

Spatial and Temporal Variability of Mesozooplankton and Tintinnid Ciliates in a Seasonally Hypersaline Estuary

DAVID T. ELLIOTT* and RONALD S. KAUFMANN

Department of Marine Science and Environmental Studies, University of San Diego, 5998 Alcalá Park, San Diego, California 92110

ABSTRACT: The zooplankton community of Mission Bay, San Diego, California, was monitored over two years, to study spatial and temporal patterns and the response of zooplankton species composition to environmental variation. Data were collected every two weeks from six stations and included hydrographic parameters, dissolved nutrient concentrations, and phytoplankton and zooplankton species composition. Hydrography varied seasonally, along a spatial gradient from the mouth to the back of the bay, and between the two years around the influence of rainfall. Spatially, Mission Bay could be divided into three regions during this study based on hydrography and zooplankton species composition. Zooplankton species composition followed a predictable seasonal progression, with different groups of species being characteristic to particular times of the year. Variability in zooplankton species composition was also evident between years, as certain species were more common in one or the other year of the study. Spatial patterns were more consistent than temporal ones, and related to distance from the mouth of the bay during much of the year and distance from freshwater inlets during the relatively short rainy season. Multivariate analysis revealed that variation in zooplankton species composition was best related to measured abiotic factors (temperature, salinity, rainfall, and tidal velocity).

Introduction

Mission Bay is an estuary located in San Diego, California, USA. It provides an important nursery for many oceanic fish species, including the commercially important white sea bass (*Atractoscion nobilis*) and California halibut (*Paralichthys californicus*; Chapman 1963; Snyder 1965). Mission Bay is located in a heavily populated urban area, and is subjected to a number of potential sources of environmental degradation (Setmire and Bradford 1980; Colt 1993; Largier et al. 1997). It is a seasonally hypersaline estuary, typical of a Mediterranean climate. The area receives little annual rainfall, so the bay undergoes little freshwater flushing. The bay has a relatively constricted connection with the open ocean, reinforcing weak tidal flushing in its inner areas, and leading to long residence times and the increased potential for environmental degradation and water quality issues (Largier et al. 1997). The sporadic nature of freshwater inflow to Mediterranean hypersaline estuaries may lead to changes in the plankton community, via freshwater input of dissolved nutrients and other allochthonous organic material, as well as rapid changes in the water column structure (e.g., salinity, temperature).

Microzooplankton and mesozooplankton are integral parts of the biological communities of estuaries, serving as intermediates between primary production and higher trophic levels. In order to understand the consequences of environmental changes on the pelagic ecology of Mission Bay, it is necessary to know how the zooplankton in the bay respond to their abiotic and biotic environment. Little information on the plankton in Mission Bay is available at present, except for two studies, both focused on phytoplankton (Fairbanks 1969; Swope 2005).

The environmental conditions in estuaries can vary across a greater range of values when compared to the open ocean. Such variability in estuaries is experienced over much smaller scales, both in terms of the spatial (shorter distances) and temporal (shorter time intervals) aspects. This increased variability results from the dynamic nature of estuaries, including reduced depth and strong gradients produced by freshwater inflow or restricted exchange with the coastal oceanic environment (Cloern and Nichols 1985). In many classical riverine estuaries, defined by a persistent source of freshwater discharge, variation in the environment and plankton are described well by a longitudinal gradient of salinity from freshwater to full seawater (e.g., Taw and Ritz 1978; Wilderman 1987; Soetaert and van Rijswijk 1993). In seasonally hypersaline estuaries like Mission Bay, there is only seasonal freshwater discharge. Temporal and spatial patterns in zooplankton species

*Corresponding author; current address: Department of Biological Sciences, Virginia Institute of Marine Science, 1208 Great Road, Gloucester Point, Virginia 23062; tele: 804/684-7887; fax: 804/684-7293; e-mail: delliottd@vims.edu

composition might be expected to differ from riverine estuaries. Temporal variation could be stronger, due to the wide range of conditions that occur at a single location over the course of a year, ranging from hypersaline to full freshwater. Spatial variation in the zooplankton might be less pronounced, due to a relatively homogeneous bay environment when compared to the gradient of freshwater influence in estuaries with persistent freshwater inflow.

The objective of this study was to characterize variation in the zooplankton community of Mission Bay over two annual cycles (July 2002–June 2004). We describe spatial and temporal variability of hydrography and nutrients, as well as zooplankton species composition. We also examine the underlying relationships between the observed variation in zooplankton species composition and variation in the abiotic and biotic environment. The ultimate goal is to obtain baseline data for interpretation of changes in zooplankton species composition as indicators of environmental change in Mission Bay and similar estuaries.

Methods

STUDY AREA

Mission Bay is a shallow mesotidal estuary located on the Pacific Coast of North America at approximately 32°46'N, 117°14'W. Depths range from over 10 m near the mouth to less than 1 m. Mission Bay has been highly engineered from its natural state as a lagoon and tidal mud flat at the mouth of the San Diego River. Alterations include extensive dredging and filling to produce a shallow embayment with several artificially created islands (Hippaka 1991). A dry weather water diversion system essentially prevents the flow of freshwater into the bay when rainfall is low or absent. The region is characterized by a dry Mediterranean climate and receives rainfall averaging 26.2 cm annually between 1964 and 2004 (San Diego County Water Authority <http://www.sdcwa.org/manage/rainfall-lindbergh.phtml>). Rainfall occurs primarily between November and April, when the bay receives most of its freshwater runoff. Freshwater inflow is never of sufficient magnitude to flush the bay, and circulation is predominantly tidally driven. Circulation is restricted, especially in the areas of the bay farthest from the mouth. Mission Bay is classified as a seasonally hypersaline estuary, with salinity sometimes reaching levels higher than adjacent coastal ocean waters. Hypersaline conditions generally occur in the back of the bay during the summer, when evaporation typically exceeds flushing rates (Fairbanks 1969; Largier et al. 1997, 2003).

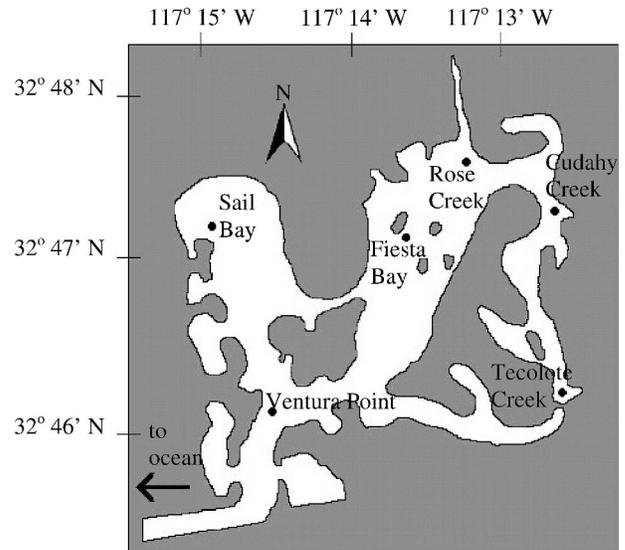


Fig. 1. Map of Mission Bay, California, indicating latitude, longitude, and the six sampling stations.

SAMPLING

Six stations were sampled biweekly between July 2002 and June 2004 (Fig. 1). Water depths at the sampling stations ranged from ca. 1 m to over 4 m. During each of 53 sampling events hydrographic profiles, dissolved nutrient concentrations, and plankton community data were collected at each station. Sampling was done in the morning, between 8:00 and 12:00 local time. No attempt was made to control for the tidal cycle in the sampling routine. Tidal velocity was considered as a potential explanatory variable for zooplankton species composition (see next section).

A vertical hydrographic profile was recorded at each station with a YSI 6820 digital multimeter. Salinity, temperature (°C), and dissolved oxygen (mg l^{-1}) were measured at 0.5 m increments from near the bottom to just below the surface. Surface water samples were collected at each station and stored in opaque bottles on ice for laboratory analysis of nutrients. The plankton community was sampled during 5-min horizontal tows using a standard conical plankton net (0.5 m mouth diameter, 53 μm mesh) equipped with a General Oceanics flowmeter. The tow was conducted at or near the surface at a speed of 0.5–1.0 m s^{-1} . The mean volume sampled was 48 m^3 (standard deviation 6.8 m^3). The contents of the net were concentrated into a 1-l volume and preserved immediately in 3.7% formalin buffered with sodium borate.

SAMPLE ANALYSIS

Water samples for nutrient analysis were filtered through a 0.45- μ m nitrocellulose filter to remove particulate material. Filtered water was analyzed for dissolved nitrate, phosphate, and silicate. Standard protocols were used to measure reactive orthophosphate (Hach ascorbic acid method 8048) and dissolved silicate (Hach silicomolybdate method 8185; Hach water analysis handbook procedures, Hach Company, Loveland, Colorado). The protocol for nitrate was altered slightly from the Hach suggested method (Hach cadmium reduction method 8039). This was done in order to minimize the effects of chloride ions, which can interfere with the indicative results of the reaction. The Hach cadmium reagent was added to a 10-ml water sample, which was shaken for 1 min and allowed to stand for 2.5 min before absorbance was measured. This protocol was developed after extensive testing of various mixing and incubation times (Bolender personal communication). A Genesys Spectronic20 spectrophotometer was used to measure the absorbance of samples at specified wavelengths for each nutrient analyzed. Nitrate and phosphate concentrations were always analyzed within 6 h of collection, and silicate within 24 h.

Plankton samples were processed using a compound microscope at a magnification of 100 \times . Three 1-ml subsamples were removed from the 1-l tow concentrate and placed on Sedgewick-Rafter slides. Ten random, nonoverlapping fields of view were selected for counting on each slide. Organisms 50% or more within a field of view were enumerated and identified to lowest possible taxon, using the available literature (Dawson and Knatz 1980; Lee et al. 1985; Young et al. 2002). Of the 1-l concentrated samples from each tow, this protocol led to analysis of 0.06 ml, equal to approximately 3 l of the initial tow volume. This method of enumeration led to unacceptably high variability (among pseudoreplicates) in the estimates of zooplankton abundance. In statistically analyzing the data, plankton counts were converted to presence-absence data and treated as sampling units in conjunction with their corresponding hydrographic data. Phytoplankton species were identified and enumerated in the same manner as zooplankton, and were treated as environmental variables in some analyses.

OTHER DATA SOURCES

Several other environmental variables also were used. The magnitude and direction of the tidal current at the time of sample collection was obtained from tidal charts. Daily rainfall measurements were obtained from the National Oceanic and Atmospheric Administration station at Sea

World, San Diego, adjacent to Mission Bay (www.wrh.noaa.gov/sgx/obs/rtp/seaworld.html). The cumulative rainfall for the two weeks before each sampling event is reported here.

Potential temperature was calculated using the standard state equation for water density given depth, salinity, and temperature. As an indication of thermal stratification, the ratio of potential temperature between 0 and 2 m was used; a ratio of less than one indicates thermal stratification.

The relationships between zooplankton species composition and environmental variables, including dissolved oxygen, nutrient concentrations, and phytoplankton abundances, were explored using time-delayed variables. This was accomplished by moving the environmental variables forward in time by 2 wk to match zooplankton abundances at the same station, but 2 wk later. These new variables were defined as lagged variables.

ANALYSIS

R-mode hierarchical agglomerative cluster analysis was performed to look for classes of zooplankton species, based on co-occurrence. The coincidence index was employed as the coefficient of dependence. This index was chosen because of its previous use as a measure of species association, and its property of not including pairs of zeros in the results (Legendre and Legendre 1998). Cluster analysis was also used to reduce the number of potential explanatory variables from the phytoplankton data that were included in the canonical multivariate analysis. Using the same method of R-mode hierarchical agglomerative cluster analysis as for the zooplankton, 10 distinct clusters of co-occurring phytoplankton species were identified. The phytoplankton abundance index was defined as the mean of the estimated abundances of all species within each of the co-occurrence clusters. This reduced the number of phytoplankton variables from 73 individual species to 10 species groups while preserving the patterns in phytoplankton abundance and species composition.

Canonical correspondence analysis (CCA) was used to describe the spatial and temporal patterns in the zooplankton (ter Braak and Verdonschot 1995). Dummy variables were created to represent spatial and temporal aspects. Variables for each station and season were created, and each sample was assigned a value of 1 if it was taken from that station or season or a 0 otherwise. CCA on the zooplankton species composition, using these explanatory variables produced two diagrams, one with stations as the variables and one with seasons.

Another potentially valuable attribute of CCA is the ability to remove (partial out) the effects of specific environmental variables by treating them as

covariables. One possible problem with the interpretation of the multivariate relationship between zooplankton species composition and environmental variables is the issue of multiple covarying variables. Many environmental parameters have predictable spatial or temporal patterns. Because of this, a parameter with a spatial gradient might be a good descriptor of variation in the zooplankton community. This apparent descriptive value also may be due to indirectly related spatial variation in the zooplankton community, rather than a true relationship. There is no way to completely eliminate this potential bias, but partial CCA can minimize its likelihood. Variation associated with chosen covariables is removed prior to analysis, and the analysis is carried out on the residual variation. Any species-environment relationships revealed using this method would be independent of the parameters partialled out. By using covariables to account for highly predictable spatial and temporal variation in the plankton data, the importance of such relationships in results can be reduced and underlying patterns made apparent (Borcard et al. 1992; Pinel-Alloul 1995; ter Braak and Verdonschot 1995).

Partial CCA was used to examine the data set for underlying relationships between the zooplankton community and its environment. The covariables used were day length and sampling station (to account for the seasonal cycle and the spatial aspect, respectively). The initial pool of potential explanatory variables included all hydrographic and abiotic variables (surface temperature, salinity, nutrients, dissolved oxygen, tidal velocity, bottom depth, and area rainfall), both collected simultaneously and 2-wk lagged (to explore potential indirect relationships with zooplankton through phytoplankton). The biotic variables included in the analysis were the phytoplankton abundance index for each of the 10 predetermined groups of co-occurring phytoplankton taxa, both simultaneously collected and 2-wk lagged.

While all of these explanatory variables were given equal consideration at the beginning of partial CCA, the explanatory variables used in the final results was a reduced set. This set was determined by the use of forward selection of variables. Criteria for selection were the amount of variation in the zooplankton species data explained and the statistical strength of the relationships as indicated by *p* values from Monte Carlo randomization (available in the program CANOCO 4.5). Not all zooplankton species were included in the partial CCA. A few species were removed prior to analysis, after determining that they were not true residents of the bay, due to extreme rarity of occurrence in samples.

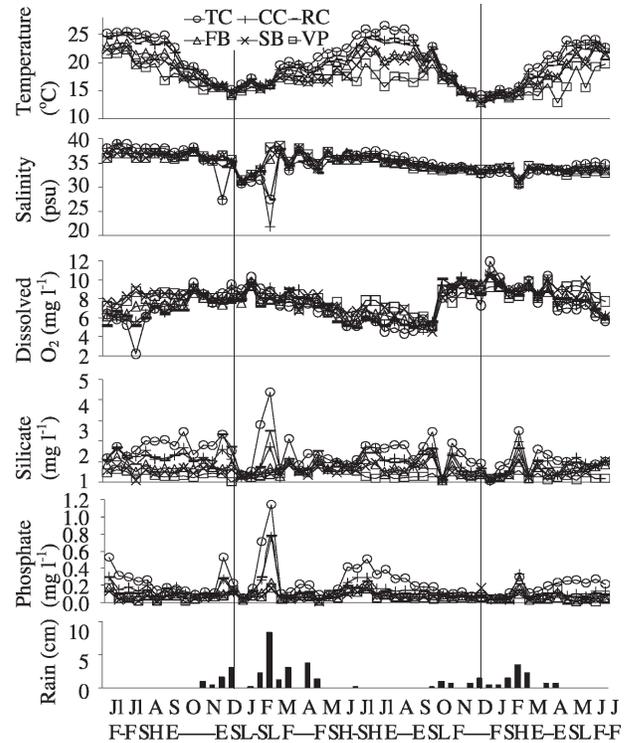


Fig. 2. Spatial and temporal distribution of main environmental variables. Temperature ($^{\circ}\text{C}$), salinity (psu), dissolved oxygen (mg l^{-1}), dissolved silica (mg l^{-1}), dissolved phosphate (mg l^{-1}), and biweekly rainfall (cm) in the area of Mission Bay, at each of the six sampling stations across the sampling period (x-axis labels are placed every 2 weeks, resulting in the occasional dual label when 3 samples were taken during a month). Hydrographic data is from 0.5 m depth at each of the six sampling stations (TC = Tecolote Creek, CC = Cudahy Creek, RC = Rose Creek, FB = Fiesta Bay, SB = Sail Bay, VP = Ventura Point); rainfall data is cumulative from the 2 weeks prior to the sampling at a weather station adjacent to Mission Bay. The approximate tidal phase during each sampling event is shown below the x-axis (F = flood, E = ebb, SL = slack low, SH = slack high).

Results

ABIOTIC ENVIRONMENT

Water temperature varied cyclically over the course of each year, with highest temperatures in July–September and lowest temperatures in December and January (Fig. 2). Temperatures were on average lower in 2003–2004 than in 2002–2003. A clear spatial gradient was evident, with lower temperatures in the front of the bay, increasing further in toward the back of the bay. Salinity essentially mirrored temperature, but with a weaker annual cycle. Salinity dropped quite noticeably several times after large rainfall events. The most pronounced of these events occurred between December 2002 and May 2003, and again in February 2004. As with temperature, salinity was consistently lower during 2003–2004 than 2002–

2003. Dissolved oxygen also showed a cyclical annual pattern, but there were no spatial trends, and values were much more variable from date to date than for temperature or salinity. Drops in oxygen concentration at stations in the back of the bay were apparent in early August 2002 and again in December 2003. There was a very pronounced rise in oxygen concentration throughout the bay between October and November 2003, coinciding with the beginning of a large prolonged bloom of the dinoflagellate *Lingulodinium polyedrum*.

Nitrate concentrations were generally low to undetectable (detection limit of assay was 4.8 μM nitrate), likely because nitrate is a growth-limiting nutrient for phytoplankton in Mission Bay (Davies 1972). Phosphate concentrations were usually low ($< 2.0 \mu\text{M}$) throughout the bay. At Tecolote Creek, phosphate levels were often elevated compared to other stations. Over the course of the study, phosphate levels were significantly different among stations according to a Kruskal Wallis test ($\chi^2 = 114$, $df = 5$, $p < 0.001$). Over time phosphate had a weak cyclical pattern, with highest values in the summer. Concentrations of silicate were variable at all stations, and especially in the back of the bay where the highest values were observed. Differences in silicate concentrations over the study period were found to be significant among stations according to a Kruskal Wallis test ($\chi^2 = 121$, $df = 5$, $p < 0.001$).

Thermal stratification, as indicated by the ratio of potential temperature between surface and 2 m depth, was virtually unobserved during the study period. While some instances occurred where potential temperature was found to be slightly lower at the surface (values < 1.0), a similar number of cases were seen where the opposite was true. This second situation suggests more dense water at the surface than at 2 m depth, an unlikely scenario, so these deviations from 1.0 were considered to be within the margin of error. Mission Bay appeared to be well mixed during the times sampled.

Rainfall in the area around Mission Bay occurred mainly in the winter and spring (Fig. 2). Approximately twice as much rainfall was received during the 2002–2003 sampling year (25.7 cm) than in 2003–2004 (13.2 cm). Several rainfall events in 2002–2003 were much larger than anything in 2003–2004, in terms of quantity of rain received. Three or more centimeters of rainfall were received during the 2 wk between sampling events on four separate occasions during 2002–2003; this is compared to only one such large rainfall event in 2003–2004.

PLANKTON

A total of 37 differentiated taxa of zooplankton were found regularly in Mission Bay (Table 1). Of

TABLE 1. Zooplankton taxa seen during the study, along with corresponding species abbreviations as used in multivariate figures, and the percentage of samples in which the species was seen (out of 318 samples).

		Percent Occurrence
Copepods		
<i>Acartia californiensis</i>	AC	30.8
<i>Acartia clausi</i>	AU	15.7
<i>Clausocalanus</i> sp.	CC	1.9
<i>Corycaeus giesbrechti</i>	CG	2.5
<i>Euterpina acutifrons</i>	EA	10.4
<i>Oithona</i> cf. <i>settigera</i>	OT	3.5
<i>Oithona oculata</i>	OO	23.6
<i>Oithona similis</i>	OS	66.7
Unknown calanoid	UC	8.8
Marine ciliates		
<i>Codonellopsis bulbulus</i>	CB	4.4
<i>Favella</i> sp.	FS	50.0
<i>Helicostomella endentata</i>	HE	18.6
<i>Rhabdonella</i> cf. <i>hebe</i>	RH	1.9
<i>Steenstrupiella steenstrupii</i>	SS	25.5
<i>Stenosemella steini</i>	SI	25.8
<i>Tintinnopsis campanula</i>	TC	29.2
<i>Tintinnopsis</i> cf. <i>beroidea</i>	TB	1.3
<i>Tintinnopsis kofoidi</i>	TY	25.2
<i>Tintinnopsis lobiancoi</i>	TL	50.0
<i>Tintinnopsis cornige</i>	TU	29.2
Larval forms		
Barnacle nauplii	BA	5.7
Bivalve veligers	BV	43.4
<i>Chrysopetalidae</i> sp.	CS	30.5
<i>Cnidarina planula</i>	CN	17.3
Gastropod veligers	GV	36.2
<i>Longipedia</i> sp.	LS	24.5
Mueller larvae	MU	13.5
<i>Polydora</i> sp.	PS	7.9
Sea cucumber gastrula	SG	2.8
Worm larvae	WM	26.1
Other holoplankton		
Cladoceran	CL	4.1
Foram A	FA	6.9
Foram B	FB	7.2
Foram C	FC	4.7
Foram D	FD	2.5
<i>Oikopleura</i> sp.	OI	5.3
Radiolarian	RA	8.8

these, 9 were copepods and 11 were tintinnid ciliates. The copepods *Acartia californiensis*, *Oithona similis*, and *O. oculata*, as well as the ciliates *Tintinnopsis lobiancoi*, *T. campanula*, *T. cornige*, *T. kofoidi*, *Favella* sp., *Steenstrupiella steenstrupii*, and *Stenosemella steini*, were the predominant species in the bay seen in at least 25% of all samples. Ten taxa identified were the planktonic larvae of marine benthic invertebrates. A few of these were also seen in 25% or more of the samples taken, including bivalve and gastropod veligers, undifferentiated worm larvae, larvae of the polychaete *Chrysopetalidae* sp., and nauplii of the benthic copepod *Longipedia* sp. Several other holoplanktonic taxa were also

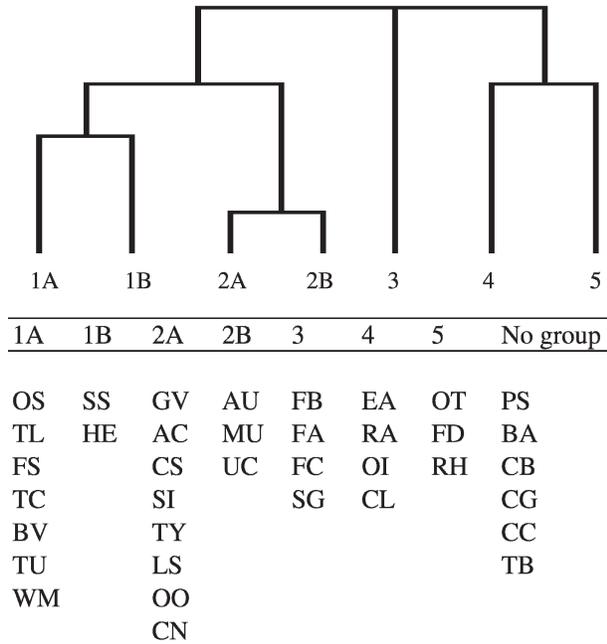


Fig. 3. Dendrogram showing functional groups of zooplankton species based on co-occurrence relationships within samples, according to R-mode hierarchical agglomerative cluster analysis. List of species belonging to each group in the hierarchical cluster analysis of zooplankton based on co-occurrence. Species are listed in order of frequency of occurrence within a group, with species listed first being more commonly observed within samples.

identified. These were all observed infrequently, and included radiolarians, forams, the appendicularian *Oikopleura* sp., and marine cladocerans.

The R-mode cluster analysis revealed five distinct co-occurring species groups, and several subclusters (Fig. 3). Members of each cluster are shown in Fig. 3, and abbreviations of the species names used are in Table 1. Cluster 1 (A and B) consisted of several species observed commonly during the sampling period and throughout the bay (Fig. 4). Cluster 1 is considered to be composed mainly of species resident to Mission Bay. Clusters 2A and 2B included species seen primarily during periods of high species richness (synonymous with high total abundances), in summer 2002 and 2004 and spring 2003 (Fig. 4). Species of this cluster were also considered to be resident to Mission Bay. Clusters 3, 4, and 5 consisted of relatively rare taxa seen mainly in the front of the bay, particularly at Ventura Point. Six of the 37 species did not cluster into one of the four main clusters. These species were rarely observed and not characteristic to any specific station or area of the bay.

Spatial variation accounted for 21% of the variance in species composition, as indicated by descriptive CCA using stations as explanatory variables. Three spatial regions were apparent (Fig. 5).

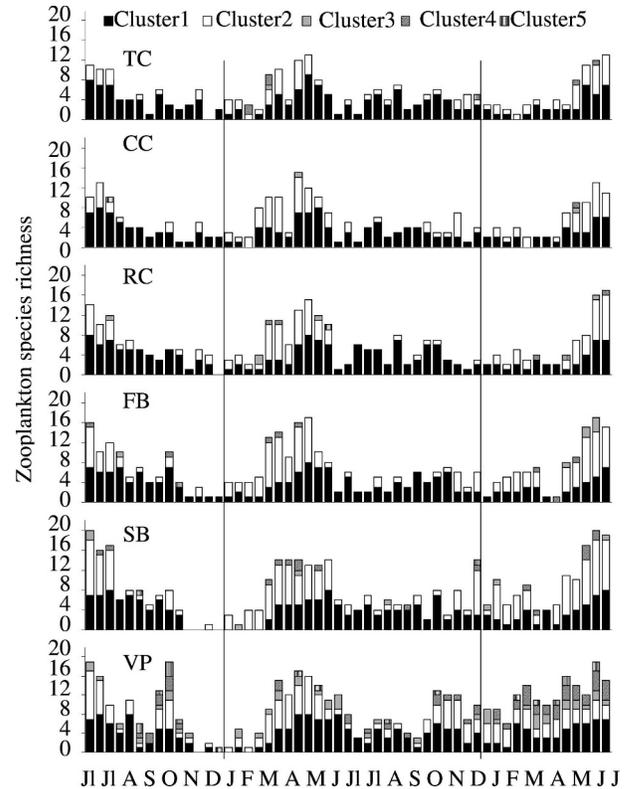


Fig. 4. Zooplankton species richness across the sampling period (x-axis labels are placed every 2 weeks, resulting in the occasional dual label when 3 samples were taken during a month) and at each of the six sampling stations (TC = Tecolote Creek, CC = Cudahy Creek, RC = Rose Creek, FB = Fiesta Bay, SB = Sail Bay, VP = Ventura Point). Values on y-axes represent proportions of the number of species occurring in a given sample, and bars are coded by co-occurrence groups (e.g., if 10 species were present in a sample, and two belonged to co-occurrence cluster 1 then the value of the bar would be 10, and the value of the black shaded area would be 2).

The first included the three creek stations, with species from co-occurrence cluster 1A characteristic to this region. This supported the classification of this cluster as a group of resident bay species. The second region was the mid bay: Fiesta and Sail Bays. Co-occurrence clusters 2A and 2B, as well as 1B, were highly associated with this region. These species also were established within the bay. Ventura Point was unique unto itself, with clusters 3, 4, and 5 species common there. Species from clusters 4 and 5, when observed, were virtually exclusive to this station (Fig. 4).

An additional 34% of the variance in the observed species composition was explained by the temporal distribution of species. Summer and autumn samples were more similar to each other, and described the temporal occurrence of the species resident to the back of the bay in cluster 1A and also those in cluster 1B, common throughout the bay (Fig. 5).

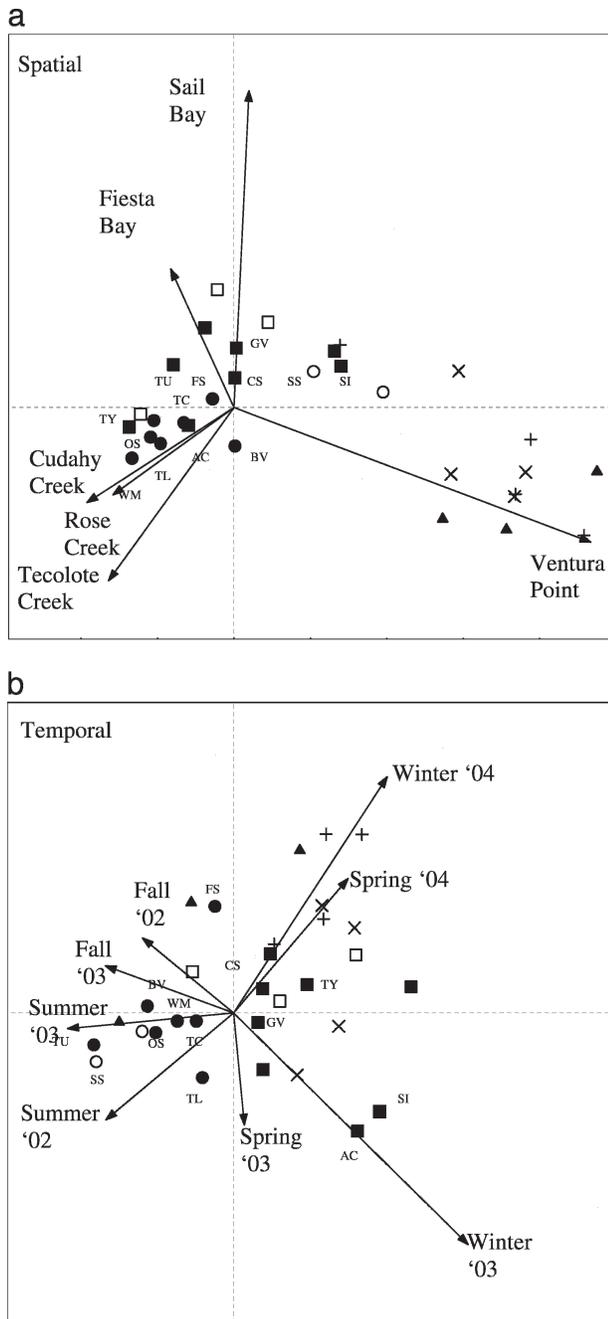


Fig. 5. Spatial and temporal distribution of and relationships among zooplankton species in Mission Bay. Each symbol represents a species (species labels included for common species seen in 25% or more of samples), and symbols correspond with co-occurrence clusters (solid circle = 1A, open circle = 1B, solid square = 2A, open square = 2B, X = 3, + = 4, solid triangle = 5, black point = species not clustered into any group). The vectors represent environmental variables, sampling stations in the case of the spatial ordination, and seasons according to year for the temporal ordination.

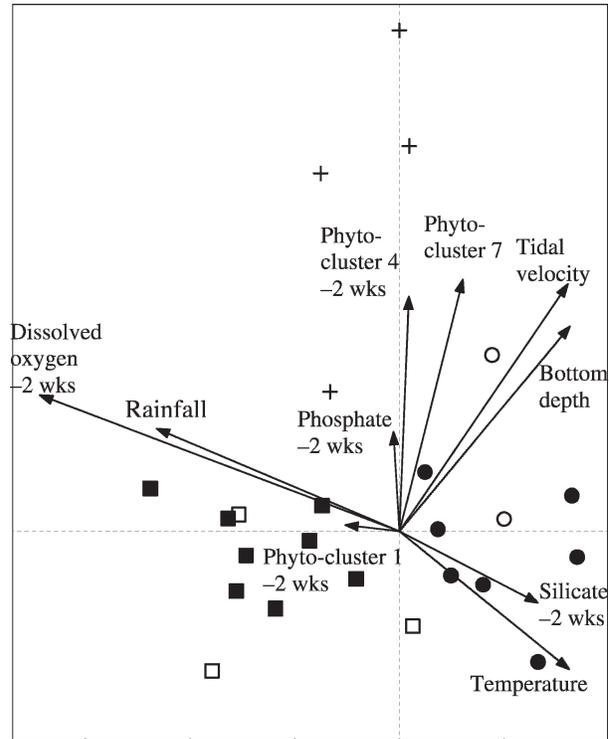


Fig. 6. Relationships between main zooplankton co-occurrence groups in Mission Bay and the environmental variables as indicated by partial canonical correspondence analysis. Each symbol represents a species, and symbols correspond to co-occurrence clusters (solid circle = 1A, open circle = 1B, solid square = 2A, open square = 2B, X = 3, + = 4, solid triangle = 5, black point = species not clustered into any group).

Spring and winter samples were also similar to each other and described the occurrences of clusters 2A and 2B species, common at the mid to front of the bay, in addition to species in cluster 3. The horizontal axis (main axis of variation) represented differences in species composition between summer–fall and winter–spring samples. There were also differences in species composition between the two years, as the winter–spring 2003 and winter–spring 2004 vectors described different zooplankton species compositions.

The species–environment relationships, as indicated by partial CCA analysis (Fig. 6), revealed that even after the spatial and temporal structure of the data set was accounted for by treating sample site and day length as covariables, the grouping of the co-occurrence clusters remained essentially intact. This suggested that even when not occurring together in a sample, these species were often associated with similar environmental conditions. The environmental variables found to have significant relationships with zooplankton species composition (as determined by Monte Carlo permutations) are shown in Table 2. These variables

TABLE 2. Biotic and abiotic environmental parameters chosen by forward selection for use in the partial canonical correspondence analysis. For the biotic set, phytoplankton species belonging to each cluster are listed as well.

Variable	Phytoplankton Species
Cluster 1, two-weeks lagged	<i>Ceratium lineatum</i> <i>Coscinodiscus</i> sp. <i>Lingulodinium polyedrum</i> <i>Akashiwo sanguinea</i>
Cluster 4, two-weeks lagged	<i>Chaetoceros radicans</i> <i>Chaetoceros</i> sp. <i>Hemiaulus hauckii</i>
Cluster 7, two-weeks lagged	<i>Ceratium fusus</i> <i>Dinophysis acuminata</i> <i>Gonyaulax spinifera</i>
Bottom depth	
Cumulative precipitation two-weeks prior	
Dissolved oxygen two-weeks lagged	
Silica two-weeks lagged	
Temperature	
Tidal velocity	

explained 15% of the variation in zooplankton species composition. Zooplankton species from co-occurrence clusters 3 and 5, as well as those not clustering, were not included in this analysis, as they were not suspected to be true bay residents. Among the remaining species, the resident zooplankton prevalent in the summer and throughout the bay (cluster 1A) were well described by the occurrence of higher temperatures and higher silicate concentrations 2-wk lagged. The resident species (clusters 2A and 2B) were well described by rainfall and dissolved oxygen concentrations 2-wk lagged. The species mostly confined to the front bay (clusters 1B and 4) were found in samples taken during strong flood tides, with relatively deep bottom depths, and during periods when phytoplankton clusters 4 and 7 had occurred at the same stations 2-wk earlier. In addition to the environmental variables mentioned so far, 2-wk lagged phosphate concentration and the occurrence of phytoplankton cluster 1 were also found to be significantly related to zooplankton species composition. The short length of the vectors representing these variables in the biplot (Fig. 6) indicated that they explained relatively little variation in species composition.

Discussion

HYDROGRAPHY

Spatial variation in the hydrographic conditions of the bay was seen as a gradient from the front to back of the bay, and was the result of either higher evaporation or freshwater input in the back areas of the bay, in concert with relatively long residence times of this water. Temporal variation in hydro-

graphy was mainly a result of the clear annual cycle. The differences in area rainfall led to within season variation in hydrography between the two years sampled.

ZOOPLANKTON

Over the entire study period, there was an assemblage of commonly observed zooplankton species in Mission Bay (e.g., some mixture of *Acartia*, *Oithona*, and *Euterpina* spp., *Tintinnopsis*, *Favella*, and *Helicostomella* spp., and bivalve and gastropod veligers). Comparable assemblages have also been reported in other areas (see Table 3), including the Tunis North Lagoon, Wilson Inlet, and Dokai Inlet (Gaughan and Potter 1995; Yye et al. 1998; Annabi-Trabelsi et al. 2005). All of these locations have temperate to tropical climates, and share many environmental characteristics with Mission Bay, including sporadic rather than persistent freshwater discharge, a constricted connection with the open coastal waters, and shallow depth. The zooplankton assemblage seen in Mission Bay seems characteristic of the plankton in such environments, perhaps due to their restricted tidal circulation, shallow depth, or inclination toward eutrophic conditions (Arfi et al. 1981; Yye 1994). In more classical riverine estuaries, where persistent freshwater discharge results in a low salinity zone throughout the year, the zooplankton species assemblage is different. The zooplankton of these estuaries often still includes *Acartia*, but smaller forms like *Oithona* spp. and tintinnid species are a less prevalent component of the zooplankton. True estuarine zooplankton species are seen (e.g., *Eurytemora affinis*).

Of the four groups of co-occurring species seen, the two key co-occurrence clusters during the study period were clusters 1A and 2A (Fig. 4 and Table 1). The prevalent metazoan zooplankton in clusters 1A and 2A were *O. similis* and *A. californiensis*, respectively. The occurrence of smaller cyclopoid copepods (*Oithona* spp.) throughout the year, and the greater relative contribution of larger copepods (*Acartia* spp.) in the spring has been reported in studies of other embayments in Mediterranean climates (Villate 1991a; Calbet et al. 2001). Copepods of the genus *Oithona* are thought to be generalists, and unable to outcompete more specialized calanoids during favorable conditions, but able to survive a wider range of less favorable conditions (Paffenhofer 1993; Sabatini and Kiorboe 1994). In summer and late in blooms, when temperatures still were warm and favorable for growth but food supplies were likely depleted, larger species such as *Acartia* spp. might have been food limited, while *O. similis* was able to do well. This is supported by the CCA analysis (Fig. 6) where

TABLE 3. Comparison of zooplankton in estuaries with sporadic and more persistent freshwater discharge.

Location of Study	Zooplankton Enumerated	Common Zooplankters	Freshwater Discharge	Narrow Mouth	Depth
Tunis North Lagoon (Annabi-Trabelsi et al. 2005)	Copepods (> 70 mm)	<i>Acartia</i> , <i>Oithona</i> , <i>Euterpina</i>	Minimal	Yes	1.5 m average
Pichavaram mangroves (Godhantaraman 1994)	Tintinnids and copepods	<i>Tintinnopsis</i> (10+ spp.), <i>Favella</i> (2 spp.), <i>Acartia</i> , <i>Acrocalanus</i> , <i>Centropages</i> , <i>Oithona</i> , <i>Euterpina</i>	Seasonal	Yes	Shallow
Dokai Inlet (Uye et al. 1998)	Microzooplankton and mesozooplankton	<i>Tintinnopsis</i> (2 spp.), <i>Favella</i> , <i>Helicostomella</i> , <i>Acartia</i> , <i>Oithona</i> , <i>Euterpina</i> , <i>Paracalanus</i> , bivalve veligers	Minimal	No	7 m average
Vranjic Basin (Vidjak et al. 2006)	Microzooplankton and mesozooplankton	Tintinnids, <i>Acartia</i> , <i>Acrocalanus</i> , <i>Centropages</i> , <i>Oithona</i> , <i>Euterpina</i> , bivalve veligers	Seasonal	Yes	> 15 m
Mondego Estuary (Vieira et al. 2003)	Metazooplankton (> 63 mm)	<i>Acartia</i> , <i>Temora</i> , <i>Oithona</i> , <i>Euterpina</i> , gastropod veligers	Seasonal	Yes	2–4 m (Lillebo et al. 2005)
Estuary of Mundaka (Villate 1991b)	Mesozooplankton (> 250 mm)	<i>Acartia</i> , <i>Paracalanus</i> , polychaete larvae	Seasonal	No	2–5 m
Wilson Inlet (Gaughan and Potter 1995)	All zooplankton (> 53 mm)	<i>Tintinnopsis</i> , <i>Favella</i> , <i>Helicostomella</i> , <i>Acartia</i> , <i>Oithona</i> , bivalve veligers, polychaete larvae	Seasonal	Yes	< 2 m most areas
Seine Estuary (Mouny and Dauvin 2002)	Mesozooplankton (> 200 mm)	<i>Acartia</i> , <i>Eurytemora</i> , <i>Acartocyclops</i> , cladocerans	Persistent	No	5–10 m
Saint John River (Carter and Dadswell 1983)	Crustacean zooplankton (> 158 mm)	<i>Acartia</i> , <i>Pseudocalanus</i> , <i>Eurytemora</i> , <i>Oithona</i> , cladocerans, barnacle nauplii	Persistent	No	7.2 m average
San Francisco Bay Estuary (Ambler et al. 1985)	All zooplankton (> 64 mm)	<i>Tintinnopsis</i> (2 spp.), <i>Eutintinnus</i> , <i>Acartia</i> , <i>Eurytemora</i> , cyclopoids, harpacticoids, barnacle nauplii, bivalve veligers, rotifers	Persistent	Yes	10–30 m
Chesapeake Bay (Brownlee and Jacobs 1987)	Microzooplankton and mesozooplankton	<i>Tintinnopsis</i> (2 spp.), <i>Acartia</i> , <i>Eurytemora</i> , cladocerans, polychaete larvae, barnacle nauplii, rotifers	Persistent (Schubel and Pritchard 1987)	No	8.4 m average
Columbia River (Haertel and Osterberg 1967)	Mesozooplankton (> 244 mm)	<i>Acartia</i> , <i>Pseudocalanus</i> , <i>Eurytemora</i> , cladocerans, rotifers	Persistent	No	10 m average

the occurrence of the *O. similis* group was explained by a phytoplankton cluster consisting of dinoflagellates and the large diatom *Coscinodiscus* sp. These species are likely less easily ingested by copepods than are smaller algal forms. The co-occurrence of *O. similis* with many tintinnids may represent a predator-prey relationship, as this copepod preferentially ingests ciliates (Atkinson 1996; Castellani et al. 2005). Selective visual predation on the larger *Acartia* spp. has been suggested as causing a similar temporal species shift in other estuaries (Fulton 1984), and similar visual predators can be found in Mission Bay (Talley 2000).

The seasonal succession of tintinnid species was similar to that reported in other estuaries (Krsinic 1987; Kamiyama and Tsujino 1996; Urrutxurtu 2004). This included winter and spring occurrence of some tintinnid species (e.g., *Stenosemella* and *Tintinnopsis* spp.), and the maximum occurrence of most species in the summer and fall (e.g., *Favella* spp., *T. campanula*, *Helicostomella* sp., and *S. steenstrupii*). Most of the tintinnid species found with any

frequency in Mission Bay were neritic or cosmopolitan forms (Pierce and Turner 1993).

Spatial variation in the zooplankton species composition of Mission Bay was less pronounced than temporal variation in Mission Bay (21% explained by site versus 34% explained by season and year in the CCA analysis). This highlights the importance of multiyear studies. Much of the temporal variation observed was a difference between the winter and spring samples in 2002–2003 and 2003–2004 (Fig. 5); if only one year of data were available, conclusions as to the importance of temporal variation in the zooplankton community of Mission Bay would have been quite different. The prominence of temporal variation is in contrast to the results found in many other estuaries (Soetaert and Van Ridjwick 1993; Laprise and Dodson 1994; Mouny and Dauvin 2002; Marques et al. 2006). It might be expected that spatial variation would be more important in riverine estuaries, and temporal variation stronger in estuaries like Mission Bay. In riverine estuaries the salinity gradient (spatial)

seems to be more of an influence on the zooplankton community. In Mission Bay, the influence of freshwater only occurs seasonally, exacerbating temporal variation.

SPECIES-ENVIRONMENT RELATIONSHIP

Some observed zooplankton species-environment relationships were more likely than others to represent species composition as a direct response to the environment (Fig. 6). Species from clusters 1B and 4 were well described by high tidal velocity (strong flood tides) and deeper bottom depth (these two were interrelated as higher tides meant deeper water), and also the occurrence of several phytoplankton species not often observed during this study. Species from these clusters were not likely true residents, even to the front of the bay. Their occurrence in samples was coincident with the intrusion of open coastal water during flood tides. The occurrence of cluster 1A species was coincident with high water temperatures and dissolved silicate concentrations 2 wk prior. Summertime had some of the highest temperatures and dissolved silicate concentrations during the study (Fig. 2). Temperature is known to affect the growth rate of zooplanktonic organisms (Huntley and Lopez 1992; Hirst and Lampitt 1998), and its relationship to the zooplankton community is not surprising. Increased silica concentrations may have led to a release of food items (diatoms) from nutrient limitation. An increase in allochthonous inputs of this nutrient seems unlikely, particularly since very little or no freshwater runoff entered the bay during the summer. The elevated silicate could be from dissolution from remnant frustules of the late spring diatom bloom as described for freshwater environments (Gibson et al. 2000; Ryves et al. 2006), which in Mission Bay began to decline by July in 2002 and April in 2003 (Swope 2005; Elliott 2006).

Species from co-occurrence cluster 2 were positively related to rainfall and dissolved oxygen concentrations. Dissolved oxygen concentrations were well above those that have been found to negatively affect zooplankton (Roman et al. 1993), and this relationship is not likely causal. Rainfall also is not likely to have any direct effect on the zooplankton community of Mission Bay, although its effects on nutrient loading and salinity may. The rainfall-freshwater inflow did result in lowered salinity for a short time following an event (Fig. 2). While it is possible that the rainfall-zooplankton relationship was the result of lower salinity, this seems improbable. Surface salinity was included as a potential explanatory variable in the partial CCA analysis, but did not relate to species composition strongly enough to have been chosen

by forward selection. The relationship between rainfall and species composition appears to have been due to some alternative indirect relationship with some unmeasured variable affected by rainfall and important to zooplankton species composition.

It is valuable to consider the relationship between rainfall and zooplankton species composition in further detail than allowed by the partial CCA biplot alone. Clear seasonal progressions in the environmental characteristics and zooplankton species composition occurred during both years of this study. There was also some substantial variability in the occurrences of certain species between the two years. This was evident in the differences in species composition between winter and fall samples in 2003 and 2004 (Fig. 5). Species from cluster 4, classified here as open coastal species, occurred more frequently in samples taken during the winter and spring of 2004, while some of the taxa in cluster 2A occurring in the spring were more commonly seen in winter and spring of 2003. While tidal phase may be important in the occurrence of these rare cluster 4 species (Fig. 6), rainfall appeared a likely explanation for the occurrence of species in cluster 2A. The winter of 2002–2003 was fairly normal in terms of rainfall in the San Diego area. Rainfall during this year was 25.7 cm, compared to the 40-yr average of 26.2 cm (1964–2004). Approximately twice as much rainfall was received during this year than either 2001–2002 (8.7 cm) or 2003–2004 (13.2 cm), so by comparison it was very wet. This translated directly to more freshwater inflow into Mission Bay. Rainfall was related to nutrient loading (Fig. 2) and potentially indirectly linked to the zooplankton species composition through phytoplankton. The higher rainfall in the winter and spring of 2003 resulted in anomalously high nutrient concentrations for the study (Fig. 2), and ultimately a larger number of zooplankton species were seen at the creek stations in the corresponding spring, as compared to the spring of 2004 (Fig. 4). A diatom bloom was seen in late winter and early spring of 2003, an anomaly not seen during the same times in 2002 or 2004 (Swope 2005; Elliott 2006). Between the two years studied, differences in the zooplankton species composition were clearly seen, coincident with differences in area rainfall and freshwater discharge.

The data cannot establish beyond all doubt the role of phytoplankton as an intermediary between rainfall and zooplankton during this study, mainly because of the lack of any strong relationship between cluster 2A species and algae. There are several potential explanations for this, two having to do with the methods used. The size of phytoplankton sampled was greater than 53 μm , on the high end for all types of grazers seen in Mission Bay,

which prefer prey in the range of 2–65 μm for ciliates (Kamiyama and Arima 2001) and 6–33 μm for similar sized copepods (Pagano et al. 2003). Standing stock was sampled, and primary production was not measured, so if top-down control of the algae was occurring, no increased algal abundance would have been observed. In copepods of the genus *Acartia* egg production and hatching success can change based on specific environmental conditions including salinity, temperature, and nutritional health (Moraitou-Apostolopoulou and Verriopoulos 1981; Barata et al. 2002; Castro-Longoria 2003). These are plausible explanations for the observations presented here, and it is not possible to confirm or reject any of them based on the data available.

Conclusions

The importance of rainfall in Mission Bay cannot be overstressed, particularly when concerning zooplankton. In 2003, high rainfall resulted in lowered salinities and high nutrient concentrations. During this year Mission Bay's zooplankton assemblage was very comparable to other shallow coastal embayments with seasonal freshwater inflow and restricted tidal exchange with the open ocean (Table 3). Species composition consisted of an assemblage with a number of copepod species (cluster 2A), which appeared following the rainfall and freshwater discharge. In 2002 and 2004, years with much lower freshwater inflow, Mission Bay behaved more like a typical Mediterranean coastal estuary with low freshwater discharge. Such environments are characterized by salinities consistently at or slightly above seawater, low nutrient concentrations, and a summer zooplankton assemblage consisting of many tintinnid species and relatively few copepod species, with smaller forms like *Oithona* spp. prevalent (Villate 1991a; Calbet et al. 2001; Gilabert 2001).

Interannual variability should be considered as an important factor in studies characterizing Mission Bay, as well as similar systems. A marked difference in annual rainfall influenced the zooplankton species composition in Mission Bay. One of the predicted consequences of global climate change is a corresponding change in global rainfall patterns (Postel 1986; Beuhler 2003; Kim 2005). From this study, it seems that changes in Mission Bay's zooplankton community would follow. These changes in the size structure of the copepod community might be seen at higher trophic levels; particularly as prey size is often an important factor for marine planktonic predators (Paffenhofer 1993; Uye 1994; Graham and Kroutil 2001).

ACKNOWLEDGMENTS

Valuable assistance was provided by P. Ajtai, E. Allen, M. Boudrias, K. Fink, R. Griggs, L. Hansen, J. Kittinger, H. Sarabia, B. Swope, and D. Twal. Thanks to B. Ripley and K. Tang for critical reviews of early drafts as well as two anonymous reviewers. Funding to support the authors and this research was provided by the City of San Diego (agreement #295495 to R. S. Kaufmann), the California State Water Resources Control Board (contract #02-184-559-1 to R. S. Kaufmann), and the University of San Diego.

LITERATURE CITED

- AMBLER, J. W., J. E. CLOERN, AND A. HUTCHINSON. 1985. Seasonal cycles of zooplankton from San Francisco Bay. *Hydrobiologia* 129: 177–197.
- ANNABI-TRABELSI, N., M. N. DALY-YAHIA, M. S. ROMDHANE, AND N. BEN MAIZ. 2005. Seasonal variability of planktonic copepods in Tunis North Lagoon (Tunisia, North Africa). *Cahiers de Biologie Marine* 46:325–333.
- ARFI, R., G. CHAMPALBERT, AND G. PATRITI. 1981. Plankton systems and urban pollution: An aspect of zooplankton populations. *Marine Biology* 6:133–141.
- ATKINSON, A. 1996. Subantarctic copepods in an oceanic, low chlorophyll environment: Ciliate predation, food selectivity and impact on prey populations. *Marine Ecology Progress Series* 130: 85–96.
- BARATA, C., M. MEDINA, T. TELFER, AND D. J. BAIRD. 2002. Determining demographic effects of cypermethrin in the marine copepod *Acartia tonsa*: Stage-specific short tests versus life-table tests. *Archives of Environmental Contamination and Toxicology* 43:373–378.
- BEUHLER, M. 2003. Potential impacts of global warming on water resources in southern California. *Water Science and Technology* 47: 165–168.
- BORCARD, D., P. LEGENDRE, AND P. DRAPEAU. 1992. Partialling out the spatial component of ecological variation. *Ecology* 73:1045–1055.
- BROWNLEE, D. C. AND F. JACOBS. 1987. Mesozooplankton and microzooplankton in the Chesapeake Bay, p. 217–269. In S. K. Majumdar, L. W. Hall, Jr., and H. M. Austin (eds.), *Contaminant Problems and Management of Living Chesapeake Bay Resources*, VOLUME. The Pennsylvania Academy of Science, Philadelphia, Pennsylvania.
- CALBET, A., S. GARRIDO, E. SAIZ, M. ALCARAZ, AND C. M. DUARTE. 2001. Annual zooplankton succession in coastal N.W. Mediterranean waters: The importance of the smaller size fractions. *Journal of Plankton Research* 23:319–331.
- CARTER, J. C. H. AND M. J. DADSWELL. 1983. Seasonal and spatial distribution of planktonic crustacea in the lower Saint John River, a multibasin estuary in New Brunswick, Canada. *Estuaries* 6:142–153.
- CASTELLANI, C., X. IRIGOIEN, R. P. HARRIS, AND R. S. LAMPITT. 2005. Feeding and egg production of *Oithona similis* in the North Atlantic. *Marine Ecology Progress Series* 288:173–182.
- CASTRO-LONGORIA, E. 2003. Production and hatching success of four *Acartia* species under different temperature and salinity regimes. *Journal of Crustacean Biology* 23:289–299.
- CHAPMAN, G. A. 1963. Mission Bay: A review of previous studies and the status of the sportfishery. *California Fish and Game* 49: 31–43.
- CLOERN, J. E. AND F. H. NICHOLS. 1985. Time scales and mechanisms of estuarine variability, a synthesis from studies of San Francisco Bay. *Hydrobiologia* 129:229–237.
- COLT, K. J. 1993. Toxicity of stormwater runoff entering San Diego and Mission Bays, California using the *Ceriodaphnia Dubia* 7-day Chronic Toxicity Test. M.S. Thesis, San Diego State University, San Diego, California.

- DAVIES, D. W. 1972. Nonconservative constituents in the waters of Mission Bay. M.S. Thesis, San Diego State University, San Diego, California.
- DAWSON, J. K. AND G. KNATZ. 1980. Illustrated key to the planktonic copepods of San Pedro Bay, California. The Allan Hancock Foundation and The Institute for Marine and Coastal Studies, University of Southern California, Los Angeles, California.
- ELLIOTT, D. T. 2006. Environmental factors affecting the zooplankton community in Mission Bay, San Diego, California. M.S. Thesis, University of San Diego, San Diego, California.
- FAIRBANKS, D. A. 1969. Environmental factors affecting phytoplankton populations in Mission Bay. M.S. Thesis, San Diego State University, San Diego, California.
- FULTON, R. S. 1984. Predation, production and the organization of an estuarine copepod community. *Journal of Plankton Research* 6:399–415.
- GAUGHAN, D. J. AND I. C. POTTER. 1995. Composition, distribution and seasonal abundance of zooplankton in a shallow, seasonally adjusted closed estuary in temperate Australia. *Estuarine, Coastal and Shelf Science* 41:117–135.
- GIBSON, C. E., G. WANG, AND R. H. FOY. 2000. Silica and diatom growth in Lough Neagh: The importance of internal recycling. *Freshwater Biology* 45:285–293.
- GILBERT, J. 2001. Seasonal plankton dynamics in a Mediterranean hypersaline coastal lagoon: The Mar Menor. *Journal of Plankton Research* 23:207–218.
- GODHANTARAMAN, N. 1994. Species composition and abundance of tintinnids and copepods in the Pichavaram mangroves (south India). *Ciencias Marinas* 20:371–391.
- GRAHAM, W. M. AND R. M. KROUTIL. 2001. Size-based prey selectivity and dietary shifts in the jellyfish, *Aurelia aurita*. *Journal of Plankton Research* 23:67–74.
- HAERTEL, L. AND C. OSTERBERG. 1967. Ecology of zooplankton, benthos and fishes in the Columbia River Estuary. *Ecology* 48:459–472.
- HIPPAKA, W. H. 1991. The history of the development of Mission Bay Aquatic Park in San Diego, California. The California State University-Real Estate and Land Use Institute, School of Business Administration, Sacramento, California.
- HIRST, A. G. AND R. S. LAMPITT. 1998. Towards a global model of in situ weight-specific growth in marine planktonic copepods. *Journal of Marine Biology* 132:247–257.
- HUNTLEY, M. E. AND M. D. G. LOPEZ. 1992. Temperature-dependent production of marine copepods: A global synthesis. *American Naturalist* 140:201–242.
- KAMIYAMA, T. AND S. ARIMA. 2001. Feeding characteristics of two tintinnid ciliate species on phytoplankton including harmful species: Effects of prey size on ingestion rates and selectivity. *Journal of Experimental Marine Biology and Ecology* 257:281–296.
- KAMIYAMA, T. AND M. TSUJINO. 1996. Seasonal variation in the species composition of tintinnid ciliates in Hiroshima Bay, the Seto Inland Sea of Japan. *Journal of Plankton Research* 18:2313–2327.
- KIM, J. 2005. A projection of the effects of the climate change induced by increased CO₂ on extreme hydrologic events in the Western U.S. *Climate Change* 68:153–168.
- KRSINIC, F. 1987. Tintinnines (Ciliophora, Oligotrichida, Tintinnina) in eastern Adriatic bays. *Estuarine, Coastal and Shelf Science* 24:527–538.
- LAPRISE, R. AND J. J. DODSON. 1994. Environmental variability as a factor controlling spatial patterns in distribution and species diversity of zooplankton in the St. Lawrence Estuary. *Marine Ecology Progress Series* 107:67–81.
- LARGIER, J. L., M. CARTER, M. ROUGHAN, D. SUTTON, J. HELLY, B. LESH, T. KACENA, P. AJTAI, L. CLARKE, D. LUCAS, P. WALSH, AND L. CARRILLO. 2003. Mission Bay Contaminant Dispersion Study Final Report. City of San Diego, California.
- LARGIER, J. L., J. T. HOLLIBAUGH, AND S. V. SMITH. 1997. Seasonally hypersaline estuaries in Mediterranean-climate regions. *Estuarine, Coastal and Shelf Science* 45:789–797.
- LEE, J. J., S. H. HUNTER, AND E. C. BOVEE. 1985. An Illustrated Guide to the Protozoa, 1st edition. Society of Protozoologists, Lawrence, Kansas.
- LEGENDE, P. AND L. LEGENDRE. 1998. Numerical Ecology, 2nd English edition. Elsevier Science, Amsterdam, Netherlands.
- LILLEBO, A. I., J. M. NETO, I. MARTINS, T. VERDELHOS, S. LESTON, P. G. CARDOSO, S. M. FERREIRA, J. C. MARQUES, AND M. A. PARDAL. 2005. Management of a shallow temperate estuary to control eutrophication: The effect of hydrodynamics on the system's nutrient loading. *Estuarine, Coastal and Shelf Science* 65:697–707.
- MARQUES, S. C., U. M. AZEITEIRO, J. C. MARQUES, J. M. NETO, AND M. A. PARDAL. 2006. Zooplankton and ichthyoplankton communities in a temperate estuary: Spatial and temporal patterns. *Journal of Plankton Research* 28:297–312.
- MORAITOU-APOSTOLOPOULOU, M. AND G. VERRIOPOULOS. 1981. Egg laying in two populations of *Acartia clausi* exposed to different degrees of pollution. *Vie et Milieu* 31:65–69.
- MOUNY, P. AND J.-C. DAUVIN. 2002. Environmental control of mesozooplankton community structure in the Seine Estuary (English Channel). *Oceanologica Acta* 25:13–22.
- PAFFENHOFER, G. A. 1993. On the ecology of marine cyclopoid copepods (Crustacea, Copepoda). *Journal of Plankton Research* 15:37–55.
- PAGANO, M., E. KOUASSI, L. SAINT-JEAN, R. ARFI, AND M. BOUVY. 2003. Feeding of *Acartia clausi* and *Pseudodiaptomus hessei* (Copepoda: Calanoida) on natural particles in a tropical lagoon (Ebrie, Cote d'Ivoire). *Estuarine, Coastal and Shelf Science* 56:433–445.
- PIERCE, R. W. AND J. T. TURNER. 1993. Global biogeography of marine tintinnids. *Marine Ecology Progress Series* 94:11–26.
- PINEL-ALLOUL, B. 1995. Spatial heterogeneity as a multiscale characteristic of zooplankton community. *Hydrobiologia* 300–301:17–42.
- POSTEL, S. L. 1986. Atmospheric warm-up. *Environmental Science and Technology* 20:1208–1209.
- ROMAN, M. R., A. L. GAUZENS, W. K. RHINEHART, AND J. R. WHITE. 1993. Effects of low-oxygen waters on Chesapeake Bay zooplankton. *Limnology and Oceanography* 38:1603–1614.
- RYVES, D. B., R. W. BATTARBEE, S. JUGGINS, S. C. FRITZ, AND N. J. ANDERSON. 2006. Physical and chemical predictors of diatom dissolution in freshwater and saline lake sediments in North America and West Greenland. *Limnology and Oceanography* 51:1355–1368.
- SABATINI, M. AND T. KIORBOE. 1994. Egg production, growth and development of the marine cyclopoid copepod *Oithona similis*. *Journal of Plankton Research* 16:1329–1351.
- SCHUBEL, J. R. AND D. W. PRITCHARD. 1987. A brief physical description of the Chesapeake Bay, p. 1–32. In S. K. Majumdar, L. W. Hall, Jr, and H. M. Austin (eds.), Contaminant Problems and Management of Living Chesapeake Bay Resources. The Pennsylvania Academy of Science, Philadelphia, Pennsylvania.
- SNYDER, H. G. 1965. Some larval fishes of Mission Bay, San Diego County, California. M.S. Thesis, San Diego State College, San Diego, California.
- SOETAERT, K. AND P. VAN RIJSWIJK. 1993. Spatial and temporal patterns of the zooplankton in the Westerschelde Estuary. *Marine Ecology Progress Series* 97:47–59.
- SWOPE, B. L. 2005. Spatial and temporal dynamics of phytoplankton in Mission Bay over a complete annual cycle. M.S. Thesis, University of San Diego, California.
- TALLEY, D. M. 2000. Ichthyofaunal utilization of newly-created versus natural salt marsh creeks in Mission Bay, California. *Wetlands Ecology and Management* 8:117–132.
- TAW, N. AND D. N. RITZ. 1978. Zooplankton distribution in relation to the hydrography of the Derwent River Estuary. *Australian Journal of Marine and Freshwater Research* 29:763–775.
- TER BRAAK, C. J. F. AND P. F. M. VERDONSCHOT. 1995. Canonical correspondence analysis and related multivariate methods in aquatic ecology. *Aquatic Sciences* 57:255–289.

- URRUTXURTU, I. 2004. Seasonal succession of tintinnids in the Nervion River Estuary, Basque Country, Spain. *Journal of Plankton Research* 26:307–314.
- UYE, S. I. 1994. Replacement of large copepods by small ones with eutrophication of embayments: Cause and consequence. *Hydrobiologia* 292/ 293:513–519.
- UYE, S. I., N. NAGANO, AND T. SHIMAZU. 1998. Biomass, production and trophic roles of micro- and net zooplankton in Dokai Inlet, a heavily eutrophic inlet, in summer. *Plankton Biology and Ecology* 45:171–182.
- VIDJAK, O., N. BOJANIC, G. KUSPILIC, I. MARASOVIC, Z. N. GLADAN, AND I. BRAUTOVIC. 2006. Annual variability and trophic relations of the mesozooplankton community in the eutrophicated coastal area (Vranjic Basin, eastern Adriatic Sea). *Journal of the Marine Biological Association of the United Kingdom* 86:19–26.
- VIEIRA, L., U. P. AZEITEIRO, R. PASTORINHO, J. C. MARQUES, AND F. MORGADO. 2003. Zooplankton distribution in a temperate estuary (Mondego estuary southern arm: Western Portugal). *Acta Oecologica* 24:S163–S173.
- VILLATE, F. 1991a. Annual cycle of zooplankton community in the Abra Harbour (Bay of Biscay): Abundance, composition and size spectra. *Journal of Plankton Research* 13:691–706.
- VILLATE, F. 1991b. Zooplankton assemblages in the shallow tidal estuary of Mundaka (Bay of Biscay). *Cahiers de Biologie Marine* 32: 105–119.
- WILDERMAN, C. C. 1987. Patterns of distribution of diatom assemblages along environmental gradients in the Severn River Estuary, Chesapeake Bay, Maryland. *Journal of Phycology* 23:209–217.
- YOUNG, C. M., M. A. SEWELL, AND M. E. RICE. 2002. Atlas of Marine Invertebrate Larvae. Academic Press, San Diego, California.

SOURCES OF UNPUBLISHED Materials

- BOLENDER, J. P. personal communication. Department of Chemistry, University of San Diego, San Diego, California 92110.
- SETMIRE, J. G. AND W. L. BRADFORD. 1980. Quality of Urban Runoff, Tecolote Creek Drainage Area, San Diego County, California. PB81-159451. Available from the National Technical Information Service, Springfield, Virginia 22161.

Received, April 17, 2006

Revised, February 12, 2007

Accepted, March 3, 2007