Lake and Reservoir Management 23:570-581, 2007

Decline of springtime abundance of the pileworm *Neanthes succinea* in relation to hydrographic conditions at the Salton Sea, California

Deborah M. Dexter, Joan S. Dainer, Paul M. Detwiler,
Marie F. Moreau and Stuart H. Hurlbert*
Department of Biology and Center for Inland Waters,
San Diego State University, San Diego, CA 92182, USA

Abstract

Dexter, D.M., J.S. Dainer, P.M. Detwiler, M.F. Moreau and S.H. Hurlbert. 2007. Decline of springtime abundance of the pileworm *Neanthes succinea* in relation to hydrographic conditions at the Salton Sea, California. Lake Reserv. Manage. 23:570-581.

The Salton Sea is the largest lake in California, and its most abundant macroinvertebrate is the pileworm (*Neanthes succinea*: Polychaeta). This is a major dietary item for three of the four most abundant fish species in the lake, and for at least one waterbird, the eared grebe (*Podiceps nigricollis*). Pileworm abundance in April 2004 was monitored at depths of 2, 6 and 10 m on seven transects distributed around the perimeter of the lake. Temperature and oxygen showed marked stratification with depth. Densities were compared to those observed in April 1999. Abundances at 2 m stations were similar to those in 1999; however, densities were greatly reduced at 6 and 10 m stations compared to 1999. The development of hypoxic or anoxic bottom conditions apparently occurred earlier in the spring in 2004 than in 1999. This was the most likely cause for the low densities at 6 and 10 m. Worm densities were higher at sites with coarser sediments (sand and/or barnacle shell debris), and lowest at 2 m sites near or downstream of freshwater inflows and at 10 m where near anoxic conditions prevailed. In March 2005, a sampling of 74 stations at depths ranging from 1 m to 10 m all around the perimeter of the lake found only a single pileworm. It was evident that the lake had just turned over and that sulfide levels were very high and had probably killed off most pileworms and many other organisms as well.

Key words: salt lake, anoxia, sulfide, mixing regime, oxygen, polychaetes, *Podiceps nigricollis*

Introduction

The Salton Sea, a large inland saline lake in southern California (Fig. 1), is an important ecosystem for several species of rare and endangered birds, has a diverse microbial and algal flora, a somewhat depauperate invertebrate fauna, and, until recently, a large sport fishery. The salinity of the Salton Sea is rising and its shoreline is receding, partially as a result of water conservation practices. The salinity levels are approaching the upper tolerance limits for many of the current fish and benthic invertebrate species, so additional increases in salinity are likely to cause major changes in the system. The most abundant macroinvertebrate in the lake during the past half century has been the pileworm (*Neanthes succinea* Frey and Leuckart).

The objective of this study was to assess the status of the status of the *Neanthes* population in 2004 and 2005 and compare it with its status in 1999, as reported in Detwiler *et al.* (2002). In April 2004 its density in sediments was measured along seven depth transects distributed around the margins of the Salton Sea. Three of these transects were sampled in March/April 1999 and thus allow estimation of population change over the past 5 years at those sites. In March 2004, an attempt to collect *Neanthes* at 74 sites distributed over the Sea for selenium analyses yielded further dramatic information on the population.

During the five year interval between sampling periods, the Sea experienced marked changes in its physical environment and in its biological community. Salinity increased ~ 2 percent, and anoxic events occurred earlier in the spring in 2004 and 2005 than in 1999 (Watts *et al.* 2001, Tiffany *et al.* 2002, Anderson *et al.* 2007; Tiffany *et al.* 2007). Fish

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* Corresponding author: shurlbert@sunstroke.sdsu.edu

and fish-eating bird populations crashed during this period (Caskey *et al.* 2007; Hurlbert *et al.* 2007), and the eared grebe population (*Podiceps nigricollis* Brehm) estimated at 0.5 and 1 million between 1990-2001, declined to approximately 50,000 from 2002 onward (Anderson *et al.* 2007). Phytoplankton abundance in 2005 was at least twice that in 1998 and 1999 (Tiffany *et al.* 2007).

Only two major studies have examined the abundance and distribution of macrobenthos in the Salton Sea (Carpelan and Linsley 1961; Detwiler *et al.* 2002). Both identified *N. succinea* as the dominant macroinvertebrate and the major species in the food chain providing energy from the benthos to fish and birds. Factors likely to influence the abundance of *Neanthes* in general include salinity, sediment composition and particle size, oxygen and sulfide concentration, and density of predators, especially tilapia (*Oreochromis mossambicus* Peters) and eared grebes at the Salton Sea (Detwiler *et al.* 2002).

Neanthes succinea, native to the north Atlantic, is found on both coasts of the Atlantic and Pacific oceans in both northern and southern hemispheres (Pettibone 1963). Throughout this range, it occurs over a wide range of microhabitats under varying conditions of temperature, oxygen level, salinity and sediment type. In the Salton Sea it is present on or in shoreline, algae-covered rocks, barnacle-covered rocks, and loose barnacle shell substrates, and in offshore sediments of sand, silt, clay, and barnacle shell debris. Estimated standing stock of *Neanthes* within the Sea in 1999 was as high as 15,125 metric tons, with numerical density reaching 21,300 m^{-2} (Detwiler *et al.* 2002).

When *N. succinea* becomes reproductively active, its morphology changes: eyes enlarge, body length decreases, and parapodia become highly modified for swimming. The reproductive males and females leave the benthic substrate as heteronereids and migrate toward the surface of the water column. Individuals reproduce only once and die after releasing their gametes (Reish 1957; Pettibone 1963). Planktonic larvae develop from the fertilized eggs. Larvae are present throughout the year at the Salton Sea, but during 1997-1999 larvae were most abundant in spring and late fall (Tiffany *et al.* 2002).

The movement of gamete-laden heteronereids from sediments to surface waters must represent a significant net transport of food, nitrogen, and phosphorus to fish and plankton populations in surface waters. All bottom-dwelling stages of *Neanthes* recycle significant amounts of phosphorus from sediments to the overlying water by means of their feeding, excreting, and burrow-ventilating activities, especially in early spring (Swan *et al.* 2006).

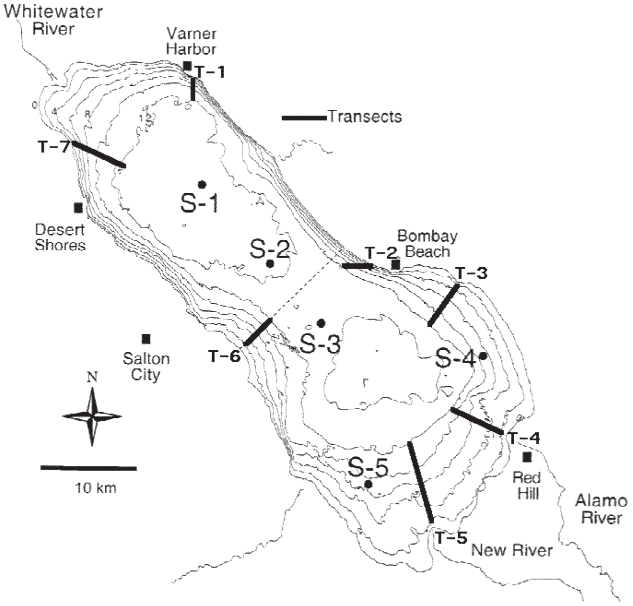

Figure 1.-Location of transects (T) and stations (S) sampled for *Neanthes succinea* in Salton Sea, April 15-16, 2004.

Methods

Sampling regime in 2004

Sampling of *Neanthes* and measurement of physical and chemical variables were carried out at three depths (2, 6, and 10 m) along each of seven transects extending out from the shoreline of the lake (Fig. 1, Table 1). Stations on transects 1-3 along the eastern shore were the ones sampled in 1999. There were, however, slight changes in the position of these stations between 1999 and 2004 due to a 0.2 m drop in lake level between April 1999 and April 2004 (Imperial Irrigation District, unpublished records), but sediment types at the 2004 sites were comparable to those of the 1999 sites. At the nearshore end of each transect, a station at 2 m depth was located precisely. From there, the 6 m and 10 m deep stations were located along the same compass headings as were used in 1999. Three of the new transects were located off the mouths of the Alamo (4), New (5), and Whitewater (7) rivers. These rivers account for 45-48%, 32-36%, and 4-5%, respectively, of the $1.5\text{-}1.6 \times 10^9$ m^3 of freshwater inflow to the lake per year (Cohen *et al.* 1999; Watts *et al.* 2001). Thus, most freshwater inflow occurs along the lake's southern margin (Fig. 1). The remaining transect (6) was located just south of Salton City far from all significant points of freshwater inflow. Sampling was carried out on April 15-16, 2004.

Table 1.-Location and time that recording of physical data began, for *Neanthes* sampling stations, April 15-16, 2004.

Transect	**Date, time, geographic coordinates, and distance (m) of station from nearest shoreline**			**Description of location & compass heading from 2 m station**
Station depth →	**2 m**	**6 m**	**10 m**	
1	Apr 16 1524 N 33° 30.551’ W 115° 55.416’ 60	Apr 16 1425 33° 30.263’ 115° 55.267’ 390	Apr 16 1450 33° 30.127’ 115° 55.701’ 960	off North Shore Marina 164°
2	Apr 16 1000 N 33° 20.744’ W 115° 43.921’ 170	Apr 16 1020 33° 20.657’ 115° 44.250’ 590	Apr 16 1054 33° 20.402’ 115° 45.035’ 1750	West of Bombay Beach 261°
3	Apr 15 1700 N 33° 20.131’ W 115° 39.292’ 380	Apr 15 1720 33° 18.617’ 115° 40.507’ 3070	Apr 15 1759 33° 19.211’ 115° 42.704’ 3400	South of Bombay Beach 244°
4	Apr 15 1513 N 33° 12.800’ W 115° 37.289’ 330	Apr 15 1542 33° 14.214’ 115° 39.117’ 4290	Apr 15 1610 33° 14.742’ 115° 39.711’ 5620	off Alamo River mouth 280°
5	Apr 15 1311 N 33° 08.121’ W 115° 41.642’ 420	Apr 15 1341 33° 10.140’ 115° 43.392’ 4990	Apr 15 1407 33° 11.155’ 115° 44.279’ 6450	off New River mouth 340°
6	Apr 15 1004 N 33° 17.014’ W 115° 52.810’ 540	Apr 15 1045 33° 18.193’ 115° 52.448’ 2600	Apr 15 1145 33° 18.941’ 115° 52.206’ 4020	South of Salton City, directly East of Tule Wash 40°
7	Apr 16 1229 N 33° 27.816’ W 116° 03.397’ 70	Apr 16 1259 33° 27.910’ 116° 02.726’ 850	Apr 16 1329 33° 28.007’ 116° 01.456’ 2520	off Whitewater River mouth, directly E of 81st Avenue 110°

Neanthes *sampling and processing*

At each sampling station three replicate samples were taken with a petite Ponar grab operated with a winch. This grab collects surface sediments from 225 cm^2 of lake bottom to a depth of 15 cm. Field and laboratory sample processing followed procedures used in 1999 (Detwiler *et al.* 2002). All material remaining on a 1000 µm mesh sieve was preserved in a solution of buffered 3.4% formaldehyde with rose Bengal added. In the lab, each sample was transferred into 70% ethanol, the worms were counted, and their total wet mass was determined after blotting with paper toweling to remove excess water.

Temperature and oxygen measurements

At each sampling site, temperature and oxygen were measured at 1 m intervals from the surface of the lake to the bottom using a YSI 85 temperature, oxygen, and conductance probe.

Sediment analysis

In the field, sediment composition and general appearance was noted and photographed for each replicate grab sample. Descriptions and photos of sediment samples were compared to those of the 1999 samples. Sediments were washed through a sieve with 1000 µm mesh, and the retained materials from each set of replicates were combined into a composite sample in the laboratory. After removal of pileworms, this composite sample was dried overnight at 105 °C and weighed. Visual estimates were made of the percentages of the total bulk contributed by a) fish bones, b) barnacle shell, and c) other material, which was mostly a dark brown granular material and sometimes cemented together in rough, flat plates. Gypsum ($Ca_2SO_4 \cdot 2H_2O$) content of this material was determined as weight loss of a mortar-pulverized, ca. 1 g sample after immersion for ca. 12 h in 500 ml of deionized water maintained at about 95 °C.

Data analysis

Analysis consisted principally of calculating geometric means (GM), for sets of replicate samples or replicate stations, and their corresponding standard error factors (SEF). The SEF is the antilog of the standard error (SE) calculated on the log-transformed data. To deal with zero values, a constant was added to all sample values prior to log transformation. For numerical densities (no. m^{-2}), this constant was 44, the lowest possible non-zero value (= 1 worm per 225 cm^2 = 44 worms per m^2). For biomass densities (g m^{-2}), the constant used was 0.0044, which was 44 times the lowest non-zero *Neanthes* biomass observed (0.0001 g) for any 225 cm^2 grab sample. Each GM was plotted along with error bars representing the GM multiplied and divided by, respectively, the standard error factor (SEF). Henceforth in this article, all references to mean pileworm abundance should be understood to refer to geometric means.

As many comparisons are of potential interest (*e.g.*, between years, among transects, among depths), we do not carry out explicit significance tests. The reader may infer the results of such by visually assessing whether appropriate extensions of the error bars for two means overlap or not. Those extended error bars are termed inferential confidence intervals (Tryon 2001). They are equal to 0.71 *times* the length of the shown error bars *times* the critical *t* value for a given degrees of freedom and selected α value. Hence, where we have 3-fold replication (*e.g.*, as in Figs. 3 and 4), two means will be "significantly different" at the 0.10 level of significance if their inferential confidence intervals are each 2.07 times the shown error bar *and* abut each other but do not overlap.

Sampling in 2005

During March 14-17, 2005 an effort by one of us (M. Moreau) was made to collect *Neanthes* for determination of their selenium levels, as part of an expanded effort to assess selenium levels in different components of the lake's food web. This provided some information on the status of the population at that time. As in 1999 and 2004, sampling was carried out using a Ponar grab; 1–3 grab samples were taken from depths ranging from 1 to 10 m at each of 74 different stations around the lake perimeter. Sediments were sieved through a 1500 µm screen, rather than a 1000 µm mesh, as we sought *Neanthes* in bulk.

Results

Temperature and oxygen

In 2004, at all sampling stations, surface (0-1 m) water temperatures ranged between 21.5 and 26.6 °C and oxygen levels between 5.2 and 26.0 mg l^{-1} (Fig. 2). Just above the lake bottom where grab samples were taken, temperatures ranged from 20.4 to 25.6 °C and oxygen from 0.2 to 19.0 mg l^{-1}. Marked stratification of both variables was usually evident in the top 4 m of the water column, at least at the 6 m and 10 m stations. Vertical profiles for temperature and oxygen varied among stations, and the variation was greater among those stations closest to shore. Over short time scales, both temperature and oxygen are strongly influenced by diel variations in photosynthesis, insolation, air temperature, and wind conditions. Some of the variation among profiles for the surface few meters may have been accounted by changes in those factors over the two days during which sampling occurred. However, large differences among profiles in deeper waters showed that different portions of the lake must have had quite different hydrodynamic behavior, at least over many days.

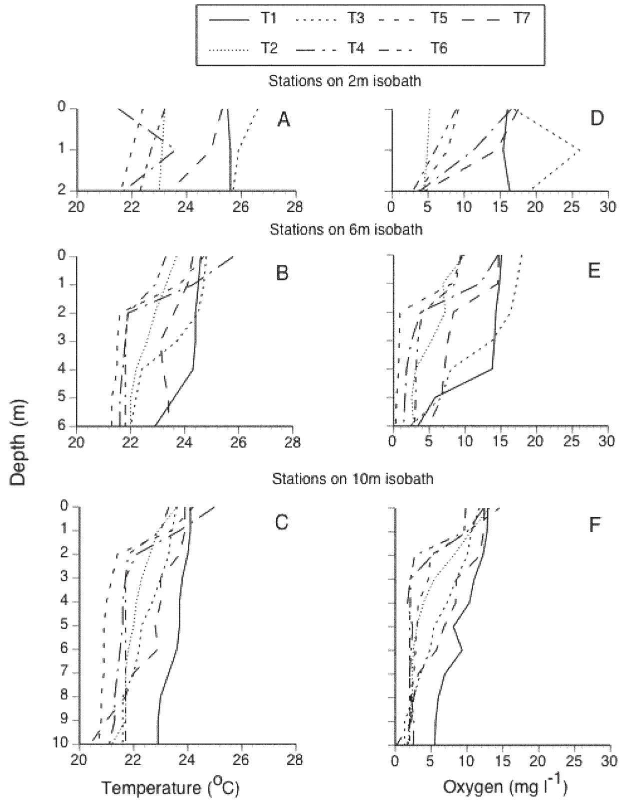

Figure 2.-Depth profiles of temperature (A-C) and oxygen (D-F) profiles at the 21 sampling stations on the 7 transects, April 15-16, 2004.

For example, the two northernmost transects (T1, T7) showed less stratification in temperature and oxygen than did other transects, especially at the 10 m stations. This was also apparent at the two southernmost transects (T4, T5) (Fig. 2C, F). These results may be due to wind-induced mixing during a brief windstorm of the previous day. However, the deeper strata also tended to have higher temperature and oxygen

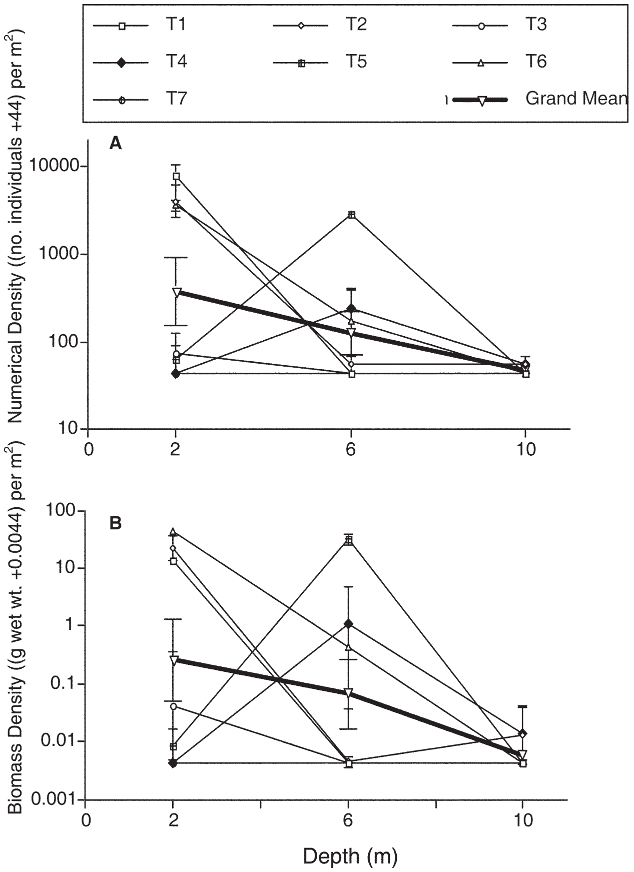

Figure 3.-Geometric mean numerical (A) and biomass (B) densities of *Neanthes* along seven depth transects, April 15-16, 2004. Error bars (most too small to be visible) represent ×/÷ 1 SEF (standard error factor), based on three replicate grab samples.

values at T1-10 m and T7-10 m than at other 10 m stations. Thus, it may have been the northernmost location of T1 and T7, and some different behavior of the northern basin in general, that accounted for their particular profiles, rather than wind conditions on April 15. It is notable that the T1-10 m water column was almost isothermal and had moderate oxygen levels (> 5 mg l^{-1}) even at 10 m, suggesting recent strong vertical mixing.

Photosynthesis by the dense phytoplankton typical of the Salton Sea (Tiffany *et al.* 2007) accounts for high oxygen values that were often, especially in surface waters near shore, well above 100 percent saturation and sometimes above 200 percent (Fig. 2D, E, F). Salinity of the Salton Sea in 2004 was about 45-46 g l^{-1} and at a temperature of about 22 °C, 100 percent oxygen saturation at the lake surface would be roughly 7 mg l^{-1} (Sherwood *et al.* 1991). Similarly, high oxygen values have been documented in previous studies of the lake (Watts *et al.* 2001; Holdren and Montaño 2002). Even the 26 mg l^{-1} recorded for a depth of 1 m at T4-2 m was credible (Fig. 2D). At that station, just off the mouth of the Alamo River, specific conductance (conductivity standardized to a temperature of 25 °C) was 43 mS at the lake surface and 52 mS at 1 m depth. It is conceivable that a halocline-stabilized stratum at 1 m could harbor a dense plate of dinoflagellates and other algae generating oxygen throughout the day prior to our late afternoon reading faster than oxygen could be lost via bubble formation.

Sediment characteristics

Though abundance of the fine (< 1000 μm) fractions was not quantified, silt appeared to be the dominant component of sediment at 6 m and 10 m depths in 2004, as it was in 1999 (Detwiler *et al.* 2002, Table 2). At 2 m depths, sediment type was variable and included barnacle shell at sites off rocky areas (T1, T6), sand (T2), and an anerobic slurry near the mouths of the New and Alamo rivers (T4, T5), and silt (T3, T7).

Abundance of coarse sediments was highly variable, ranging from 0 to 201 cm^3 per 100 cm^2 of lake bottom (Table 2). Barnacle shell made up ≥ 20% of coarse sediments at 9 of the 21 stations. Fish bones were a minor but conspicuous component at 14 stations. Gypsum was present at all stations except the two where only a black slurry was present. At the other stations it made up 8 to 52% of the coarse sediments, averaging 27%. There was a slight tendency for both the relative and absolute amount of gypsum in coarse materials to increase with depth (Fig. 5 and Table 2). Only one of the seven 2 m stations had more than 5 g gypsum per 100 cm^2 of lake bottom, but 8 of the 14 6 m and 10 m stations did. The 2 m stations averaged 1.7 g, the 6 m stations 10.2 g, and the 10 m stations 12.2 gypsum per 100 cm^2 of lake bottom (Table 2).

All sediments obtained during the March 2005 sampling effort showed evidence of anoxia, and released a strong hydrogen sulfide odor. Surface layers consisted of slimy, black organic matter, possibly derived from recent massive die-offs of plankton populations and other organisms. Only two of the 21 stations sampled in April 2004 (T4-2 m and T5-2 m) yielded sediment samples of this sort.

Abundance of Neanthes

In 2004, mean numerical density of *Neanthes* decreased by two orders of magnitude with depth, from 333 and 84 per m^2 for the 2 m and 6 m stations, respectively, to 3 per m^2 for the 10 m stations (Fig. 3). Mean biomass per m^2 was 258 mg for the 2 m stations, 64 mg for the 6 m, and 2 mg for the 10 m. *Neanthes* was present at only two of the seven 10 m stations.

Mean body mass of individual worms varied by two orders of magnitude among stations (Table 3). For example, in

Table 2.-Some characteristics of sediments at the 21 Neanthes sampling stations, April 15-16, 2004.

		Coarse sediments (particle size > 1000 µm)					
		Percent of total bulk					
Transect no. & Station depth	**Dominant sediment type**	**Barnacle shell**	**Fish bones**	**Gypsum**	**Other coarse**	**Bulk volume (cm^3 per 100 cm^2)**	**Gypsum (g per 100 cm^2)**
T1							
2 m	barnacle shells	88	4	8	0	34	2.7
6 m	brown silt	44	1	24	31	45	11
10 m	brown silt	1	2	36	61	31	11
T2							
2 m	sand	20	1	34	45	12	4.0
6 m	dk brown silt, some clay	0	1	21	78	2.5	0.5
10 m	dk brown silt	0	2	52	46	14	5.0
T3							
2 m	brown silt	20	1	26	53	1.7	0.45
6 m	dk brown silt, some clay	10	0	29	61	1.5	0.43
10 m	black silt, clay	0	1	36	63	32	12
T4							
2 m	black, anaerobic, fluid	-	-	-	-	0	0
6 m	sand	10	0	33	57	33	11
10 m	brown silt	1	0	27	72	37	10
T5							
2 m	black, anaerobic, fluid	-	-	-	-	0	0
6 m	gray clay	2	0	23	75	66	15
10 m	brown clay,some silt	2	2	21	75	15	3.1
T6							
2 m	sandy silt, barnacle shells	30	0	39	31	70	27
6 m	dk brown silt, some clay	62	1	16	21	158	25
10 m	brown silt	60	5	21	14	201	42
T7							
2 m	brown silt	74	1	17	8	29	4.8
6 m	brown silt	77	1	13	9	43	5.5
10 m	brown silt, soupy	5	5	41	49	5.2	2.2

going from T5-2 m to T5-6 m, numerical density increased ~140-fold while biomass density increased by ~7200-fold (Fig. 3). Wherever only 1 or 2 worms were present in the sample, these invariably were very small (< 5 mm), perhaps representing new recruits originating from sites with high adult densities.

Great variation among transects existed in the depth-abundance relation (Fig. 3). No *Neanthes* were collected south of the Whitewater River on transect T7. On four transects (T1, T2, T3, T6), densities were greater at the 2 m than the 6 m station, while on two transects (T4, T5) densities were greater at the 6 m than the 2 m station. For 2 m stations, lowest absolute densities were found near or just downcurrent from freshwater inflows (T3, T4, T5, T7). Among 6 m stations, greatest observed densities were at T5-6 m, which is usually bathed by waters coming from midlake in the counter-clockwise gyre of the southern basin (Arnal 1961; Cook *et al.* 2002).

The sampling effort in March 2005 was so dramatically unsuccessful that no tables or figures are warranted: our grab hauls at 74 sampling stations yielded a single *Neanthes* measuring 30 mm in length. The specimen was found in the northernmost part of the lake a few km south of the mouth of the Whitewater River (or Coachella Valley Floodwater Channel). We did not measure physical or chemical variables on this occasion, but the odor of hydrogen sulfide was present over the whole lake, all sampled sediments appeared anoxic, and tiny gypsum crystals, an indicator of sulfide events (Watts *et al.* 2001), were present in water samples taken from the southwestern corner of the lake. Additionally, no

Table 3.-Mean individual body mass of *Neanthes succinea* collected at sampling stations in April 1999 and 2004. Stations without worms are not included.

Transect	Station depth (m)	Number of worms per 3 grabs	Total mass (mg) per 3 grabs	Mass per worm (mg)
		1999		
T1	2	42	227	5.4
	6	5	216	43
	10	8	213	27
T2	2	10	56	5.6
	6	47	682	15
	10	42	830	20
T3	2	63	646	10
	6	16	479	30
	10	49	1087	22
		2004		
T1	2	583	923	1.6
T2	2	320	1881	5.9
	6	1	1	1
	10	1	2.7	2.7
T3	2	4	78.2	20
T4	6	17	216	13
	10	1	2.9	2.9
T5	2	2	0.7	0.4
	6	191	2264	12
T6	2	249	2948	12
	6	21	407	19

live *Neanthes*, amphipods (*Gammarus mucronatus* Say), or adult barnacles (*Balanus amphitrite* Darwin) were observed along the many portions of lake shoreline examined in days following sampling, though air-breathing water boatmen (*Trichocorixa reticulata* Guérin-Menéville) were abundant in many places.

Changes since 1999

In 2004, while there was no significant change in *Neanthes* mean abundance since 1999 at the 2 m stations, abundance at 6 and 10 m stations was much lower than in 1999 (Fig. 4). Mean body mass of *Neanthes* along these three transects was both much higher and less variable among stations in 1999 than it was in 2004 (Table 3). The only exception was at the 2 m depth at T3 in 2004, where mean body mass was twice as high as in 1999. Mean individual mass was highest at the 6 m stations and lowest at the 10 m. These differences reflect a greater proportion of very small worms (length < 5 mm), recently recruited to the sediment in the 2004 samples. The largest *Neanthes* observed both years were on the order of 50 mm long, although no measurements of sizes of individual worms were made in either year. In 2005 pileworms were obviously dramatically lower than in 1999.

Discussion

Factors causing decline

Given the absence of any strong evidence of marked change between 1999 and 2004 in mean abundance at the 2 m stations, and the presence at many stations of robust adults as well as recently settled juveniles, we initially concluded that the *Neanthes* population remained in good condition in 2004 and that its reduced abundance at the 6 m and 10 m stations on the three transects in 2004 might simply have reflected a more rapid seasonal onset of reduced oxygen conditions in 2004 than in 1999. The near total absence of *Neanthes* over the whole lake in March 2005, reflects an even earlier onset of reduced oxygen and high sulfide conditions. It may signal a longer term change in state of the lake that bodes ill for the *Neanthes* population. The recent decline in eared grebe numbers at the Salton Sea may be due to drastic reduction of the *Neanthes* population by increasingly severe or frequent periods of anoxia and high sulfide levels (Anderson *et al.* 2007).

Lack of temperature and oxygen profiles for benthic sampling stations in 1999 prohibits a direct comparison with those for 2004. But mid-lake data from Watts *et al.* (2001) and C. Holdren (unpublished data) are informative. In 1999, hypoxic conditions (< 1 mg O_2 l^{-1}) at the three midlake stations (S-1, 2, 3; Fig. 1) were not detected anywhere in the water column (0-12 m) until June 8, although oxygen profiles had also been measured on March 16, April 7 and 25, and May 10 and 25 of that year. In contrast, in 2004, hypoxic conditions were detected – below 8 m at S-1, below 10 m at S-2, and below 4 m at S-3 – as early as March 30 (Fig. 1) (C. Holdren, unpublished data).

Earlier onset of hypoxic conditions at depth could develop as a result of markedly different wind and current regimes during March and April of 2004 and 1999. Thermal stratification can also inhibit downward mixing of oxygen. However, there was evidence that overall seasonal warming occurred in the central region of the lake at about the same pace in both years. For the three mid-lake stations (S-1, 2, 3, in Fig. 1) mean water column (2-12 m) temperature was 16.8 °C on April 7, 1999 (Watts *et al.* 2001 and unpublished data) and 17.4 °C on March 30, 2004 (C. Holdren, unpublished data).

Detwiler *et al.* (2002) noted tentative evidence of the *Neanthes* population in the Salton Sea being much lower in 1999 than in 1956. While we are cognizant of the danger of concluding that there has been a long-term decline in such a

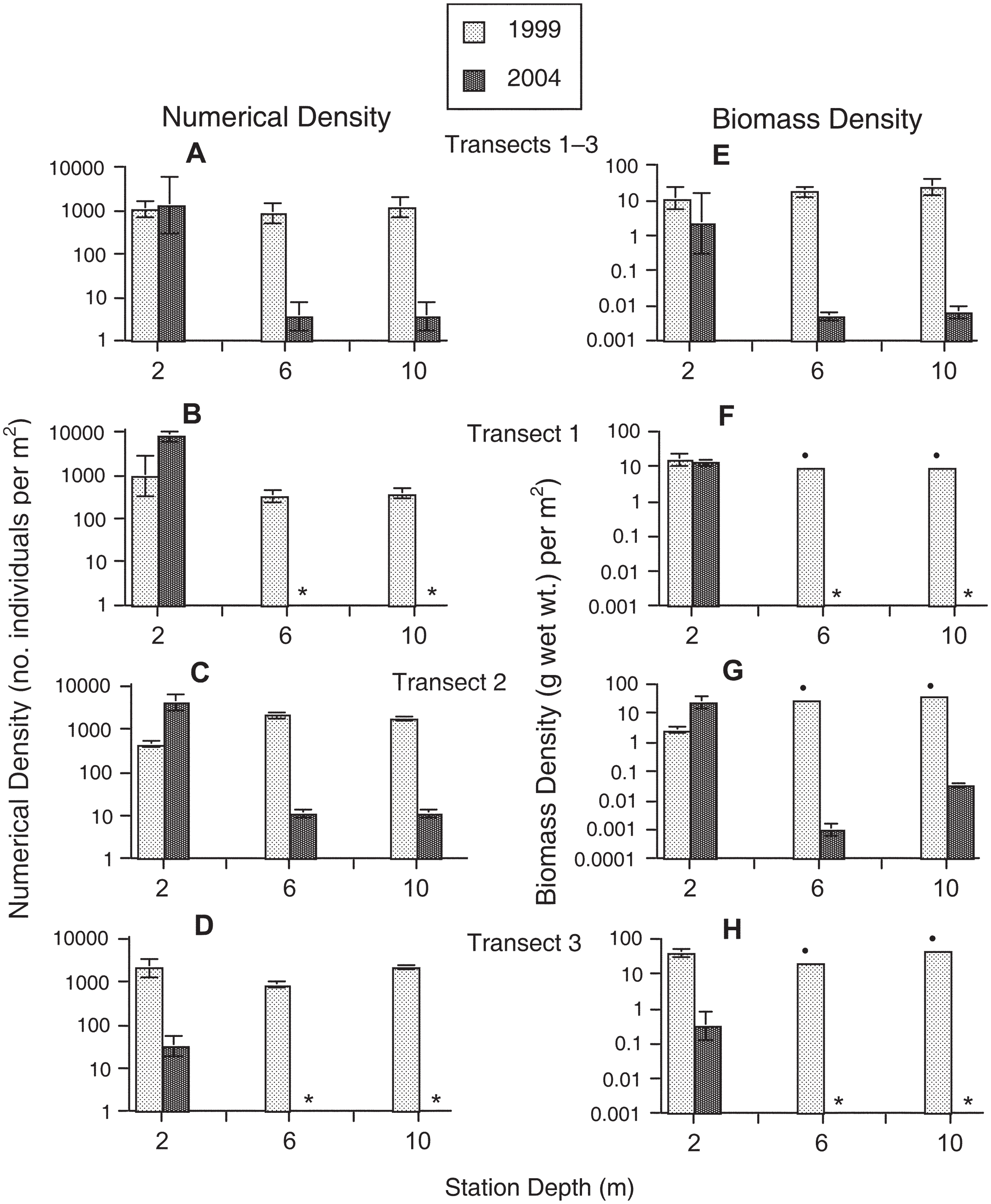

Figure 4.-Comparison of geometric mean numerical (A-D) and biomass (E-H) densities of *Neanthes succinea* for three sampling transects in 1999 and 2004. Biomass values marked with a dot (•) are based on a single measurement, so SEF could not be computed. Asterisks (*) indicate geometric means equal to zero.

variable system, the data of 2004 and 2005 suggest a decrease in *Neanthes* abundance relative to both the 1956 and 1999 populations. Whatever factors are involved, the decrease of *Neanthes* may pose a major reduction in current food supplies for those fish and waterbirds, such as the eared grebe (Jehl and McKernan 2002; Anderson *et al.* 2007), that have historically relied on the abundance of this invertebrate in the lake.

Detwiler *et al.* (2002) emphasized the importance of shoreline habitats as a refuge for the *Neanthes* population after anoxia during the warmer months had eliminated the populations at depths deeper than 2 m. The barnacle- and/or algal-covered rocky substrates and the barnacle shell sediments along the shoreline harbored high densities of *Neanthes* all year in 1999. Similarly, in January 2006, *Neanthes* were abundant in the sediments underneath rocks at the shoreline near Red Hill Marina (J. Gafney, personal communication).

Spatial variation in Neanthes *abundance in 2004*

The absence or near absence of *Neanthes* at all 10 m stations on April 15-16, 2004 and throughout the lake on March 14-17, 2005 can be attributed, as implied above, to the fact that early thermal stratification had already led to hypoxic or anoxic conditions in deep waters, killing *Neanthes*. Anoxia was not observed on April 15-16, even at 10 m, but it could have developed a bit earlier in the season, under the influence of another period of density stratification, and then been eliminated by a strong mixing event.

More complex must be the set of factors that produced the high variability in *Neanthes* abundance among the 2 m and 6 m stations in 2004. We anticipated that abundance of *Neanthes* might be higher offshore (T4, T5) and downcurrent (T3, T7) of river mouths than at other locations. This polychaete thrives over a wide range of salinities, temperatures, and oxygen levels (Detwiler *et al.* 2002). Reduced salinities occurring offshore of the river mouths and associated increased nutrient levels might create favorable conditions for phytoplankton (Reifel *et al.* 2007) and organic matter sedimentation, leading to increased densities of *Neanthes*.

Despite the lower salinities and presumed increased food supply, *Neanthes* was absent or scarce at most 2 m (T3, T4, T5, T7) and 6 m stations (T3, T7) in these areas (Fig. 3). Observed bottom oxygen levels (2.3-19.0 mg l^{-1}) at these stations seemed adequate for *Neanthes* but could have been much lower on some earlier date in the season. If vertical mixing is restricted in these areas due to salinity gradients produced by river inflows moving out over the lake surface, then hypoxia could occur reducing the density of *Neanthes*.

Sediment quality may also be a controlling factor for *Neanthes*. Sediments at 2 m on T3 and T7 were silty, but those at 2 m on T4 and T5 were black, soup-like, lacked a coarse fraction, contained some vascular plant detritus, and seemed anoxic. *Neanthes* have not been collected in such fluid sediments, so it is likely that these sediments do not provide a suitable stable substrate for this species.

The 6 m stations with highest *Neanthes* densities were the ones - on T4 and T5 - with the lowest bottom oxygen concentrations (1.4 and 0.3 mg l^{-1}, respectively) at the time of sampling (Figs. 2 and 3) and these were located further from shore (Table 1) and the ones with the firmest substrates. *Neanthes* can tolerate complete anoxia for up to 27 h and survive for at least a month at 1.8 mg O_2 l^{-1} in the laboratory (Carpelan and Linsley 1961). The combination of suitable substrate and productive overlying waters may have more than canceled out negative influence of low oxygen levels. The interactions between substrate, food supply, and oxygen level on the survival of *Neanthes* need to be experimentally investigated.

Additionally, predation on *Neanthes* by tilapia might also account for some spatial variation. Small numbers of 0+ and 1+ year class tilapia were in the lake in April 2004 (J. Crayon, California Dept. Fish and Game, pers. comm.). Caskey *et al.* (2007) obtained higher catches of tilapia (an *Oreochromis mossambicus* Peters x *O. urolepis hornorum* (Trewavas) hybrid) in gillnets set in 2 m deep water off the mouths of the New and Alamo rivers than in those set elsewhere in the Sea. That might explain the low *Neanthes* densities found in a little deeper water off those areas.

Significance of gypsum and sulfide

Increasing salinity has long been regarded as the main threat to the future health of the Salton Sea *Neanthes* population. Since November 1956, salinity has risen by about 10 g l^{-1} (Detwiler *et al.* 2002) and the present salinity 45-47 g l^{-1} is approaching the physiological tolerance of this species (Kuhl and Oglesby 1979). However, we believe that the sulfur biogeochemistry of the lake is presently a more critical influence on *Neanthes* than is salinity. Gypsum and sulfide abundances are two reflections of that biogeochemistry.

The abundance of gypsum in the sediments reflects the fact that the lake reached saturation with calcium sulfate about 1980, and ever since all sulfate ion arriving via inflow waters has been precipitating as gypsum (Tostrud, 1997). Some of the gypsum present in the sediments may also be a result of *in situ* dissolution and precipitation processes. Wardlaw and Valentine (2005) found evidence of large vertical gradients in several porewater ions. Some of these ions, including sulfate, showed large increases in concentration with sediment depth. It is possible that *in situ* gypsum formation occurs as a result of interactions between sulfate and calcium porewater concentrations. Other studies (Walker 1996; K. Bertine and M. Klinger, Dept. Geol. Sciences, SDSU, unpubl. data) have also reported high gypsum content of sediments at this lake, often as high as 30-40%. The gypsum itself may somewhat impede the burrowing activity of *Neanthes*, especially if it occurs as a competent, uninterrupted crust over large areas of lake bottom. We have found gypsum-cemented plates up to ~100 cm^2 in some of our grab samples and have observed high rates of gypsum crystal production over large portions of the lake during overturn events (Watts *et al.* 2001; Tiffany *et al.* 2007). Such plates would also be expected to greatly influence vertical geochemical fluxes of diverse elements both within the sediments and across the sediment-water interface. Rapid production and precipitation of gypsum crystals is associated with sulfide events in the lake (Watts *et al.* 2001; Tiffany *et al.* 2002, 2007). Greater abundance of gypsum in deepwater sediments (Fig. 5) might be expected for two reasons. It is sulfide in the deeper parts of the water column that, when mixed upward, results in formation of gypsum crystals. These will usually precipitate out of the water column not too far from where they form. Also, fine gypsum crystals that do settle out in shallower waters are liable to resuspension by turbulence and currents and, eventually, redeposition in deeper water. M. Anderson *et al.* (2007) discuss and model how those same processes account for sediment organic carbon and correlated variables showing marked increases below depths of about 9 m in the Salton Sea.

Sulfide is generated both by decomposition of sulfur-containing proteins derived from dead organisms and by bacterial sulfate reduction (Goldhaber and Kaplan 1974). Following the decline of tilapia (Caskey *et al.* 2007; Hurlbert *et al.* 2007) between 1999 and 2004 in the Salton Sea, phytoplankton increased dramatically, greatly adding to the amount of particulate organic matter delivered to the sediments, and anoxic conditions and sulfide events were more frequent (Anderson *et al.* 2007). Under the anoxic conditions that are rapidly produced by high decomposition rates, sulfide does not undergo chemical oxidation to sulfate but instead accumulates to high levels in bottom waters and sediments. When after a period of stratification the water column is suddenly mixed, lethal levels of sulfide can occur throughout it and massive die-offs of phytoplankton, zooplankton, and fish result (Watts *et al.* 2001; Caskey *et al.* 2007; Tiffany *et al.* 2002, 2007). This is what appears to have happened at least in deeper parts of the lake some time prior to our April 2004 sampling for *Neanthes* and over the entire lake just a day or two prior to our March 2005 sampling. As discussed above, such die-offs were not observed in the 1950s when anthropogenic phosphorus and nitrogen enrichment was less and sulfide levels may have been lower.

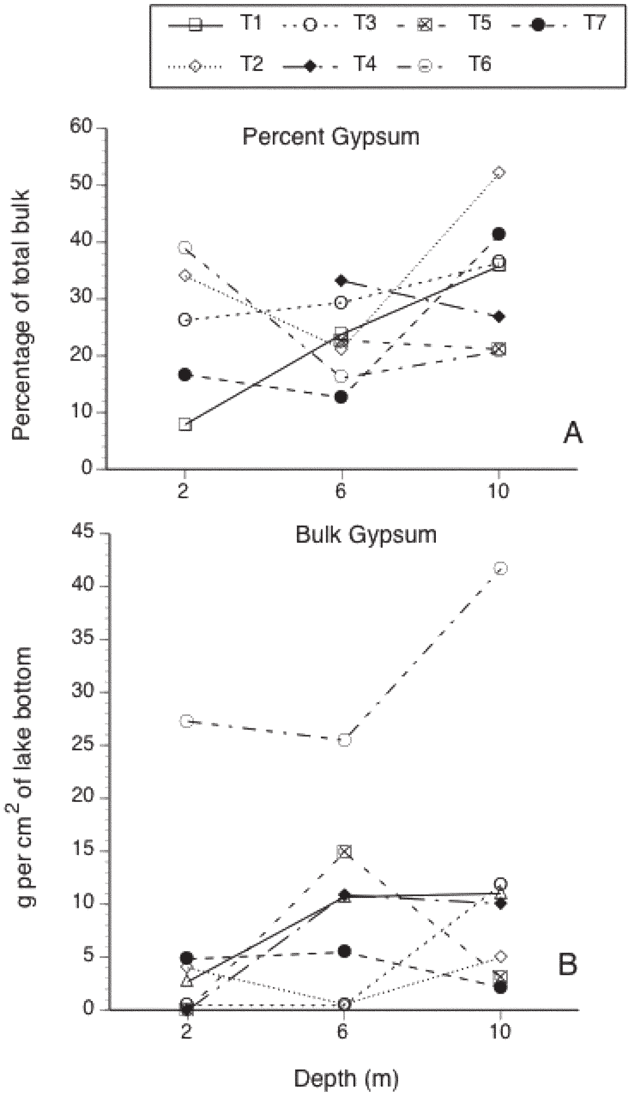

Figure 5.-Gypsum abundance in sediments as a percentage of total coarse (> 1000 μm) sediments (A) and as mass per unit area of lake bottom (B).

Implications for Neanthes *monitoring*

Because of the important role of *Neanthes* in the Salton Sea ecosystem, its distribution and abundance should be monitored at least yearly using a modification of the array of sampling transects used here. From this study, it is apparent that such sampling should occur earlier in the year, in January or February, when *Neanthes* is more likely to be at its peak abundance, and before early episodes of stratification and anoxia are likely. We would also predict less station-to-station variability in January or February than we found in April, and that would increase precision of estimates. A second sampling date in April would provide information on how well this fish food supply persists into spring.

For such future efforts, we recommend that stations be sampled on each transect at the same depths – 2, 4, 6, 8, 10, and 12 m – sampled in 1999. The seven transects used in the 2004 sampling might be sufficient, but additional deep (12-14 m) water stations might be added to better cover the large central portion of the lake. Temperature, oxygen, and specific conductance profiles should be determined at each sampling station.

Conclusions

This study found a marked overall reduction in springtime abundance of *Neanthes* between 1999 and 2004-2005. Though its food supply is abundant, the physical and chemical environment is clearly suboptimal for *Neanthes*, and the evidence stands that the worm is much less abundant than during the 1950s. The data from March 2005 clearly indicates that the population crashed very early in that year. Recovery of *Neanthes* during the spring, summer, or early fall of the year will be difficult because most of the lake bottom is anoxic during those seasons. Only the shoreline substrates provide a potential refuge from which *Neanthes* can recolonize offshore sediments.

Acknowledgments

Funding for this project was provided Agreement No. 04FG3000020 from the U.S. Bureau of Reclamation, Lower Colorado Region. Scientific oversight was provided by the U.S. Geological Survey Salton Sea Science Office. Field sampling in 2005 was funded by the California Department of Water Resources through a contract to CH2MHill. Field assistance was provided by Jim Zimmer, Tom Anderson, Walter Atkins, and Tim Hamaker. Boat support was provided by the Salton Sea Authority and Bryan and Mac Brinegar of Environmental Recovery Services, Salton City, California. For helpful comments on the manuscript, we thank Lisa Levin, Joe Rachlin, Cheryl Rodriguez, Robert Ross, Barbara Warkentine, and an anonymous reviewer.

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