEMALES	MALES	5TH COP.	4TH COP.	3RD COP.	TOTAL	
000Y 21	23.5539	14.7212	5.8885	0	0	44.1636	
000Y 29	1227.7471	1183.3747	2041.3144	2840.0896	4230.5502	11523.0720	
000Y 39	2235.4932	1992.1743	565.7167	456.2231	328.4806	5578.0879	
000Y 45	617.9359	492.7793	72.8223	59.5818	46.3414	1199.4698	
TOLEDO	48.2025	6.8051	1.1342	1.1342	0	57.2760	
TOL +2.5	1.5594	0	0	0	0	1.5594	
ESTIMATES FOR 09/14							
	FEMALES	MALES	5TH COP.	4TH COP.	3RD COP.	TOTAL	
000Y 21	23.5101	.9796	7.8367	0	0	32.3263	
000Y 29	991.6419	1359.9660	2351.6079	1473.2965	396.8714	6875.3837	
000Y 39	2888.8167	2256.8880	1421.8395	716.9197	789.9108	8065.3747	
000Y 45	2545.3293	1302.6097	146.7417	68.8736	32.9396	4090.4939	
TOLEDO	163.5916	43.7324	8.0986	3.2394	0	218.6621	
ESTIMATES FOR 09/18							
	FEMALES	MALES	5TH COP.	4TH COP.	3RD COP.	TOTAL	
000Y 21	.1594	0	0	0	0	.1554	
000Y 29	589.3798	665.9227	443.9484	375.0599	459.2570	2533.5679	
000Y 39	989.3830	1041.3982	489.3806	718.5288	151.8637	4290.5543	
000Y 45	2357.2744	2332.7195	313.1574	441.9890	38.4285	6083.5687	
TOLEDO	1145.4223	728.9200	29.5975	29.5975	46.3405	1979.5777	
TOL +2.5	62.3465	17.5849	0	0	1.5986	81.5361	
ESTIMATES FOR 09/21							
	FEMALES	MALES	5TH COP.	4TH COP.	3RD COP.	TOTAL	
000Y 21	0	0	0	0	0	0	
000Y 29	37.4907	33.7116	14.9827	11.2375	7.4913	104.8757	
000Y 39	1538.4361	1726.0503	1294.5377	1386.3448	1538.4361	7485.8051	
000Y 45	1215.9410	1239.5523	417.1192	590.2630	731.9261	4194.8025	
TOLEDO	215.3572	237.5263	22.1691	28.5032	25.3361	528.8919	

ESTIMATES FOR 09/25							
	FEMALES	MALES	5TH COP.	4TH COP.	3RD COP.	TOTAL	
BUOY 21	J	L	0	0	0	0	0
BUOY 29	14.5727	2.1859	29.1453	14.5727	14.5727	75.9492	
BUOY 39	433.9443	348.7214	405.2696	480.6686	518.3681	2186.5711	
BUOY 45	1050.3270	965.1653	2022.5891	3406.4659	4661.3107	12305.8581	
TOLEDO	721.0952	685.7474	161.1860	249.9090	405.4393	2223.3769	
TOL +2.5	20.9672	5.2418	3.4945	6.9891	8.7363	45.2490	
ESTIMATES FOR 09/28							
	FEMALES	MALES	5TH COP.	4TH COP.	3RD COP.	TOTAL	
BUOY 21	15.8079	L	7.9040	0	7.9040	31.6156	
BUOY 29	1690.7768	1790.2343	1790.2343	3083.1812	3306.9605	11661.3871	
BUOY 39	1542.2439	1610.2840	453.6011	623.7016	963.9024	5193.7330	
BUOY 45	145.8251	62.4965	32.4056	64.8112	74.0699	379.6082	
TOLEDO	4.2995	1.4332	1.4332	1.4332	0	8.5990	
ESTIMATES FOR 10/02							
	FEMALES	MALES	5TH COP.	4TH COP.	3RD COP.	TOTAL	
BUOY 21	30.4400	8.4556	25.3667	15.2200	5.0733	84.5556	
BUOY 29	2009.6397	2767.3727	4216.3488	3426.2709	3556.8853	16977.1175	
BUOY 39	2165.6094	1790.4645	1313.0073	1074.2787	739.0355	7082.3955	
BUOY 45	965.0414	598.3257	177.5676	111.9448	77.2033	1930.9828	
TOLEDO	11.9475	5.1204	.8534	0	0	17.9212	
TOL +2.5	.1723	0	0	0	0	.1723	
ESTIMATES FOR 10/05							
	FEMALES	MALES	5TH COP.	4TH COP.	3RD COP.	TOTAL	
BUOY 21	J	L	0	0	0	0	
BUOY 29	68.6928	9.8133	22.8976	3.2711	0	104.6747	
BUOY 39	987.6048	753.5950	480.9206	171.7574	62.9777	2461.8556	
BUOY 45	2480.9313	2387.8012	2109.6107	1390.9521	514.4299	8983.3253	
TOLEDO	277.9234	259.9441	56.4584	48.3930	24.1965	666.9154	
ESTIMATES FOR 10/09							
	FEMALES	MALES	5TH COP.	4TH COP.	3RD COP.	TOTAL	
BUOY 21	J	L	0	0	0	0	
BUOY 29	28.8750	9.0252	4.8126	0	0	43.3134	
BUOY 39	352.7808	88.3978	153.2228	100.0773	79.5560	820.6368	
BUOY 45	1017.6261	689.0177	347.6809	169.6044	220.4857	2444.4228	
TOLEDO	546.1711	675.9867	65.5405	27.3086	40.9628	1359.8697	
TOL +2.5	7.5683	10.0911	0	0	0	17.6594	
ESTIMATES FOR 10/12							
	FEMALES	MALES	5TH COP.	4TH COP.	3RD COP.	TOTAL	
BUOY 21	J	L	0	0	0	0	
BUOY 29	817.7283	258.4731	129.2365	64.6163	58.1564	1318.2127	
BUOY 39	1217.4170	1361.2341	35.4156	39.8428	44.2697	2698.2398	
BUOY 45	1155.9614	1820.9526	47.5053	9.5011	4.7505	3046.6708	
TOLEDO	10.1908	10.1908	0	0	0	20.3816	
ESTIMATES FOR 10/16							
	FEMALES	MALES	5TH COP.	4TH COP.	3RD COP.	TOTAL	
BUOY 21	7.0040	4.3779	2.9186	0	0	14.3010	
BUOY 29	358.6561	249.4998	59.2562	37.4250	28.0857	732.9058	
BUOY 39	793.2380	382.7169	101.4036	88.3193	127.5723	1493.2501	
BUOY 45	1718.4004	1642.4032	109.4935	30.4149	36.4978	3537.2499	
TOLEDO	16.4120	22.7244	1.2625	1.2625	J	41.6613	
TOL +2.5	1.4094	.9396	.9396	0	J	3.2686	

ESTIMATES FOR 10/19							
	FEMALES	MALES	5TH COP.	4TH COP.	3RD COP.	TOTAL	
BUOY 21	0	0	0	0	0	0	0
BUOY 29	5.4046	0	0	0	0	5.4046	
BUOY 39	227.0530	123.8498	61.9249	46.4437	38.7031	497.9794	
BUOY 45	547.6357	573.6093	260.8311	250.3477	250.3477	1882.7715	
TOLEDO	15.4111	30.8221	0	0	0	46.2332	
ESTIMATES FOR 10/23							
	FEMALES	MALES	5TH COP.	4TH COP.	3RD COP.	TOTAL	
BUOY 21	0	0	0	0	0	0	0
BUOY 29	12.7448	6.3724	1.5931	0	0	20.7103	
BUOY 39	318.9735	138.4225	54.1653	42.1266	48.1469	601.8368	
BUOY 45	592.6526	470.8833	196.8629	142.8844	104.7819	1508.0650	
TOLEDO	19.0677	38.1354	12.7118	31.7795	12.7118	114.4061	
TOL +2.5	1.6169	4.0422	0	0	0	5.6591	
ESTIMATES FOR 10/26							
	FEMALES	MALES	5TH COP.	4TH COP.	3RD COP.	TOTAL	
BUOY 21	0	0	0	0	0	0	0
BUOY 29	50.2676	22.8489	13.7093	4.5658	0	91.3956	
BUOY 39	305.1020	295.6656	78.6345	59.7622	81.7799	820.9445	
BUOY 45	152.1838	216.6323	35.0941	11.6434	17.5471	433.1006	
TOLEDO	4.4663	7.4439	1.4888	2.9776	0	16.3766	
ESTIMATES FOR 10/30							
	FEMALES	MALES	5TH COP.	4TH COP.	3RD COP.	TOTAL	
BUOY 21	0	0	0	0	0	0	0
BUOY 29	3.1807	1.5903	1.5903	0	0	6.3614	
BUOY 39	164.1755	69.5961	32.1213	7.1361	5.3535	278.3845	
BUOY 45	104.3613	107.1921	28.5846	17.8654	8.9327	326.9360	
TOLEDO	7.3901	5.9121	.8868	.8868	0	15.0759	
TOL +2.5	.7751	.7751	0	0	0	1.5502	
ESTIMATES FOR 11/06							
	FEMALES	MALES	5TH COP.	4TH COP.	3RD COP.	TOTAL	
BUOY 21	0	0	0	0	0	0	0
BUOY 29	14.0314	7.0157	0	0	0	21.0471	
BUOY 39	78.1590	63.5042	24.4247	4.8849	0	170.9727	
BUOY 45	19.8424	12.4015	0	0	0	32.2439	
TOLEDO	0	0	0	0	0	0	
ESTIMATES FOR 11/13							
	FEMALES	MALES	5TH COP.	4TH COP.	3RD COP.	TOTAL	
BUOY 21	0	0	0	0	0	0	0
BUOY 29	4.8857	.8143	.8143	0	0	6.5142	
BUOY 39	44.4769	19.4586	2.7738	0	0	66.7153	
BUOY 45	18.0415	2.7756	1.3678	0	0	22.2049	
TOLEDO	0	0	0	0	0	0	
ESTIMATES FOR 11/20							
	FEMALES	MALES	5TH COP.	4TH COP.	3RD COP.	TOTAL	
BUOY 21	0	0	0	0	0	0	0
BUOY 29	24.7974	8.2656	0	0	0	33.0632	
BUOY 39	26.9063	10.4638	0	0	0	37.3705	
BUOY 45	1.7034	5.1251	0	0	0	6.8335	
TOLEDO	0	0	0	0	0	0	