

# Seasonal cycles of zooplankton from San Francisco Bay

Julie W. Ambler<sup>1, 2</sup>, James E. Cloern<sup>2</sup> & Anne Hutchinson<sup>2, 3</sup>

<sup>1</sup>Department of Oceanography, Texas A&M University, College Station, TX 77843, USA

<sup>2</sup> U.S. Geological Survey, 345 Middlefield Rd., MS496, Menlo Park, CA 94025, USA

<sup>3</sup>RFD 2, West Stockbridge, MA 01266, USA

**Keywords:** San Francisco Bay, zooplankton densities, seasonal cycles, estuarine circulation, spatial distribution, estuarine ecology

## Abstract

The two estuarine systems composing San Francisco Bay have distinct zooplankton communities and seasonal population dynamics. In the South Bay, a shallow lagoon-type estuary, the copepods *Acartia* spp. and *Oithona davisae* dominate. As in estuaries along the northeast coast of the U.S., there is a seasonal succession involving the replacement of a cold-season *Acartia* species (*A. clausi* s.l.) by a warm-season species (*A. californiensis*), presumably resulting from the differential production and hatching of dormant eggs. *Oithona davisae* is most abundant during the fall. Copepods of northern San Francisco Bay, a partially-mixed estuary of the Sacramento-San Joaquin Rivers, organize into discrete populations according to salinity distribution: *Sinocalanus doerrii* (a recently introduced species) at the riverine boundary, *Eurytemora affinis* in the oligohaline mixing zone, *Acartia* spp. in polyhaline waters (18–30‰), and neritic species (e.g., *Paracalanus parvus*) at the seaward boundary. *Sinocalanus doerrii* and *E. affinis* are present year-round. *Acartia clausi* s.l. is present almost year-round in the northern reach, and *A. californiensis* occurs only briefly there in summer-fall. The difference in succession of *Acartia* species between the two regions of San Francisco Bay may reflect differences in the seasonal temperature cycle (the South Bay warms earlier), and the perennial transport of *A. clausi* s.l. into the northern reach from the seaward boundary by nontidal advection.

Large numbers ( $>10^6 \text{ m}^{-3}$ ) of net microzooplankton ( $>64 \mu\text{m}$ ), including the rotifer *Synchaeta* sp. and three species of tintinnid ciliates, occur in the South Bay and in the seaward northern reach where salinity exceeds about 5–10‰. Maximum densities of these microzooplankton are associated with high concentrations of chlorophyll. Meroplankton (of gastropods, bivalves, barnacles, and polychaetes) constitute a large fraction of zooplankton biomass in the South Bay during winter-spring and in the northern reach during summer-fall.

Seasonal cycles of zooplankton abundance appear to be constant among years (1978–1981) and are similar in the deep ( $>10 \text{ m}$ ) channels and lateral shoals ( $<3 \text{ m}$ ). The seasonal zooplankton community dynamics are discussed in relation to: (1) river discharge which alters salinity distribution and residence time of plankton; (2) temperature which induces production and hatching of dormant copepod eggs; (3) coastal hydrography which brings neritic copepods of different zoogeographic affinities into the bay; and (4) seasonal cycles of phytoplankton.

## Introduction

Studies of seasonal cycles of estuarine zooplankton have usually focused on net collections of mesozooplankton ( $>200 \mu\text{m}$ ), which are primarily co-

pepods, rotifers, and meroplankton. Much of our knowledge about estuarine copepods has come from studies along the U.S. East coast where copepods of the genus *Acartia* usually dominate (Deevey, 1948, 1956, 1960; Conover, 1956; Cronin

*et al.*, 1962; Herman *et al.*, 1968; Hulsizer, 1976). *Eurytemora* species reach high densities in estuaries with extensive oligohaline reaches (Deevey, 1948, 1960; Jeffries, 1962b; Haertel & Osterberg, 1967; Haertel *et al.*, 1969; Sage & Herman, 1972; Jones & Bottom, 1984). Less well studied are the seasonal cycles of net microzooplankton (tintinnids and rotifers), which also occur in high abundances in estuaries (Deevey, 1948; Hollowday, 1949; Hulsizer, 1976; Hargraves, 1981; Hernroth, 1983). In the present study, we describe seasonal cycles of the dominant net (>64  $\mu\text{m}$ ) holozooplankton (copepods, rotifers, and tintinnids) of San Francisco Bay in relation to the estuarine circulation, formation of dormant eggs, and the seasonal cycles of phytoplankton.

The most striking feature of zooplankton populations in many estuaries is the seasonal disappearance of planktonic species which form benthic dormant eggs. Dormant eggs are produced by a variety of zooplankton taxa: tintinnids, rotifers, cladocerans, and copepods (Gilbert, 1974; Onb , 1978; Paranjape, 1980; Grice & Marcus, 1981). Copepods produce diapause eggs that undergo a refractory period, or quiescent eggs that are inhibited from hatching by unfavorable environmental conditions of temperature, light, or dissolved oxygen. The production and hatching of dormant eggs, predominantly a species-specific response to temperature (Grice & Marcus, 1981), appears to cause the well-documented seasonal succession of *Acartia* species of the U.S. East coast in which a cold-water form (e.g. *A. clausi*) is replaced by a warm-water species (e.g. *A. tonsa*) during summer. Seasonal appearances observed for other *Acartia* species in an Indian monsoonal lagoon (Tranter & Abraham, 1971) and in two South African estuaries (Woolridge & Melville-Smith, 1979) may also be caused by dormant egg production.

The causes of production and hatching of rotifer resting eggs and tintinnid cysts are not well understood, although seasonal disappearances of estuarine rotifers have been attributed to dormant egg production since the 1940's (Deevey, 1948; Hollowday, 1949). Production of resting eggs in monogonont rotifers such as the estuarine genus *Synchaeta* is associated with sexual reproduction of the population, which may be controlled by photoperiod, population density, or diet. Cyst formation by marine tintinnids has only been recently described

from preserved samples (Reid & John, 1978; Paranjape, 1980). Photoperiod may be important for cyst formation, because cysts formed at the same time in a field and laboratory population of *Helicostomella subulata* (Paranjape, 1980).

In addition to seasonal variations in temperature or photoperiod, other mechanisms can induce temporal changes in the zooplankton community. Because planktonic populations are maintained in estuaries by reproducing at rates above the flushing rate (Ketchum, 1954; Barlow, 1955), river discharge has a direct and obvious influence on zooplankton distribution mediated through its control of advective residence time and salinity distribution. When river discharge is high and residence time short, growth rates of copepods are insufficient to maintain estuarine populations, as demonstrated for *Eurytemora affinis* in the Columbia River estuary (Haertel *et al.*, 1969). River discharge directly controls salt distribution in estuaries and therefore also determines the habitat available to different copepod species. The longitudinal salinity gradient causes estuarine circulation, characterized by net nontidal landward advection in the bottom layer, that can transport and concentrate copepods that migrate to deep water (Cronin *et al.*, 1962; Haertel *et al.*, 1969).

When advective residence time increases (e.g. during periods of low river discharge), biological processes become more important causes of temporal variability in estuarine zooplankton populations. Predators on zooplankton, for example, occur seasonally. In Narragansett Bay, dramatic decreases in *A. tonsa* abundance during the late summer have usually been correlated with the seasonal increase of its ctenophore predator *Mnemiopsis leidyi* (Kremer, 1979; Deason & Smayda, 1982). For two West coast *Acartia* populations, high mortality rates calculated from cohort analysis were attributed to the seasonal appearance of planktivorous fishes (Landry, 1978; Johnson, 1980b). Although phytoplankton biomass is maximal during the spring and summer months of many estuarine environments (see Cloern *et al.*, 1985), food may be limiting for copepod egg production even when chlorophyll concentrations are high perhaps due to inadequate food quality (Durbin *et al.*, 1983; Ambler, 1985). Interactions between phytoplankton and zooplankton abundance cycles vary among estuaries, and among years and seasons within the same estuary (Deason & Smayda, 1982;

Smayda, 1983; Jones & Bottom, 1984). In the Kiel Bight, zooplankton biomass increases regularly followed peaks in phytoplankton biomass during a one year study (Smayda, 1983). However, in other estuaries abundances of phytoplankton and zooplankton are not strongly related (Deevey, 1948; Hulsizer, 1976; Landry, 1978; Johnson, 1980b). In Narragansett Bay, Deason & Smayda (1982) suggested that both phytoplankton and zooplankton abundances are controlled by the carnivore *Mnemiopsis leidyi*. Since detrital carbon and ciliates may also provide food for estuarine copepods (Heinle & Flemer, 1975; Poulet, 1976; Heinle *et al.*, 1977; Berk *et al.*, 1977; Robertson, 1983), the relationship between abundance cycles of copepods and their food is further complicated.

And finally, because coastal copepods are present in estuaries, their seasonal occurrences may reflect changes in coastal hydrography (Jeffries, 1962a). For example, along the U.S. West coast northerly winds cause upwelling during the spring and summer, bringing fauna with northern zoogeographic affinities to the coastal areas. During winter, however, the Davidson current flows north close to the coast transporting a different planktonic fauna with southern zoogeographic affinities. Coastal copepod species in Yaquina Bay, Oregon are indicators of these seasonal changes in coastal water type (Frolander *et al.*, 1973).

Although there have been sporadic studies of the zooplankton community in San Francisco Bay (see Hutchinson, 1981), there has been no sustained baywide investigation that documents seasonal population dynamics of zooplankton in this large estuarine system. Here we present the results of zooplankton surveys done either monthly or semi-monthly from 1978 through spring 1981. The purpose of this contribution is to: (1) define the numerical and biomass dominants of the zooplankton community, (2) describe seasonal changes in abundance and distribution of copepods and net microzooplankton throughout San Francisco Bay using results from 1980 to represent the annual cycle, (3) describe interannual variations in the zooplankton community using data collected from 1978 to 1981, and (4) present hypotheses concerning mechanisms of temporal variability in the zooplankton community of this estuary.

## The San Francisco Bay estuary

San Francisco Bay comprises two estuaries that connect, via Central Bay, to the Pacific Ocean at the narrow and deep (>100 m) inlet of Golden Gate (Fig. 1). The South Bay and northern reach (including San Pablo and Suisun Bays) share the bathymetric feature of a central channel (about 10–30 m deep) that incises broad shallows (mean depth <3 m). The two estuaries have distinct circulation patterns (Walters *et al.*, 1985), distributions of salinity, suspended sediments and nutrients (Peterson *et al.*, 1985), and biological communities (see other papers in this volume). Most of these differences result from the differential proximity to the largest source of freshwater inflow, the Sacramento and San Joaquin Rivers (Fig. 1). The northern reach is the partially-mixed estuary of the Sacramento-San Joaquin Rivers. It is characterized by a longitudinal salinity gradient from freshwater at the riverine boundary to near-seawater at Golden Gate, high suspended sediment concentrations especially near the riverine boundary, and persistent estuarine circulation in which net nontidal flow is seaward at the surface and landward at depth. In contrast, the South Bay has no large direct source of freshwater and is usually well-mixed, has a small longitudinal

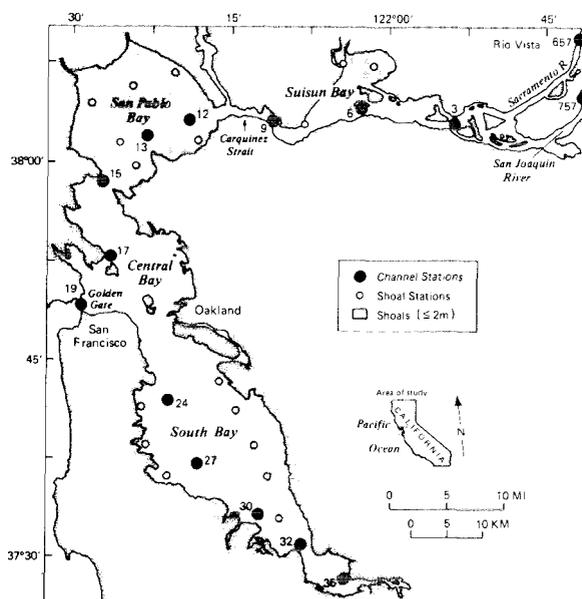


Fig. 1. Map of San Francisco Bay showing locations of stations sampled for zooplankton during 1978–1981.

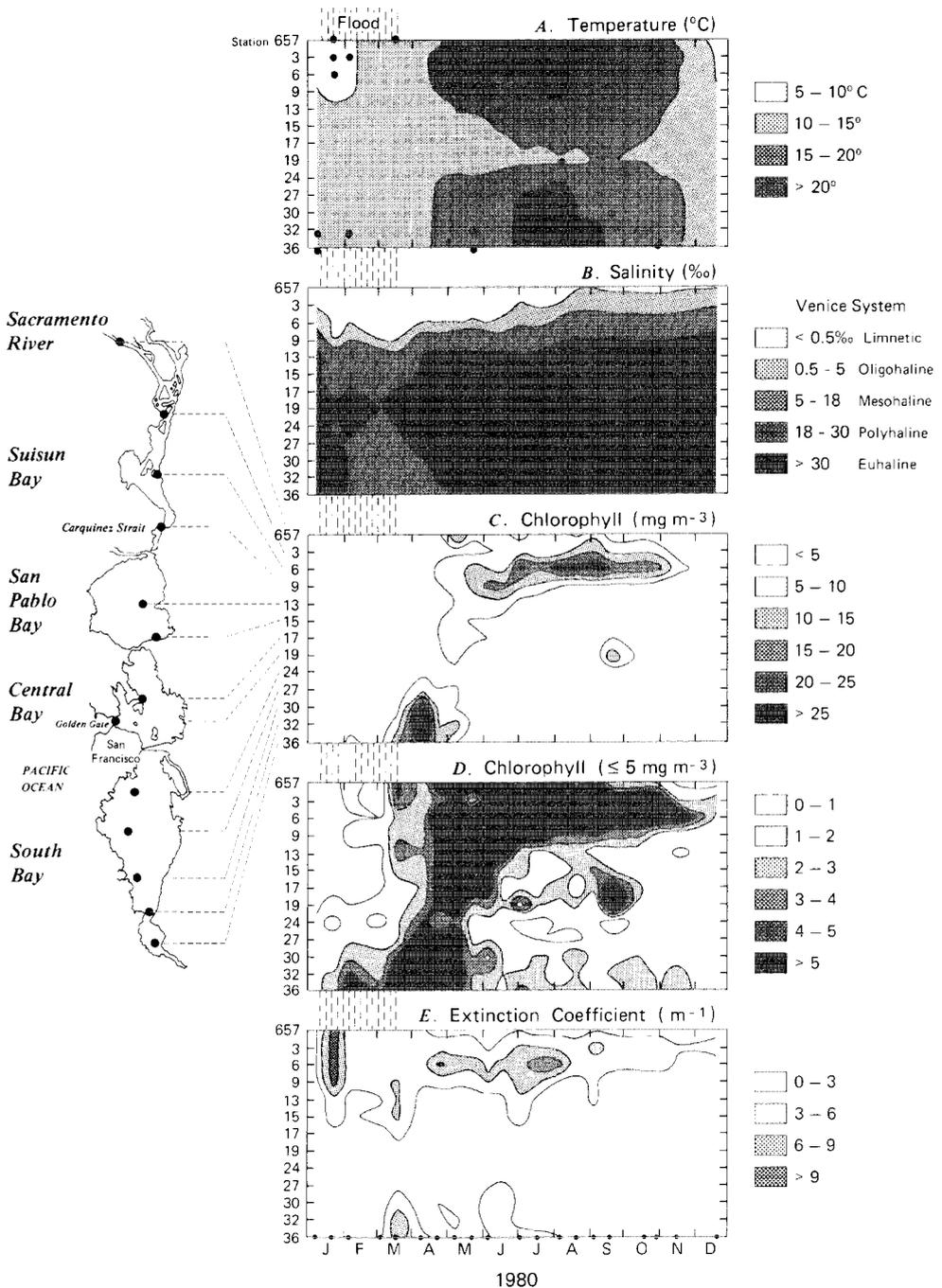


Fig. 2. Contoured concentrations along the channel of San Francisco Bay during 1980 for values integrated over the water column of temperature (A), salinity (B), chlorophyll (C), chlorophyll  $\leq 5 \text{ mg m}^{-3}$  (D), and extinction coefficient (E). Concentrations contoured by computer program (Reid 1981). In (A), large dots in contour map represent interpolated values, and in (E), small dots along abscissa represent sampling dates.

salinity gradient, and slow circulation. Exceptions occur during brief periods in winter-spring when river discharge is sufficient to induce salinity stratification (Cloern, 1984) and generate nontidal currents (Walters *et al.*, 1985). The South Bay is less turbid than the northern reach and therefore has higher annual primary production (Cloern *et al.*, 1985).

Seasonal changes in hydrography are mostly direct responses to the annual periodicity of river discharge, which is high ( $1000\text{--}10\,000\text{ m}^3\text{ s}^{-1}$ ) in winter-spring and consistently low ( $100\text{--}500\text{ m}^3\text{ s}^{-1}$ ) during summer-fall. During 1980, the year of an intensive baywide plankton investigation, water temperature ranged from about  $10\text{--}20^\circ\text{C}$ , peaked in July–August, and was highest at the landward extremities during the dry season (Fig. 2A). Large peaks in river discharge occurred in January and February, displacing salinity contours seaward in the northern reach and causing the intrusion of low-salinity water into South Bay (Fig. 2B). During winter floods, advective residence time in the northern reach is short (on the order of days; Walters *et al.*, 1985), phytoplankton biomass was low baywide (Figs. 2C, D) and turbidity was very high in the upper estuary (Fig. 2E) as suspended sediment loads increased. After river discharge receded in spring, salt progressively moved landward in the northern reach and salinity increased in the South Bay because of evaporation and tidal exchange with coastal waters (Fig. 2B). As observed in other years, phytoplankton dynamics were very different in the two estuaries. The South Bay had a brief spring bloom of nanoplankton, and the northern reach had a more prolonged summer bloom of netplankton localized around Suisun Bay (Fig. 2C). This chlorophyll maximum coincided with a turbidity maximum (Fig. 2E), and both features presumably result from accumulation of suspended sediments and diatoms in the null zone where nontidal bottom currents converge with river currents (Peterson *et al.*, 1975).

## Methods

During 1980, zooplankton were sampled twice monthly (on neap tides) at 32 fixed locations throughout San Francisco Bay (Fig. 1). Sample sites were chosen to provide information about the zooplankton communities of the major embayments, at the estuary boundaries, and along the

salinity gradient of the northern reach. Sample volumes of  $1.5\text{ m}^3$  were collected by a Jabsco pump with a 5-cm diameter hose, and strained through  $64\text{ }\mu\text{m}$  mesh. At the channel stations, two to six depths were sampled from near the surface to near the bottom. Average zooplankton densities were calculated by integrating the densities over the water column using the trapezoid rule, and dividing by water depth (the vertical distribution of zooplankton will be reported later). One mid-depth sample was collected at the shallow-water sites. During 1978 and 1979, sampling was done monthly and we used an  $80\text{-}\mu\text{m}$  mesh net; during 1981 sampling was done almost weekly through spring.

One-hundred and twenty-four taxa were identified to the lowest level, which for copepods was the larval stage (Hutchinson, 1981, 1982a, 1982b). Some zooplankton were not sampled quantitatively by the pump. Large zooplankton such as mysids and decapod larvae avoided the pump, and fragile gelatinous zooplankton such as ctenophores, medusae, chaetognaths, and fish larvae were destroyed by the pump. Nonloricate ciliates, heterotrophic flagellates, and small tintinnids were not sampled, since these organisms must be collected with water samples (Smetacek, 1981). Community biomass was calculated from estimates of carbon weight associated with each taxon; these were either estimated from the literature or were determined by direct analysis with a CHN analyzer for common taxa (Hutchinson, 1981). Results presented below emphasize observations in the central channel along a transect from the Sacramento River to the southern limit of South Bay (Fig. 2).

## Zooplankton composition

The zooplankton community of San Francisco Bay (Tables 1 and 2) is described by frequencies of occurrence of the common taxa within ten geographic areas and for two 'seasons', defined on the basis of river discharge, salinity distribution, and water temperature. The most frequently observed zooplankton taxa during 1980 were *Acartia clausi* s.l.<sup>1</sup>, *Acartia californiensis*, *Oithona davisae*<sup>2</sup>,

<sup>1</sup> The form *Acartia clausi sensu lato* refers to the U.S. West coast species of the subgenus *Acartiura*, which includes all forms of *A. clausi* (see Bradford 1976).

<sup>2</sup> Originally referred to as *Oithona* sp. (Hutchinson 1981, 1982a, 1982b). Ferrari & Orsi (1984) described it as a new species, *Oithona davisae*.

Table 1. Frequency of occurrence (percent occurrence of a taxon) for all sampling dates during January–May 1980. All stations included. A taxon was included if it had at least one frequency of occurrence  $\geq 25\%$  at one geographical location during either the 'wet' or 'dry' season. Densities for the channel stations are average densities integrated over the water column. GG-C = Golden Gate Channel, SO-C = South Bay channel, SO-S = South Bay shoals, SP-C = San Pablo Bay channel, SP-S = San Pablo Bay shoals, CS-C = Carquinez Strait channel, SU-C = Suisun Bay channel, SU-S = Suisun Bay shoals, SR-C = Sacramento River channel, SJR-C = San Joaquin River channel, TOTBAY = Total bay.

Frequency of occurrence (%), January–May 1980											
	GG-C	SO-C	SO-S	SP-C	SP-S	CS-C	SU-C	SU-S	SR-C	SJR-S	TOTBAY
<b>COPEPODS</b>											
<i>Acartia clausi</i> CI–CVI	100	100	98	100	75	55	12	7	0	0	81
<i>Acartia californiensis</i> CI–CVI	7	0	1	0	0	0	0	0	0	0	1
<i>Paracalanus parvus</i> CI–CVI	61	10	1	38	6	0	0	0	0	0	12
<i>Eurytemora affinis</i> CI–CVI	0	17	1	44	45	55	68	64	0	0	26
<i>Sinocalanus doerrii</i> CI–CVI	0	1	0	11	15	33	62	57	28	50	13
Cyclopoid spp.	0	8	1	38	25	66	93	85	100	50	27
<i>Oithona davisae</i>	53	1	0	16	4	0	6	7	0	0	7
<i>Oithona similis</i>	30	1	0	0	0	0	0	0	0	0	3
<i>Corycaeus</i> sp.	46	10	1	16	0	0	0	0	0	0	7
Harpacticoid spp.	92	57	31	83	38	66	81	92	100	50	58
<i>Microsetella</i> sp.	38	7	0	22	4	0	0	0	0	0	6
<i>Acartia</i> spp. nauplii	100	98	98	100	61	33	0	0	0	0	76
Other copepod nauplii	92	38	24	66	31	55	50	78	71	25	45
<b>CLADOCERANS</b>											
Cladoceran spp.	0	0	0	16	2	44	37	28	42	25	8
<i>Bosmina</i> sp.	0	0	0	0	0	11	37	21	57	50	6
<i>Daphnia pulex</i>	0	0	0	0	0	0	31	14	42	25	3
<b>ROTIFERS</b>											
Rotifer spp.	7	7	3	22	2	11	31	14	57	0	10
<i>Synchaeta</i> sp.	30	50	28	33	18	22	0	0	0	0	28
<i>Brachionus</i> sp.	0	0	0	0	0	11	0	0	42	0	1
<i>Keratella</i> sp.	0	1	0	11	0	22	12	14	28	0	4
<b>TINTINNIDS</b>											
<i>Tintinnopsis</i> sp. A	23	42	21	55	40	44	6	0	0	0	31
<i>Tintinnopsis</i> sp. B	53	66	65	88	70	55	6	28	0	0	61
<i>Eutimnus neriticus</i>	30	40	10	44	27	22	0	0	0	0	24
<i>Parafavella</i> sp.	23	1	0	11	0	0	0	0	0	0	3
<b>MEROPLANKTON</b>											
Barnacle nauplii	61	52	46	61	36	44	0	7	14	0	43
Barnacle cyprids	7	5	0	5	4	0	0	0	0	0	3
Gastropod veligers	30	24	12	11	4	0	0	0	0	0	12
Bivalve veligers	100	49	24	66	18	22	0	0	0	0	35
Polychaete trochophores	30	19	15	11	0	11	0	0	0	0	12
Spionid larvae	92	68	71	61	27	11	0	0	0	0	52
Scaleworm larvae	46	43	22	27	4	0	0	0	0	0	23
Number of samples per geographic area											
	13	57	66	18	44	9	16	14	7	4	248

Table 2. Frequency of occurrence (%) for June–December 1980. Codes for geographic areas as in Table 1

Copepods	Frequency of occurrence (%), June–December 1980										
	GG-C	SO-C	SO-S	SP-C	SP-S	CS-C	SU-C	SU-S	SR-C	SJR-S	TO1BAY
<b>COPEPODS</b>											
<i>Acartia clausi</i> CI–CVI	100	41	30	66	41	58	12	3	8	9	38
<i>Acartia californiensis</i> CI–CVI	9	83	83	50	56	41	8	9	0	0	51
<i>Paracalanus parvus</i> CI–CVI	81	11	6	50	16	25	0	0	0	0	17
<i>Eurytemora affinis</i> CI–CVI	0	11	1	4	3	25	100	84	0	54	23
<i>Sinocalanus doerrii</i> CI–CVI	0	0	0	0	0	8	79	54	75	100	18
Cyclopoid spp.	45	25	12	12	1	0	58	39	75	54	25
<i>Oithona davisae</i>	45	48	37	29	25	41	4	15	8	0	31
<i>Oithona similis</i>	54	5	0	8	5	8	0	0	0	0	6
<i>Corvaceus</i> sp.	36	5	3	20	10	8	0	0	0	0	7
Harpacticoid spp.	100	96	72	87	40	75	87	66	66	45	76
<i>Microsetella</i> sp.	18	6	10	4	5	0	0	0	0	0	6
<i>Acartia</i> spp. nauplii	90	95	90	100	92	100	8	12	0	0	75
Other copepod nauplii	90	81	84	54	16	50	87	81	50	18	67
<b>CLADOCERANS</b>											
Cladoceran spp.	0	0	0	0	0	8	12	0	8	0	1
<i>Bosmina</i> sp.	0	0	0	0	0	0	8	0	58	100	6
<i>Daphnia pulex</i>	0	0	0	0	0	0	16	0	16	45	3
<b>ROTIFERS</b>											
Rotifer spp.	9	1	0	0	0	0	0	0	8	0	0
<i>Synchaeta</i> sp.	63	15	13	29	5	41	29	6	0	9	18
<i>Brachionus</i> sp.	0	0	0	0	0	0	4	3	16	27	2
<i>Keratella</i> sp.	0	1	0	0	0	0	0	0	0	0	0
<b>TINTINNIDS</b>											
<i>Tintinnopsis</i> sp. A	0	11	4	75	45	91	20	3	0	0	23
<i>Tintinnopsis</i> sp. B	45	53	27	62	56	58	8	0	0	0	37
<i>Eutintinnus neriticus</i>	9	30	10	29	16	16	0	0	0	0	14
<i>Parafavella</i> sp.	63	3	1	0	0	0	4	0	0	0	6
<b>MEROPLANKTON</b>											
Barnacle nauplii	90	50	33	95	76	100	45	57	0	0	58
Barnacle cyprids	36	6	3	20	0	16	29	3	8	0	10
Gastropod veligers	63	93	62	54	21	41	0	0	0	0	45
Bivalve veligers	90	80	59	83	45	66	29	6	16	36	56
Polychaete trochophores	63	26	36	16	9	8	0	3	0	0	20
Spionid larvae	100	86	80	87	54	50	41	30	0	0	66
Scaleworm larvae	54	25	22	54	23	33	4	0	0	0	23
Number of samples per geographic area											
	11	60	66	24	55	12	24	33	12	11	308

harpacticoid copepods, tintinnids, and the mero-plankton of gastropods, bivalves, barnacles, and polychaetes (IOTBAY in tables 1 and 2). Most taxa seen were estuarine species, and were found in South Bay, San Pablo Bay, and Carquinez Strait, but not in the more freshwater areas upstream:

Suisun Bay and the river stations. Zooplankton communities at these latter sites were dominated by *Eurytemora affinis*, *Sinocalanus doerrii*, cyclopoid copepods, *Bosmina* sp., *Daphnia pulex*, *Brachionus* sp., and bivalve veligers.

Within all embayments, the same taxa were usu-

ally found in both the channel and shoals, although most taxa were more frequently found in the channels (Tables 1 and 2). Adult *Acartia* spp. and *Eurytemora affinis* were usually found more often in the channel, but copepodites and nauplii were found with about equal frequency in the channel and shoal area. The greater frequency of occurrence of some taxa in the channel compared to the shoals may be caused by their preference for deeper water in the channel, which would inhibit horizontal transport into shallow waters. In fact, during all seasons adult *Acartia* spp. in the South Bay were more abundant in the bottom samples than in the surface samples, but the copepodites and especially the nauplii were most abundant near the surface (Fig. 3).

Several taxa probably have their origin in the neritic ocean. *Acartia clausi* s.l., *Paracalanus parvus*, *Oithona similis*, spionid larvae, bivalve veligers, and scalewormlarvae occurred most frequently at the Golden Gate station. In contrast, *A. californiensis* was rarely seen at the Golden Gate station but, instead, was most frequently seen in the South Bay.

Average densities and carbon biomass (Tables 3 and 4) were calculated only from nonzero values to compare the maximum contribution of each taxon. Since the taxa with the highest frequencies of occurrence were usually the most abundant, the potential bias of this method towards taxa with low frequency of occurrence and high abundance is probably not serious. A list of the ten taxa having highest population densities during each season

Table 3. Average density.  $\log_{10}(\text{No. m}^{-3} + 1)$ , for the most abundant rooplankton in San Francisco Bay including all taxa and geographic areas in Tables 1 and 2. The calculation of average density included only densities when a taxon was present and did not include zeroes. Rank order of abundance for the top ten in parentheses.

	January– May 1980	June– December 1980
<i>Tintinnopsis</i> sp. B	4.92 (1)	4.59 (1)
<i>Acartia</i> spp. nauplii	4.11 (2)	3.63 (5)
<i>Acartia clausi</i> CI-CVI	4.03 (3)	3.69 (4)
<i>Tintinnopsis</i> sp. A	3.91 (4)	3.38 (8)
Spionid larvae	3.42 (5)	2.94 (–)
<i>Bosmina</i> sp.	3.35 (6)	2.79 (–)
<i>Synchaeta</i> sp.	3.30 (7)	3.14 (10)
<i>Eutiminnus neriticus</i>	3.29 (8)	3.54 (6)
Copepod nauplii	3.27 (9)	3.48 (7)
<i>Daphnia pulex</i>	3.22 (10)	2.48 (–)
<i>Acartia californiensis</i> CI-CVI	2.97 (–)	3.95 (2)
<i>Oithona davisae</i>	2.36 (–)	3.84 (3)
Barnacle nauplii	2.83 (–)	3.35 (9)

(Table 3) shows that the most abundant components of the San Francisco Bay zooplankton community were microzooplankton (tintinnid ciliates, rotifers, copepod nauplii) and *Acartia* spp. Further, there were some large seasonal differences in community composition. With a few exceptions, all of the common taxa occurred at higher densities during the 'wet' season (January–May) than during the 'dry' season (June–December).

Seasonal changes in community biomass were also apparent, although the patterns were different among the two estuaries (Table 4). Mean zooplankton biomass ranged from about 10–50 mg C m<sup>-3</sup>, and was composed primarily of contributions from copepods and meroplankton. Biomass was highest in South Bay during winter-spring (because of the spring population increase of *A. clausi* s.l. and meroplankton), but was highest in the northern reach during summer-fall (because of increased abundances of *A. californiensis*, *Eurytemora*, *Sinocalanus*, and meroplankton). Zooplankton biomass was highest in those reaches of San Francisco Bay (South Bay and San Pablo Bay shoals) where net primary productivity was highest (Cloern *et al.*, 1985). This suggests that, at least for long (seasonal or annual) time scales, zooplankton dynamics may be partly influenced by food availability or quality.

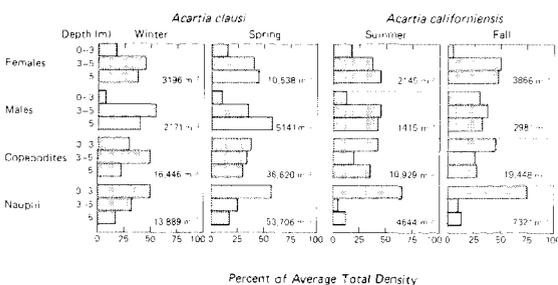


Fig. 3. Vertical distributions for developmental stages of *Acartia* species in the South Bay channel (1980). Maximum abundances of each species occurred during seasons shown: *A. clausi* (winter and spring), and *A. californiensis* (summer and fall). The average total density (No. m<sup>-3</sup>) shown in lower right.

Table 4. Average carbon biomass ( $\text{mg C m}^{-3}$ ) for zooplankton in the channels (C, integrated over the water column) and shoals (S) of South Bay (SO), San Pablo Bay (SP), and Suisun Bay (SU). Carbon biomass was calculated from average density (includes only nonzero values) of taxa listed in Table 1, and individual carbon values from Hutchinson (1981).

	January–May 1980						June–December 1980					
	SO-C	SO-S	SP-C	SP-S	SU-C	SU-S	SO-C	SO-S	SP-C	SP-S	SU-C	SU-S
<i>Acartia clausi</i> CI-CVI	21.0	16.9	6.2	9.9	0.3	0.4	3.6	2.9	4.5	17.1	5.1	0.4
<i>Acartia californiensis</i> CI-CVI	0.0	4.9	0.0	0.0	0.0	0.0	11.1	8.1	8.4	19.0	3.3	1.5
Neritic copepods CI-CVI	1.0	0.1	0.3	0.9	0.0	0.0	0.4	0.6	0.4	1.0	0.0	0.0
<i>Eurytemora affinis</i> CI-CVI	2.9	0.1	1.3	2.3	3.9	2.3	0.5	0.1	0.0	0.3	2.8	4.3
<i>Sinocalanus doerrii</i> CI-CVI	1.1	0.0	0.7	5.0	7.1	4.6	0.0	0.0	0.0	0.0	5.9	6.5
Cyclopoids	1.0	1.2	1.9	1.7	2.8	3.2	6.2	11.9	0.5	1.9	2.1	3.0
Harpacticoids	0.7	0.8	0.4	1.2	1.5	0.7	0.8	1.7	0.5	0.8	0.5	0.6
Copepod nauplii	1.9	1.4	1.5	3.7	0.2	0.2	0.7	1.4	0.8	2.4	0.5	1.1
Cladocerans	0.0	1.1	0.0	0.2	1.7	1.6	0.1	0.0	0.0	0.0	1.1	0.0
Rotifers	0.2	0.2	0.0	0.1	0.0	0.0	0.0	0.1	0.0	0.1	0.0	0.0
Protozoans	1.5	0.9	0.4	0.8	0.0	0.0	0.1	0.5	0.0	1.1	0.2	0.0
Meroplankton	11.7	11.0	2.3	5.5	0.0	0.2	2.1	7.4	5.6	9.4	10.5	9.9
Total	42.9	38.6	15.0	31.2	17.4	13.2	25.6	34.8	20.7	53.1	32.1	27.5

## The annual cycle of zooplankton distribution and abundance

### Copepods

Contour plots, summarizing the distribution of five copepod species along the longitudinal axis of San Francisco Bay, show that each copepod occupied a unique portion of the time-space domain during 1980 (Fig. 4). Four groups of copepods occurred within distinct segments of the northern reach channel, presumably according to salinity tolerances, and the sequence *Sinocalanus* → *Eurytemora* → *Acartia* → *Paracalanus* (and other neritic species) was usually observed between the Sacramento River and Golden Gate. Such discrete separation among populations was less apparent in South Bay where the longitudinal salinity gradient was small and *Acartia* spp. were dominant. *Oithona davisae* was abundant ( $10^3$ – $10^4$   $\text{m}^{-3}$ ) only during the fall in South Bay. Peak abundances (22 000–44 000  $\text{m}^{-3}$ ) occurred at stations 30 and 32 during October and November.

*Species whose distributions are influenced by river flow.* *Sinocalanus doerrii*, a copepod native to main-

land China rivers, was introduced accidentally to the Sacramento River in 1978 (Orsi *et al.*, 1983). Subsequently, this copepod has spread throughout Suisun Bay and the tributaries of the Sacramento-San Joaquin Delta. During 1980, *S. doerrii* was present almost year-round and had maximum densities just upstream of the chlorophyll maximum in Suisun Bay during the spring and summer (Figs. 2C, 4B). During the winter periods of high river inflow, *S. doerrii* was advected downstream into San Pablo Bay. In the late summer and fall, *S. doerrii* was not as abundant in Suisun Bay as earlier. The population maximum may have been progressively transported upstream into the Sacramento River as discharge declined and salt intruded further landward during the dry season. A plot of the abundance of *Sinocalanus* (Fig. 5) against temperature and salinity shows that this species usually occurred at salinities  $<5\text{‰}$ .

Maximum densities of *Eurytemora affinis* occurred downstream from *Sinocalanus doerrii*, within the chlorophyll maximum zone in Suisun Bay (Figs. 2C, 4A). Winter floods also dispersed this maximum and carried *E. affinis* downstream to mesohaline areas as far south as northern Central Bay. Throughout 1980, the distribution of *E. affinis*

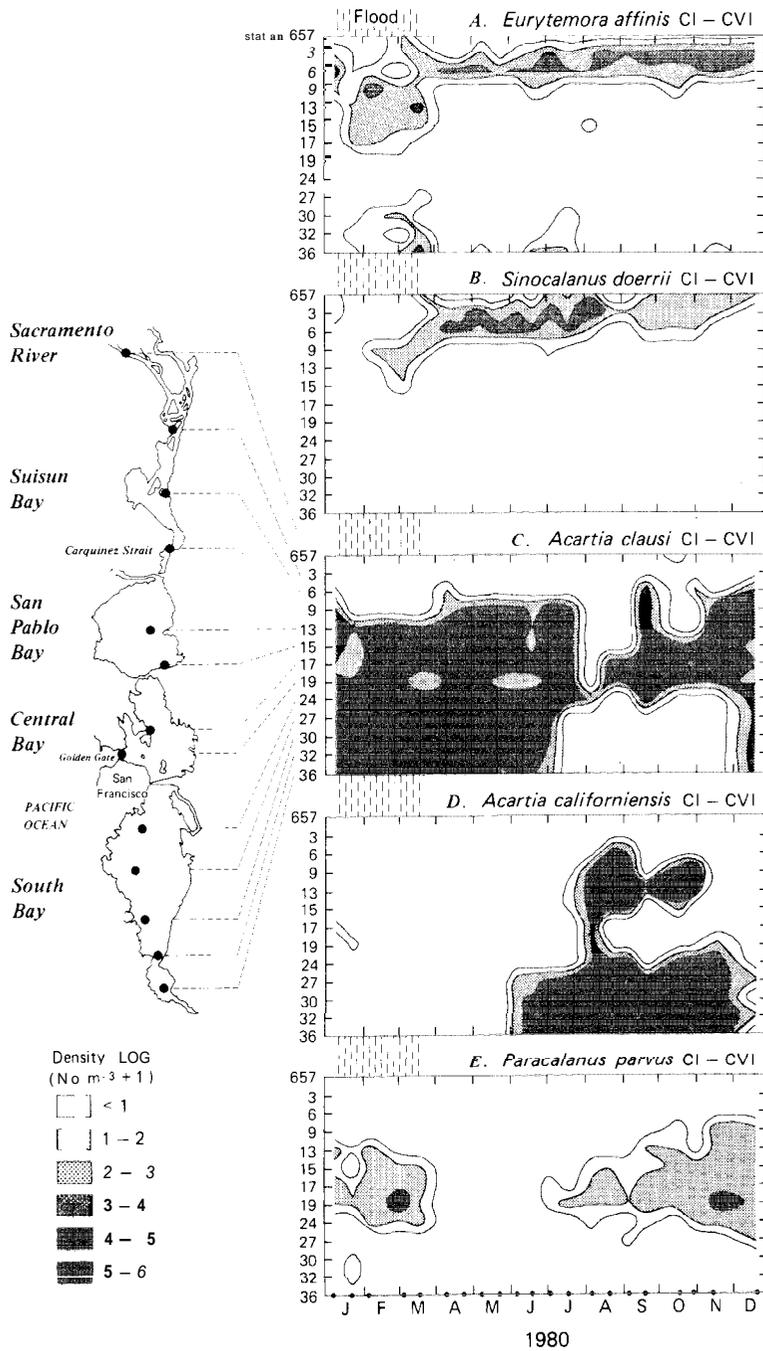


Fig. 4. Contoured densities along the channel of San Francisco Bay during 1980 for values integrated over the water column of the copepodites and adults (CI-CVI) of *Eurytemora affinis* (A), *Sinocalanus doerrii* (B), *Acartia clausi* (C), *Arartia californiensis* (D), and *Paracalanus parvus* (E). In (E), small dots along abscissa represent sample dates.

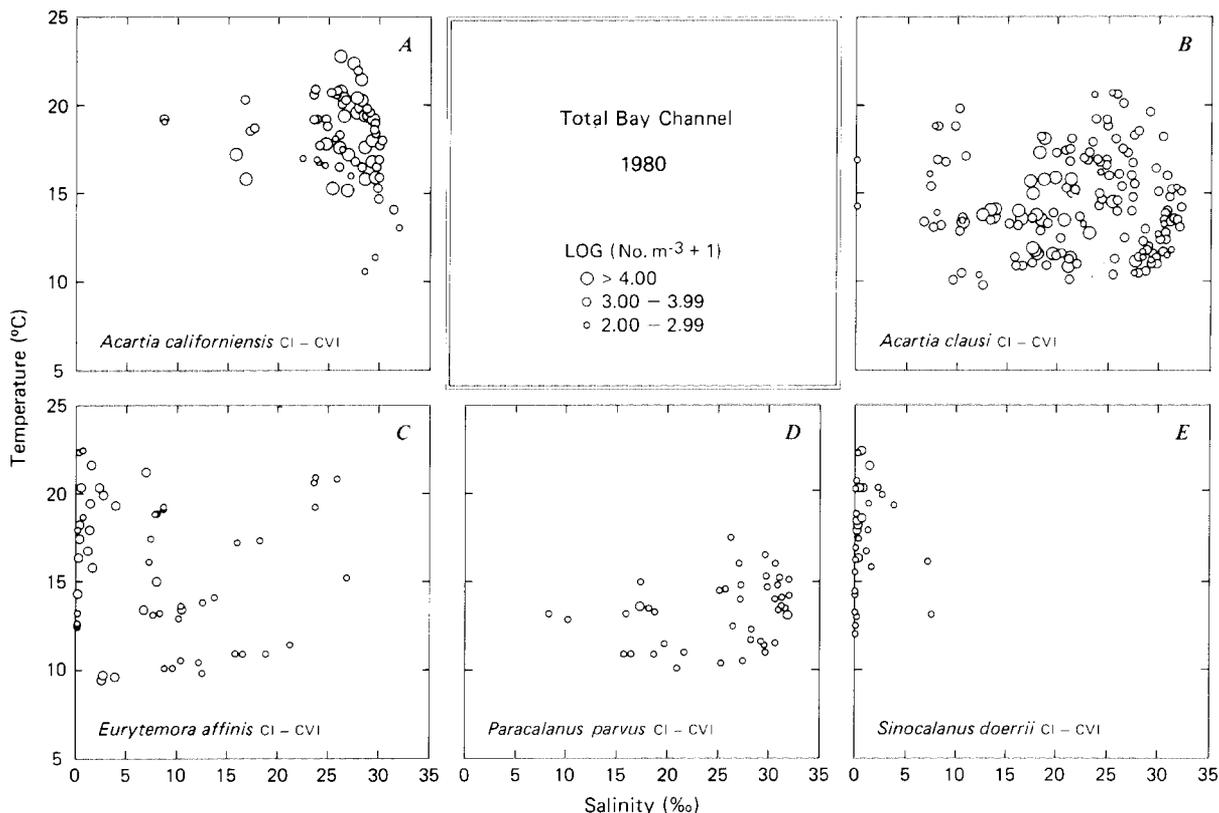


Fig. 5. Temperature-salinity plots for abundances (integrated over the water column) of the copepodites and adults (CI - CVI) of *Acartia californiensis* (A), *Acartia clausi* (B), *Eurytemora affinis* (C), *Paracalanus parvus* (D), and *Sinocalanus doerrii* (E). Abundances are from samples collected in 1980 along the entire San Francisco Bay.

in the northern reach had well defined boundaries, implying that a single population occupied Suisun Bay. *Eurytemora affinis* were not found at the Golden Gate station or in northern South Bay, although they occurred periodically in the southern part of South Bay (Fig. 4A). Perhaps a population of *E. affinis* inhabits the sloughs of lower South Bay and was sampled during peaks in local discharge or on low tides.

*Eurytemora affinis* was found in a wide range of temperatures (10–20°C) and salinities (0.5–30‰, Fig. 5C). Laboratory studies of *E. affinis* from the U.S. East coast have shown that successful reproduction occurs from 5–23.5°C and from 5–33‰ salinity (Katona, 1970). Although the San Francisco Bay *E. affinis* were within these limits, highest abundances usually occurred at salinities lower than 5‰ (Fig. 5C). Also, Roddie *et al.* (1984) have shown that highest survival rates of *E. affinis* adults

and copepodites occurred at salinities between 3 and 10‰. *Eurytemora affinis* can produce a benthic resting egg (Johnson, 1980a), but this stage was probably not present in San Francisco Bay because these eggs hatch at temperatures above 10°C. Hence, this copepod species, like *Sinocalanus doerrii*, persists throughout the annual cycle.

*Acartia species.* During 1980 the two *Acartia* species were the dominant copepods of San Francisco Bay where salinity exceeded 10‰. A seasonal replacement of *A. clausi* *s.l.* by *A. californiensis* was apparent, but the nature of this succession was different in the two estuaries (Figs. 4C, D). In the South Bay, *A. clausi* *s.l.* reached peak abundances ( $10^4$ – $10^5$   $m^{-3}$ ) from January through April and it was replaced by *A. californiensis* from July through November. In the northern reach, however, *A. clausi* *s.l.* was present almost year-round (a brief disappearance occurred in August and September)

and *A. californiensis* was present only from August to November. The two species had nearly non-overlapping distributions (compare Figs. 4C, D). The temperature-salinity plots (Figs. 5A, B) show that *A. californiensis* was most abundant when water temperature exceeded 15°C and salinity exceeded 25‰, reflecting its dominance during the dry-warm season. In contrast, *A. clausi s.l.* was most abundant during the wet-cold season and it occurred at temperatures less than 20°C and over a broad salinity range, 5–30‰ (Fig. 5B).

The mechanism of differential responses to temperature or salinity is presumed to be species-specific production or hatching of dormant eggs at different temperatures. For example, the dramatic disappearance of *A. clausi s.l.* in South Bay during summer is consistent with the observation by Uye & Fleminger (1976) who found that *A. clausi s.l.* eggs ceased hatching at temperatures greater than 17.5°C when salinity was less than 30‰. Further, Uye *et al.* (1979) reported decreased hatching (40%) at 25°C of *A. clausi* eggs collected from bottom sediments, and no hatching at 30°C (31–32‰ salinity). Therefore, *A. clausi s.l.* egg hatching probably stops at salinities lower than 30‰ and temperatures higher than at least 17.5°C. The summer appearance of *A. californiensis* presumably results from the hatching of diapause eggs laid by females the previous winter when temperature decreased below 15°C (Johnson, 1980a). The upstream penetration of *A. californiensis* is probably limited by decreased hatching success of its eggs at salinities below 10‰ (Uye & Fleminger, 1976; Johnson 1980a).

Note that *A. californiensis* did not reach maximum densities in San Francisco Bay until two months after the temperature exceeded 15°C, and that the population decreased rapidly when the temperature fell below 15°C (Figs. 2A, 4D). Conversely, *A. clausi s.l.* copepodites and adults disappeared about one month after the water temperatures exceeded 17.5°C in South Bay (Fig. 4C). The one exception to the temperature control of *Acartia* succession occurred in the northern reach where the *A. clausi s.l.* population persisted into fall, long after water temperature exceeded 17.5°C. This disparity may result from the coupling of neritic populations between the Golden Gate (where temperature was always cold enough to permit egg hatching) and the northern reach through estuarine circulation. Since *A. clausi s.l.* was always present

in the cooler, higher salinity waters of Central Bay (Tables 1 and 2), it is possible that eggs hatch in the Central Bay. Copepodites and adults, which are most abundant at depth, are then transported north into San Pablo Bay with the bottom currents (Conomos, 1979). Hence, maintenance of a nearly perennial *A. clausi s.l.* population in the northern reach may be a direct consequence of estuarine circulation. This conclusion is supported by evidence that residual currents are stronger in the northern reach than in the South Bay during summer (Walters *et al.*, 1985).

Both *Acartia* species were more abundant in the southern reach than in the northern reach (Figs. 4C, D). High abundances of *A. clausi s.l.* in South Bay during the wet season coincided with the spring blooms by phytoplankton and tintinnids, which would allow high copepod growth rates. In the northern reach *A. clausi s.l.* was present when advection due to river flow was maximal; perhaps then it was advected from the northern to the southern reach. The higher abundances of *A. californiensis* in South Bay than in San Pablo Bay probably resulted from longer periods of favorable temperatures for egg hatching and longer water residence times.

Predation by planktivorous fish may be more intense on *A. californiensis* than on *A. clausi s.l.* The northern anchovy, the numerically dominant fish in San Francisco Bay, was most abundant during the summer and fall in 1980; and Pacific herring, the second dominant, was most abundant during the spring and summer (Armor & Herrgesell, 1985). During the optimum season for growth of each species, *A. clausi s.l.* reached a higher average density ( $10.7 \times 10^3 \text{ m}^{-3}$  during the wet season) than *A. californiensis* ( $8.9 \times 10^3 \text{ m}^{-3}$  during the dry season, Table 3).

*Oceanic indicator species.* The oceanic influence in the Central Bay (stations 17 and 19) is indicated by lower temperatures, higher salinities, lower extinction coefficients and generally lower chlorophyll concentrations than are found in the rest of the bay (Fig. 2). During 1980 ten coastal copepod species were found in Central, San Pablo, and South Bays (Table 5). Copepod species with either southern or northern zoogeographic affinities were present. Higher frequencies of occurrence for coastal species were observed during the dry season (June–December) than during the wet season (January–

Table 5. Coastal copepod species found in San Francisco Bay during 1980, and their zoogeographic affinities.

<i>Acartia tonsa</i>	temperate-sub tropical <sup>4</sup>
<i>Calanus pacificus</i>	transitional <sup>1</sup>
<i>Calanus tenuicornis</i>	temperate-subtropical <sup>2</sup>
<i>Centropages abdominalis</i>	boreal-subarctic <sup>1</sup>
<i>Epilabidocera longipedata</i>	boreal-temperate <sup>1</sup>
<i>Meiridia pacifica</i>	boreal-temperate <sup>2</sup>
<i>Paracalanus parvus</i>	temperate-subtropical <sup>1</sup>
<i>Pseudocalanus</i> sp. <sup>3</sup>	temperate
<i>Tortanus discaudatus</i>	boreal-temperate <sup>1</sup>
<i>Oithona similis</i>	subarctic <sup>1</sup>

<sup>1</sup> Fleminger 1967.

<sup>2</sup> Brodsky 1950.

<sup>3</sup> Same species that was found in the Oregon upwelling zone by Peterson *et al.* (1979).

<sup>4</sup> Ferrari & Orsi 1984.

May), probably because of reduced seaward flow in the surface layer when river discharge was low. For both seasons, higher frequencies of occurrence were found in San Pablo Bay than in South Bay. The highest densities of *Paracalanus parvus* were also north of the Golden Gate station (Fig. 4E), which again may result from stronger residual landward currents in the northern reach. Only *P. parvus* copepodites and adults had frequencies of occurrence usually greater than 10% (Tables 1 and 2). *Paracalanus parvus* was absent in the bay during the upwelling season (April–June) when coastal currents are from the north. Only during the winter when coastal waters are of southern origin was *P. parvus* found in the bay.

### Microzooplankton

The rotifer *Synchaeta* sp. (probably *S. bicornis*; J. Orsi, pers. comm.), *Tintinnopsis* sp. A (length 190 µm), *Tintinnopsis* sp. B (length 70 µm), *Eutintinnus neriticus*, and *Acartia* spp. nauplii were the most abundant and frequently occurring microzooplankton species (Tables 1–3). The seasonal abundance distribution of *Acartia* nauplii paralleled that of the adults and copepodites. The rotifer and tintinnids were found in all the embayments but in decreased abundance in oligohaline areas such as Suisun Bay. Their seasonal distributions were distinct (Fig. 6), suggesting that populations of these species may be controlled by different mechanisms. *Tintinnopsis* sp. B was the most abundant and frequently occurring tintinnid, reaching densities  $>10^5$  m<sup>-3</sup>. Blooms of *Synchaeta* sp. and *Tintinnop-*

*sis* sp. B coincided with the beginning of the phytoplankton bloom in South Bay during March, but the bloom of *Tintinnopsis* sp. A occurred when the phytoplankton bloom was at its maximum in April (Figs. 2, 6B). Higher abundances of *Tintinnopsis* sp. A were found in Carquinez Strait from March to November. Seasonal distributions of the microzooplankton tended to be more discontinuous than those of copepods. These patchy distributions might result from the short generation times of tintinnids that allow populations to increase rapidly (Heinbokel, 1978a), as well as the production of dormant eggs (Gilbert, 1974; Reid & John, 1978).

Predation of *Tintinnopsis* sp. B by the larger *Tintinnopsis* sp. A and *Eutintinnus neriticus* probably does not happen because Heinbokel (1978b) found that tintinnids will ingest prey only up to 45% of their oral diameters. The diameter of *Tintinnopsis* sp. B is 50% of the oral diameter of *Tintinnopsis* sp. A (Hutchinson, 1981). The major predators of the San Francisco Bay tintinnids are probably adult *Acartia* spp. (Robertson, 1983), and possibly *Acartia* copepodites.

### Interannual variations

Estuaries are subjected to large interannual variations in physical forcings, including river discharge and meteorological events, that induce interannual variability in biological processes and communities. For example, within San Francisco Bay, interannual variability of phytoplankton dynamics (Cloern *et al.*, 1985), shrimp abundance (Hatfield, 1985), fish populations (Armor & Herrgesell, 1985), and benthic infauna (Nichols & Thompson, 1985) is driven in part by interannual variations in freshwater inflow. Long-term records of zooplankton abundance are not available for San Francisco Bay, but the collections made over two annual cycles (1979, 1980) in San Pablo Bay and over 3.5 years in South Bay can be used to determine whether the seasonal variations observed during 1980 were unique to that year, or whether they represent persistent features that characterize a typical annual cycle. During this study period, mean annual freshwater inflow ranged from 450 m<sup>3</sup> s<sup>-1</sup> during 1981 (a dry year) to 1070 m<sup>3</sup> s<sup>-1</sup> during 1980 (a wet year).

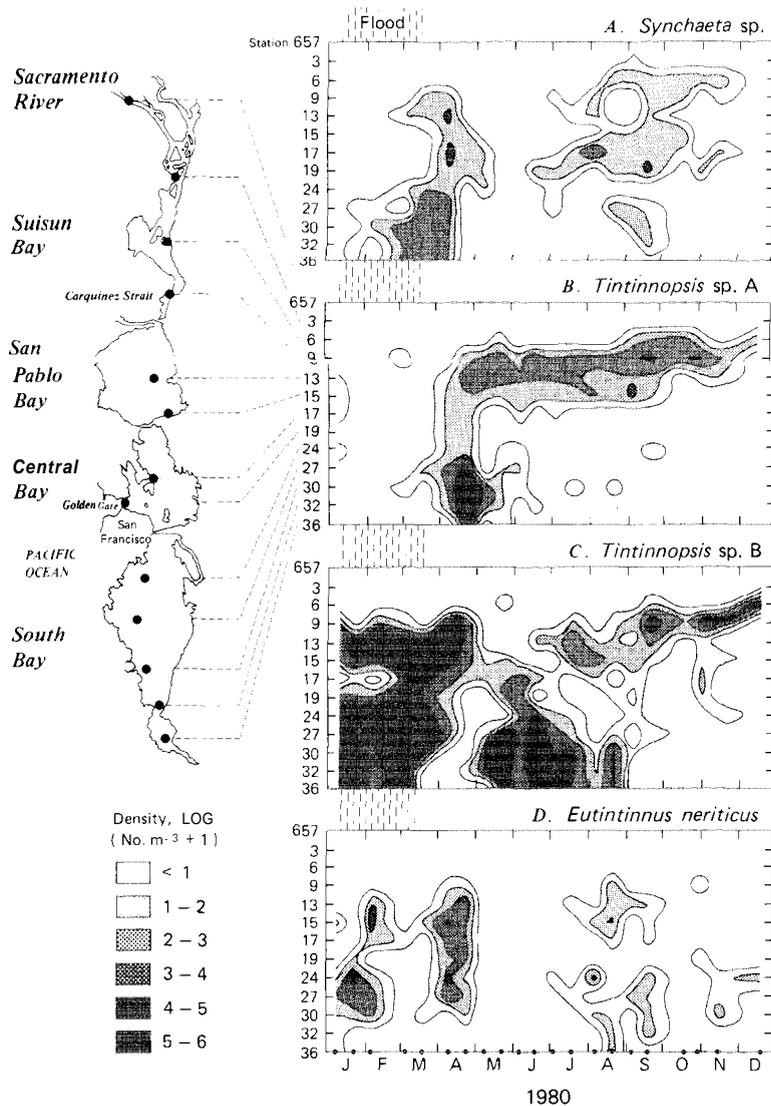


Fig. 6. Contoured densities along the channel of San Francisco Bay during 1980 for values integrated over the water column of *Synchaeta* sp. (A), *Tintinnopsis* sp. A (B), *Tintinnopsis* sp. B (C), and *Eutintinnus neriticus* (D). In (D), small dots along abscissa represent sampling dates.

### Acartia species

From 1978 to 1981, the two *Acartia* species exhibited a seasonal periodicity in South Bay, and the succession between *A. clausi* s.l. and *A. californiensis* observed there in 1980 appears to be a regular feature in this estuary (Fig. 7A). Moreover, the timing of this succession varied only slightly between years (Table 6), and the maximum annual abundance of these copepods was fairly constant among years at  $\geq 10^4$  m<sup>-3</sup>. As observed in 1980, *A. clausi* s.l. consistently reached higher abundances

in spring than *A. californiensis* in summer. The two-year record for San Pablo Bay (Fig. 8A) confirms that *A. clausi* s.l. is nearly a perennial species there, and that the short-term appearance of *A. californiensis* in summer may also be a regular feature. As in 1980, both *Acartia* species were more abundant in South Bay than San Pablo Bay during 1979. These general conclusions regarding seasonal abundance and distribution of *Acartia* also hold for the earlier (1972–1974) annual studies of Caskey (1976), indicating that population dynamics of *Acartia* could be fairly stable from year to year.

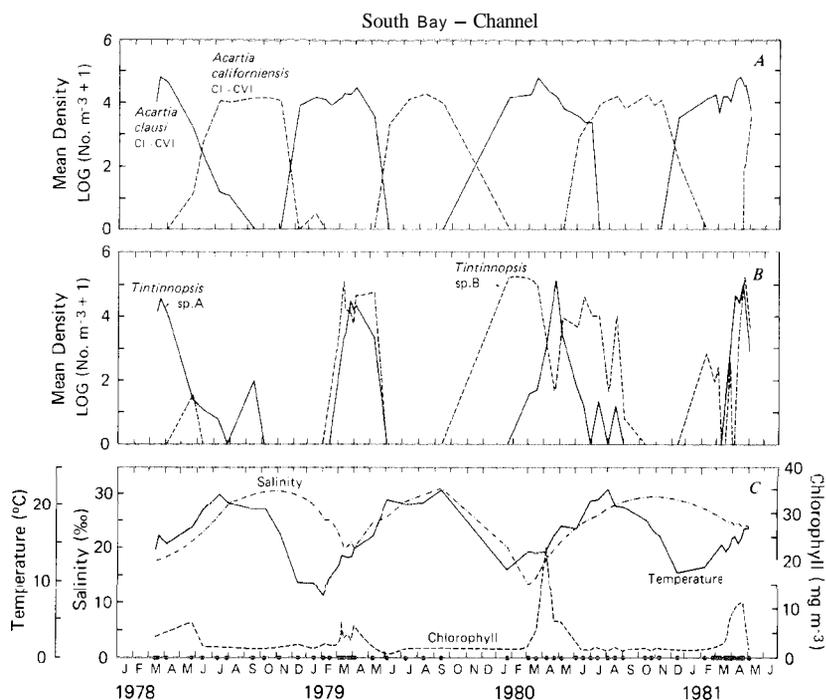


Fig. 7. Annual comparisons of average densities (integrated over the water column) of *Acartia* species (A), tintinnid species (B), and the ancillary data (C) for the channel of South San Francisco Bay from 1978 to 1981. For 1981, data are only from Station 30.

Table 6. First appearance and first disappearance of *Acartia* species in South Bay (Channel Stations 27, 30, and 32) and San Pablo Bay (Channel Stations 13 and 15). T = temperature ( $^{\circ}\text{C}$ ), S = salinity ( $\text{‰}$ ).

*Acartia clausi*

	Appearance			Disappearance		
	Date	T	S	Date	T	S
South Bay	Dec. 78	9.7	29.7	July 78	21.4	25.6 Copepodites
	Jan. 80 <sup>1</sup>	11.5	20.2	Sept. 78	19.3	29.6 Adults
	Dec. 80	11.1	29.1	June 79	20.6	25.6
				June 80	20.6	26.0
San Pablo Bay	Sept. 79	19.7	27.9	June 79	17.8	22.6
	Sept. 80	17.4	26.6	Aug. 80	18.8	24.8

*Acartia californiensis*

South Bay	May 78	17.0	20.9 Adults	Dec. 78	9.7	29.7
	June 78	19.4	23.1 Copepodites	Feb. 79	11.8	26.9
	June 79	20.6	25.6	Jan. 80 <sup>1</sup>	11.5	20.2
	June 80	16.8	24.1	Feb. 81 <sup>2</sup>	11.8	26.9
	May 81	16.9	24.0	no data	-	-
San Pablo Bay	June 79	17.8	22.6	Jan. 80 <sup>3</sup>	10.9	21.3
	July 80	18.0	22.3	Nov. 80	14.3	26.2

<sup>1</sup> No sampling in December

<sup>2</sup> No sampling in January

<sup>3</sup> No sampling October–December in 1979

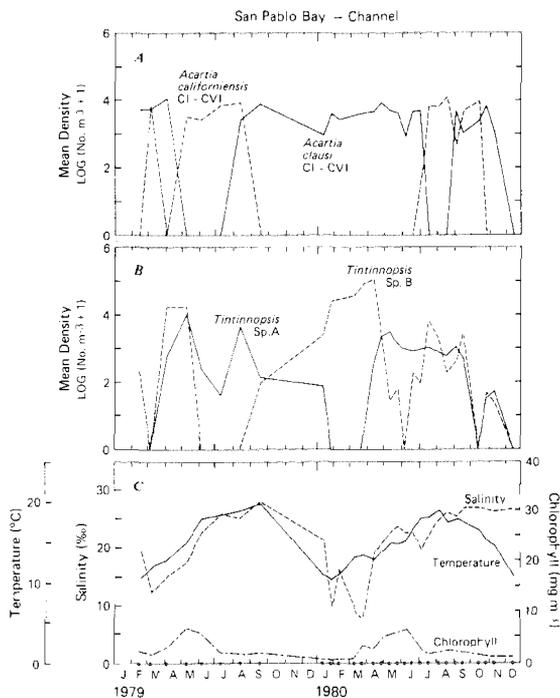


Fig. 8. Annual comparisons of average concentrations (integrated over the water column) of *Acartia* species (A), tintinnid species (B), and the ancillary data (C) for the channel of San Pablo Bay during 1979 and 1980.

Given the large interannual variability of river discharge and biota, the stability of *Acartia* periodicity in South and San Pablo Bays is surprising. For example, the annual minimum salinity in South Bay ranged from 15‰ during 1980 to 25‰ during 1981. Phytoplankton biomass and annual primary productivity in South Bay were also very different during 1978–1981. The spring bloom was of short duration during 1981 when annual primary productivity was estimated to be only  $100 \text{ g C m}^{-2}$ , compared to 1980 when the magnitude and duration of the spring bloom were enhanced (Fig. 7C) and primary productivity was  $150 \text{ g C m}^{-2}$  (Cloern, 1985). During this 3.5 year period there was no strong relationship between population dynamics of the *Acartia* species and the timing or magnitude of phytoplankton blooms, although *A. clausi* s.l. generally had maximum abundance during the spring blooms. These observations support our hypothesis that the succession of *Acartia* species in South Bay results primarily from the annual perio-

dicity of water temperature: *A. clausi* s.l. first appears in December or January when temperature drops to about  $10^\circ\text{C}$ , and it disappears in June or July when temperature warms to about  $20^\circ\text{C}$  (Table 6). Conversely, *A. californiensis* first appears in May or June and disappears in December.

### Tintinnids

The annual variations of microzooplankton abundance in both South and San Pablo Bays were much more erratic than those of the copepods (Figs. 7B, 8B). *Tintinnopsis* sp. A did reach annual maximum abundance at the same time each year in South Bay, coinciding with the timing of the phytoplankton bloom in April. However, maximum abundance was constant among years (about  $10^5 \text{ m}^{-3}$ ), and it is not clear whether this population responded directly to increased food availability during the bloom or to other features such as increased water column stability and density stratification that also occur in spring (Cloern, 1984). The other *Tintinnopsis* species had more random occurrences and was highly variable among years (Fig. 7B). In San Pablo Bay the tintinnids were almost always present, but there were no obvious relations between abundance and either food availability or physical properties of the estuary (Fig. 8B). We observed highest abundances of tintinnids in the shoals of San Pablo Bay. If this habitat represents a source of high productivity by ciliates, then populations observed in the channel may be highly influenced by the rate of lateral exchange between water masses of the channel and shoals. Given the high potential growth rates of tintinnid populations and the erratic occurrence patterns observed, we can speculate that the nature and causes of temporal variability in these populations will not become apparent until sampling is done with sufficient frequency to document discrete changes in population growth (i.e., almost daily).

### The seasonal cycle: Comparison with other estuaries

The seasonal succession of *Acartia* species observed in San Pablo and South Bays is analogous to that observed in East coast estuaries from Massachusetts to New York (Deevey, 1948, 1956; Conov-

er, 1956; Jeffries, 1962c; Hulsizer, 1976). In all cases, a form of *A. clausi* is the dominant winter-spring species and *A. tonsa* or *A. californiensis* are dominant during the summer and fall. These seasonal patterns are chiefly a function of temperature mediated through the production and hatching of diapause eggs of *A. tonsa* and *A. californiensis*, and an unknown type of dormant egg by *A. clausiformis* (Grice & Marcus, 1981). The first known change from this pattern north of San Francisco Bay is at Yaquina Bay, Oregon where *A. clausi s.l.* occurs year-round and *A. californiensis* occurs seasonally in the summer and fall (Miller, 1983). This seasonal cycle is analogous to that reported for a Maine estuary by Lee & McAlice (1979).

The only seasonal zooplankton study south of San Francisco Bay is Pace's (1978) study of Elkhorn Slough, California where three *Acartia* species occur year-round. *Acartia tonsa* and *Acartia californiensis* were the dominant species and *Acartia clausi s.l.* occurred in lower densities. *Acartia californiensis* was most abundant in the upper reaches of Elkhorn Slough during the summer and fall. *Acartia tonsa* and *A. clausi s.l.* were found throughout Elkhorn Slough but were more abundant at the seaward end. Thus, on the U.S. West coast, *A. clausi s.l.* has been reported the most frequently occurring and abundant *Acartia* species in estuaries from Washington to San Francisco Bay (Landry, 1978; Johnson, 1980b; Miller, 1983, present study), but *A. californiensis* and *A. tonsa* become dominant in estuaries south of San Francisco (Trinast 1976; Pace, 1978).

One *Eurytemora* species, *E. affinis*, occurs year-round at densities ranging from  $10^2$ – $10^3$   $m^{-3}$  in the oligohaline waters of San Francisco Bay. During the winter floods of 1980, *E. affinis* was advected as far downstream as San Pablo Bay, but most of the year this species was found in the mixing zone located in Suisun Bay. *Eurytemora* species are usually located in the mixing zone of estuaries, although the mechanism for their maintenance there has not been well studied (Arthur & Ball, 1979; Miller, 1983; Roddie *et al.*, 1984). Densities of *E. affinis* are higher in the Columbia River estuary where this is the dominant copepod species year-round (Haertel *et al.*, 1969; Jones & Bottom, 1984). Densities there typically were between  $10^3$ – $10^4$   $m^{-3}$ , except when the population reached peak densities up to  $10^5$   $m^{-3}$  during late spring. Low abundances in

the Columbia River estuary were associated with the two maxima in river flow. In East coast estuaries, *E. affinis* has a seasonal peak in abundance during the winter and spring, and is absent or present in very low numbers during the rest of the year (Jeffries, 1967; Herman *et al.*, 1968; Heinle & Flemer, 1975).

Since its introduction in 1978, *Sinocalanus doerrii* has become the dominant freshwater copepod species in San Francisco Bay, ranging in density from  $10^2$ – $10^3$   $m^{-3}$ . Its distribution appears to oscillate between Suisun Bay and the rivers depending upon river flow (Orsi *et al.*, 1983). Before its introduction, *Diaptomus* spp. and *Cyclops* sp. were the dominant copepod species but never very abundant, usually found at densities  $<10^2$   $m^{-3}$  and  $<10^3$   $m^{-3}$ , respectively. Orsi *et al.* (1983) suggested that *S. doerrii* probably competes with these species rather than with the brackish species *E. affinis*, since the population maximum of *S. doerrii* is upstream of that of *E. affinis*. The fact that blooms of neritic diatoms typically occur in Suisun Bay during years with average river discharge (Cloern *et al.*, 1983) suggests that competition for food may not exist. Other factors probably determine the dominance of *S. doerrii* in freshwater.

The major occurrence of *Synchaeta* sp. in San Francisco Bay was a short six-week population explosion (maximum  $10^4$   $m^{-3}$ ) in South Bay coinciding with the spring phytoplankton bloom. Similar population explosions have been reported for *Synchaeta* species in other estuaries and coastal areas (Hollowday, 1949; Eriksson *et al.*, 1977; Hernroth, 1983). Hernroth (1983) attributed the rapid population increase to parthenogenetic growth and the rapid decline to competition for food from other grazers such as larval copepods. An alternative explanation for the rapid decline and disappearance is the formation of resting eggs, perhaps in response to population density (Gilbert, 1974). Rotifers in Narragansett Bay were present and abundant for a longer period, from January to May (Hulsizer, 1976). *Synchaeta littoralis*, the most abundant rotifer in Tisbury Great Pond, made erratic appearances throughout the year and reached peak densities of  $10^5$   $m^{-3}$  (Deevey, 1948).

As in our study, densities of tintinnid species varied greatly spatially and temporally in a seasonal study of Narragansett Bay (Hargraves, 1981). Different species of *Tintinnopsis* were dominant dur-

ing different seasons, but their densities were not obviously correlated with chlorophyll concentrations. In San Francisco Bay, no correlations between chlorophyll concentration and densities of *Tintinnopsis* sp. B or *Eutintinnus neriticus* were observed. Densities of *Tintinnopsis* sp. A, however, were strongly correlated with phytoplankton blooms in South Bay and San Pablo Bay shoals. The factors affecting the seasonal distributions of tintinnids probably occur at much shorter time intervals than were sampled in both of these studies.

Although tintinnid densities in San Francisco Bay were impressive (up to  $10^6 \text{ m}^{-3}$ ), our sampling technique missed other protozoan taxa that can be more abundant than the tintinnids. In a comparison of methods, Smetacek (1981) demonstrated that water samples concentrated with nets yielded much less ciliate biomass ( $<20 \text{ mg m}^{-2}$ ) than unconcentrated water samples (usually  $>100 \text{ mg m}^{-2}$ , and up to  $600 \text{ mg m}^{-2}$ ). Nonloricate ciliates of all sizes were not adequately sampled by nets even with mesh as small as  $20 \mu\text{m}$ . These nonloricate ciliates were numerically more important than the tintinnids, a result also seen for coastal waters off southern California (Beers & Stewart, 1970), Chesapeake Bay (Berk *et al.*, 1977), and the Bothnian Sea off Sweden (Eriksson *et al.*, 1977).

Microzooplankton are considered an important link between nanoplankton and larger grazers such as adult copepods because the microzooplankton may more efficiently consume the smaller cells than adult copepods, that can prey on ciliates (Berk *et al.*, 1977; Hernroth, 1983; Robertson, 1983). This situation might apply to the plankton of South San Francisco Bay because nanoplankton always dominated even during the spring bloom. Although the total microzooplankton biomass is unknown in San Francisco Bay, the smaller phytoplankton provided much more carbon biomass (100 to 1000 times) than either tintinnids or rotifers (Table 4). If zero values were included, the average microzooplankton biomass would be even less. Although differences in food selection of nanoplankton and ciliates by copepods have not been studied, nanoplankton may be a major food item due to their high relative abundance. In the Bothnian Sea off Sweden, phytoplankton carbon was also much higher (10 to 100 times) than the microzooplankton composed mainly of rotifers and nonloricate ciliates (Eriksson *et al.*, 1977).

## Summary

1. In San Francisco bay, copepods and mero-plankton dominated zooplankton carbon biomass, but *Tintinnopsis* spp. were the most numerous taxa.

2. Copepod species were aligned along the salinity gradient in the northern reach: *Sinocalanus doerrii* in the Sacramento-San Joaquin Rivers, *Eurytemora affinis* in Suisun Bay, *Acartia* spp. in San Pablo Bay, and *Paracalanusparvus* in Central Bay. Winter peaks in river discharge advected *S. doerrii* and *E. affinis* from Suisun Bay into San Pablo Bay showing that river flow is an important mechanism of temporal variation in the distribution of estuarine zooplankton.

3. Zooplankton species composition changed between the cold wet season when *A. clausi s.l.* and *Tintinnopsis* spp. were dominant, and the warm dry season when *A. californiensis* and veligers were dominant. Carbon biomass was higher in the southern than the northern reach during the wet season. During the dry season, carbon biomass was similar between reaches, except for the high values found in the San Pablo Bay shoals.

4. Seasonal succession patterns of *Acartia* spp. were different between the reaches. In South Bay, *A. clausi s.l.* was present during the wet season and *A. californiensis* during the dry season. In San Pablo Bay, *A. clausi s.l.* was present most of the year except for August and September, and *A. californiensis* was present only briefly from August to October. The two species did not often co-occur. Warmer temperatures in South Bay than in San Pablo Bay affecting production and hatching of dormant eggs may explain some of the observed differences.

5. Both *Acartia* species reached maximum densities in South Bay rather than San Pablo Bay. *Acartia clausi s.l.* attained higher densities during the wet season when the phytoplankton bloomed than *A. californiensis* during the dry season when planktivorous fish were most abundant and chlorophyll concentrations were minimal.

6. Neritic copepods were observed most frequently in Central Bay, and they occurred more frequently in the northern than the southern reach consistent with observations that oceanic bottom currents flow north (Walters *et al.*, 1985). Although *Oithona similis* was often found at the Golden Gate

station, *Paracalanus parvus* was the only neritic copepod frequently found in both Central and San Pablo Bays. *Paracalanus parvus*, a warm water species, was absent from San Francisco Bay during the spring upwelling season when coastal waters of northern origin enter the bay.

7. Seasonal patterns of microzooplankton were much more patchy in time and space than the mesozooplankton. The dominant microzooplankton species had different seasonal patterns, suggesting that different mechanisms control their dynamics. Maximum abundances were usually associated with phytoplankton blooms.

8. Seasonal patterns observed in the channels of San Francisco Bay during 1980 were also observed during 1978–1981 in South Bay and 1979–1980 in San Pablo Bay.

9. Zooplankton composition during the two major seasons and seasonal cycles in the shoals were similar to those in the channel of the same embayment. However, taxa usually did not occur as frequently in the shoals as in the channels; this probably results from some taxa preferentially occurring at depth in the channel.

10. Introductions of exotic species of plankton can be an important mechanism of long-term variation in estuarine zooplankton communities, and this appears to have occurred in the upper reaches of San Francisco Bay with the introduction of *Sinocalanus doerrii*.

## References

- Ambler, J. W., 1985. Seasonal factors affecting egg production and viability of eggs of *Acartia tonsa* in East Lagoon, Galveston. Texas. Estuar. coast. shelf. Sci. In press.
- Armor, C. & P. L. Herrgesell. 1985. Flow-related variation in San Francisco Bay fish communities: 1980–1982. Hydrobiologia (this volume).
- Arthur, J. F. & M. D. Ball. 1979. Factors influencing the entrapment of suspended material in the San Francisco Bay-Delta estuary. In T. J. Conomos (ed.), San Francisco Bay, the urbanized estuary. Pac. Div. Am. Assoc. Adv. Sci., San Francisco: 143–174.
- Barlow, J. P., 1955. Physical and biological processes determining the distribution of zooplankton in a tidal estuary. Biol. Bull. 109: 211–225.
- Beers, J. R. & G. L. Stewart, 1970. Numerical abundance and estimated biomass of microzooplankton. In J. D. H. Strickland (ed.), The ecology of the plankton of La Jolla, California, in the period April through September. 1967. Bull. Scripps Insti. Oceanogr. (New Ser.) 17: 67–87.
- Berk, S. G., D. C. Brownlee, D. R. Heinle, H. J. Kling & R. R. Colwell, 1977. Ciliates as a food source for marine planktonic copepods. Microb. Ecol. 4: 27–40.
- Bradford, J. M., 1976. Partial revision of the *Acartia* subgenus *Acartiura* (Copepoda: Calanoida: Acartiidae). N.Z. J. mar. freshwater Res. 10: 159–202.
- Brodsky, K. A., 1950. Calanoida of the far eastern seas and polar basin of the U.S.S.R. (trans. from Russian by A. Mercado, Israel Program for Scientific Translations, Jerusalem. 1967). Opred. Faune U.S.S.R. 35, 441 pp.
- Caskey, P. S., 1976. Spatial and temporal aspects of the zooplankton distribution in San Francisco Bay. Hayward, California State Univ., M.S. Thesis, 89 pp.
- Cloern, J. E., 1984. Temporal dynamics and ecological significance of salinity stratification in an estuary (South San Francisco Bay, U.S.A.). Oceanol. Acta. 7: 137–141.
- Cloern, J. E., 1985. Empirical models of water column stability and phytoplankton dynamics in an estuary. Submitted.
- Cloern, J. E., A. E. Alpine, B. E. Cole, R. L. J. Wong, J. F. Arthur & M. D. Ball, 1983. River discharge controls phytoplankton dynamics in the northern San Francisco Bay estuary. Estuar. coast. shelf. Sci. 16: 415–429.
- Cloern, J. E., B. E. Cole, R. L. J. Wong & A. E. Alpine. 1985. Temporal dynamics of estuarine phytoplankton: A case study of San Francisco Bay. Hydrobiologia (this volume).
- Conomos, T. J., 1979. Properties and circulation of San Francisco Bay waters. In T. J. Conomos (ed.), San Francisco Bay, the urbanized estuary. Pac. Div. am. Assoc. Adv. Sci., San Francisco: 47–84.
- Conover, R. J., 1956. Oceanography of Long Island Sound, 1952–1954. 6. Biology of *Acartia clausi* and *A. tonsa*. Bull. Bingham Oceanogr. Coll. 15: 156–233.
- Cronin, L. E., J. C. Daiber & E. M. Hulbert, 1962. Quantitative seasonal aspects of zooplankton in the Delaware River estuary. Ches. Sci. 3: 63–93.
- Deason, E. E. & T. J. Smayda. 1982. Ctenophore-zooplankton interactions in Narragansett Bay, Rhode Island, USA, during 1972–1977. J. Plankton Res. 4: 203–218.
- Deevey, G. B., 1948. The zooplankton of Tisbury Great Pond. Bull. Bingham Oceanogr. Coll. 12: 1–44.
- Deevey, G. B., 1956. Oceanography of Long Island Sound, 1952–1954. V. Zooplankton. Bull. Bingham Oceanogr. Coll. 15: 113–155.
- Deevey, G. B., 1960. The zooplankton of the surface waters of the Delaware Bay region. Bull. Bingham Oceanogr. Coll. 17: 5–53.
- Durbin, E. G., A. G. Durbin, T. J. Smayda & P. G. Verity, 1983. Food limitation of production by adult *Acartia tonsa* in Narragansett Bay, Rhode Island. Limnol. Oceanogr. 28: 1199–1213.
- Eriksson, S., L. Sellei & K. Wallstrom, 1977. The structure of the plankton community of the Oregrundsgrepen (southwest Bothnian Sea). Helgolander wiss. Meeresunters 30: 582–597.
- Ferrari, F. D. & J. J. Orsi, 1984. *Oithona davisae*, new species, and *Limnoithona sinensis* (Burckhardt, 1912) (Copepoda: Oithonidae) from the Sacramento–San Joaquin Estuary. California. J. crust. Biol. 4: 106–126.
- Fleminger, A., 1967. Distribution atlas of calanoid copepods in the California Current region. Part 2. Calif. coop. ocean. fish. Invest. Atlas 7. 213 pp.

- Frolander, H. F., C. B. Miller, J. J. Flynn, S. C. Meyers & S. T. Zimmerman. 1973. Seasonal cycles of abundance in zooplankton populations of Yaquina Bay, Oregon. *Mar. Biol.* 21: 277-288.
- Gilbert, J. J.. 1974. Dormancy in rotifers. *Trans. Amer. Micros. Soc.* 93: 490-513.
- Grice, G. D. & N. H. Marcus, 1981. Dormant eggs of marine copepods. *Oceanogr. mar. Biol. Ann. Rev.* 19: 125-140.
- Haertel, L. & C. Osterberg. 1967. Ecology of zooplankton, benthos, and fishes of the Columbia River estuary. *Ecology* 48: 459-472.
- Haertel, L., C. Osterberg, H. Curl, Jr. & P. K. Park, 1969. Nutrient and plankton ecology of the Columbia River estuary. *Ecology* 50: 962-978.
- Hargraves, P. E., 1981. Seasonal variations of tintinnids (Ciliophore: Oligotrichidae) in Narragansett Bay, Rhode Island, U.S.A. *J. Plankton Res.* 3: 81-91.
- Hatfield, S., 1985. Seasonal and interannual variation in the distribution and abundance of the shrimp *Crangon franciscorum* in San Francisco Bay. *Hydrobiologia* (this volume).
- Heinbokel, J. F., 1978a. Studies on the functional role of tintinnids in the Southern California Bight. I. Grazing and growth rates in laboratory cultures. *Mar. Biol.* 47: 177-189.
- Heinbokel, J. F., 1978b. Studies on the functional role of tintinnids in the Southern California Bight. 2. Grazing rates of field populations. *Mar. Biol.* 47: 191-197.
- Heinle, D. R. & D. A. Flemer. 1975. Carbon requirements of a population of the estuarine copepod *Eurytemora affinis*. *Mar. Biol.* 31: 235-247.
- Heinle, D. R., R. P. Harris, J. F. Ustach & D. A. Flemer, 1977. Detritus as food for copepods. *Mar. Biol.* 40: 341-353.
- Herman, S. S., J. A. Mihursky & A. J. McErlean, 1968. Zooplankton and environmental characteristics of the Patuxent River estuary. *Ches. Sci.* 9: 67-82.
- Hernroth, L., 1983. Marine pelagic rotifers and tintinnids - important trophic links in the spring plankton community of the Gullmar Fjord, Sweden. *J. Plankton Res.* 5: 835-846.
- Hollowday, E. D., 1949. A preliminary report on the Plymouth marine and brackish-water rotifera. *J. mar. biol. Assoc. U.K.* 28: 239-253.
- Hulsizer, E. E., 1976. Zooplankton of lower Narragansett Bay. 1972-1973. *Ches. Sci.* 17: 260-270.
- Hutchinson, A., 1981. Plankton studies in San Francisco Bay. 3. Zooplankton species composition and abundance in the South Bay, 1978-1979. U.S. Geological Survey, Open-File Report 81-132. 107 pp.
- Hutchinson, A., 1982a. Plankton studies in San Francisco Bay. 5. Zooplankton species composition and abundance in the South Bay, 1980-1981. U.S. Geological Survey, Open-File Report 82-1002. 135 pp.
- Hutchinson, A., 1982b. Plankton studies in San Francisco Bay. 6. Zooplankton species composition and abundance in the North Bay, 1979-1980. U.S. Geological Survey, Open-File Report 82-1003. 185 pp.
- Jeffries, H. P., 1962a. Copepod indicator species in estuaries. *Ecology* 43: 730-733.
- Jeffries, H. P., 1962b. Salinity-space distribution of the estuarine copepod genus *Eurytemora*. *Int. Revue ges. Hydrobiol.* 47: 291-300.
- Jeffries, H. P., 1962c. Succession of two *Acartia* species in estuaries. *Limnol. Oceanogr.* 7: 354-364.
- Jeffries, H. P., 1967. Saturation of estuarine zooplankton by congeneric associates. In G. H. Lauff (ed.), *Estuaries*. *Publ. am. Assoc. Adv. Sci.* 83: 500-508.
- Johnson, J. K., 1980a. Effects of temperature and salinity on production and hatching of dormant eggs of *Acartia californiensis* (Copepoda) in an Oregon estuary. *Fish. Bull. U.S.A.* 77: 567-584.
- Johnson, J. K., 1980b. Population dynamics and cohort persistence of *Acartia californiensis* (Copepoda: Calanoida) in Yaquina Bay, Oregon. Ph.D. dissertation. Oregon State University, 305 pp.
- Jones, K. & D. Bottom, 1984. Zooplankton and larval fishes of the Columbia River Estuary. Final Report to Columbia River Estuary Data Development Program, POB 175. Astoria, Oregon 97103.
- Katona, S. K., 1970. Growth characteristics of the copepods *Eurytemora affinis* and *E. hermoni* in laboratory cultures. *Helgolander wiss. Meeresunters.* 20: 373-384.
- Ketchum, B., 1954. Relation between circulation and plankton populations in estuaries. *Ecology* 35: 191-200.
- Kremer, P., 1979. Predation by the ctenophore *Mnemiopsis leidyi* in Narragansett Bay, Rhode Island. *Estuaries* 2: 97-105.
- Landry, M. R., 1978. Population dynamics and production of a planktonic marine copepod, *Acartia clausi*, in a small temperate lagoon on San Juan Island. Washington. *Int. Revue ges. Hydrobiol.* 63: 77-119.
- Lee, W. Y. & B. J. McAlice, 1979. Seasonal succession and breeding cycles of three species of *Acartia* (Copepoda: Calanoida) in a Maine estuary. *Estuaries* 2: 228-235.
- Miller, C. B., 1983. The zooplankton of estuaries. In B. H. Ketchum (ed.), *Ecosystems of the world* 26, Estuaries and enclosed seas. Elsevier Sci. Pub. Co.: 103-149.
- Nichols, F. H. & J. K. Thompson, 1985. Time scales of change in the San Francisco Bay benthos. *Hydrobiologia* (this volume).
- Onbé, T., 1978. The life cycle of marine cladocerans. *Bull. Plankton Soc. Japan* 25: 41-54.
- Orsi, J. J., T. E. Bowman, D. C. Marelli & A. Hutchinson. 1983. Recent introduction of the planktonic calanoid copepod *Sinocalanus doerrii* (Centropagidae) from mainland China to the Sacramento-San Joaquin estuary of California. *J. Plankton Res.* 5: 357-375.
- Pace, S. D., 1978. Distribution, abundance and rates of fecundity and growth of *Acartia tonsa* Dana and *Acartia californiensis* Trinast (Copepoda) in Elkhorn Slough, California. M.S. Thesis. San Jose State University. Calif., 113 pp.
- Paranjape, M. A., 1980. Occurrence and significance of resting cysts in a hyaline tintinnid. *Helicosromella subulata* (Ehre.) Jorgensen. *J. exp. mar. Biol. Ecol.* 48: 23-34.
- Peterson, D. H., T. J. Conomos, W. W. Broenkow & P. C. Doherty, 1975. Location of the non-tidal current null zone in northern San Francisco Bay. *Estuar. coast. mar. Sci.* 3: 1-11.
- Peterson, D. H., R. E. Smith, S. W. Hager, D. D. Harmon, R. Herndon & L. E. Schemel, 1985. Interannual variability in dissolved inorganic nutrients in northern San Francisco Bay. *Hydrobiologia* (this volume).

- Peterson, W. T., C. B. Miller & A. Hutchinson, 1979. Zonation and maintenance of copepod populations in the Oregon upwelling zone. *Deep Sea Res.* 26A: 467-494.
- Poulet, S. A., 1976. Feeding of *Pseudocalanus minutus* on living and nonliving particles, *Mar. Biol.* 34: 117-125.
- Reid, P. C. & A. W. G. John, 1978. Tintinnid cysts. *J. mar. biol. Ass. U.K.* 58: 551-557.
- Reid, T., 1981. Computer graphics software for the Amdahl, second edition. Data Processing Center, Texas A&M University, College Station, Texas.
- Robertson, J. R., 1983. Predation by estuarine zooplankton on tintinnid ciliates. *Estuar. coast. shelf Sci.* 16: 27-36.
- Roddie, B. D., R. J. G. Leakey & A. J. Berry, 1984. Salinity-temperature tolerance and osmoregulation in *Eurytemora affinis* (Poppe) (Copepoda: Calanoidea) in relation to its distribution in the zooplankton of the upper reaches of the Forth Estuary. *J. exp. mar. Biol. Ecol.* 79: 191-211.
- Sage, L. E. & S. S. Herman, 1972. Zooplankton of the Sandy Hook Bay area. *N.J. Ches. Sci.* 13: 29-39.
- Smayda, T. J., 1983. The phytoplankton of estuaries. In B. H. Ketchum (ed.), *Ecosystems of the world* 26. Estuaries and enclosed seas. Elsevier Sci. Pub. Co.: 65-102
- Smetacek, V., 1981. The annual cycle of protozooplankton in the Kiel Bight. *Mar. Biol.* 63: 1-11.
- Tranter, D. J. & S. Abraham, 1971. Coexistence of species of Acartiidae (Copepoda) in the Cochin Backwater, a monsoonal estuarine lagoon. *Mar. Biol.* 11: 222-241.
- Trinast, E. M., 1976. A preliminary note on *Acartia californiensis*, a new calanoid copepod from Newport Bay, California. *Crustaceana* 31: 54-58.
- Uye, S. & A. Fleminger, 1976. Effect of various environmental factors on egg development of several species of *Acartia* in southern California. *Mar. Biol.* 38: 253-262.
- Uye, S., S. Kasahara & T. Onbé, 1979. Calanoid copepod eggs in sea-bottom muds. 4. Effects of some environmental factors on the hatching of resting eggs. *Mar. Biol.* 51: 151-156.
- Walters, R. A., R. T. Cheng & T. J. Conomos, 1985. Time scales of circulation and mixing processes of San Francisco Bay waters. *Hydrobiologia* (This volume).
- Wooldridge, T. & R. Melville-Smith, 1979. Copepod succession in two South African estuaries. *J. Plankton Res.* 1: 329-341.