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Role of the polychaete *Neanthes succinea* in phosphorus regeneration from sediments in the Salton Sea, California

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Abstract The Salton Sea currently suffers from several well-documented water quality problems associated with high nutrient loading. However, the importance of phosphorus regeneration from sediments has not been established. Sediment phosphorus regeneration rates may be affected by benthic macroinvertebrate activity (e.g. bioturbation and excretion). The polychaete *Neanthes succinea* (Frey and Leuckart) is the dominant benthic macroinvertebrate in the Salton Sea. It is widely distributed during periods of mixing (winter and spring), and inhabits only shallow water areas following development of anoxia in summer. The contribution of *N. succinea* to sediment phosphorus regeneration was investigated using laboratory incubations of cores under lake temperatures and dissolved oxygen concentrations typical of the Salton Sea. Regeneration rates of soluble reactive phosphorus (SRP) were lowest (–0.23–1.03 mg P m^{-2} day^{-1}) under saturated oxygen conditions, and highest (1.23–4.67 mg P m^{-2} day^{-1}) under reduced oxygen levels. *N. succinea* most likely stimulated phosphorus regeneration under reduced oxygen levels via increased burrow ventilation rates. Phosphorus excretion rates by *N. succinea* were 60–70% more rapid under reduced oxygen levels than under saturated or hypoxic conditions. SRP accounted for 71–80% of the dissolved phosphorus excreted under all conditions. Whole-lake SRP regeneration rates predicted from *N. succinea* biomass densities are highest in early spring, when the lake is mixing frequently and mid-lake phytoplankton populations are maximal. Thus, any additional phosphorus regenerated from the sediments at that time has potential for contributing to the overall production of the lake.

Keywords Bioturbation · Polymictic · Nutrient excretion · Sediment cores

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Saline Water and their Biota

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Introduction

The effects of benthic macroinvertebrates on the transport of nutrients from sediments to overlying water have been extensively documented in aquatic environments (Aller, 1978; Gallepp, 1979; Clavero et al., 1992). Because of the importance of phosphorus in the eutrophication of many lakes and estuaries, the effects of macroinvertebrate activity in sediments on phosphorus cycling have been a primary focus. Effects include upward transport of phosphorus associated with sediment and pore water during physical activities of benthic macroinvertebrates within burrows, excretion of phosphorus by the organism directly into surrounding sediments or burrows (Gardner et al., 1981), and the excretion of sediment-derived phosphorus directly into overlying waters (Wilhelm et al., 1999). Organism characteristics such as size, behavior, and feeding mode are important determinants of what processes will be dominant and under which environmental conditions (Matisoff & Wang, 1998; Christensen et al., 2000).

Temporal and spatial distributions of benthic macroinvertebrates are strongly affected by seasonal changes in abiotic features of the environment. Specifically, low dissolved oxygen concentrations (hypoxia) or anoxia, along with the presence of toxic substances such as hydrogen sulfide can directly affect the physiology and behavior of many macroinvertebrates (Miron & Kristensen, 1993; Riedel et al., 1997). Depending on the duration of such conditions, populations of benthic macroinvertebrates may experience high mortality and temporary extirpation events. The ability of macroinvertebrate species to tolerate anoxia/hypoxia and the presence of hydrogen sulfide is a strong determining factor as to which species persist under these conditions, and therefore which species will successfully recolonize these environments (Rosenberg et al., 1991; Bartoli et al., 2000). Thus, shifts in environmental conditions can indirectly affect sediment phosphorus regeneration through regulation of organism activity and density, and can determine the relative importance of bioturbation as a transport process for phosphorus (Guérin & Labroue, 1991).

The polychaete *N. succinea* is the dominant macroinvertebrate in the sediments of the Salton Sea, in both number of individuals and biomass (Detwiler et al., 2002). It was most likely introduced into the Salton Sea around 1930 to provide a forage base for fish populations (Carpelan & Linsley, 1961). This animal constructs U-shaped burrows lined with mucus, which it actively irrigates by pulling overlying water through the burrow via undulations of its body. This and related species tolerate hypoxia and anoxia as well as hydrogen sulfide for short periods of time (1–3 days) by switching to anaerobic metabolism (Kristensen, 1981), which makes them suitable colonizers of regions that experience depressed oxygen levels (Theede et al., 1973; Jørgensen, 1980). *N. succinea* typically inhabits Salton Sea sediment at all depths during months when oxygen is present in bottom waters. As anoxia develops in the deeper waters during summer months, *N. succinea* is not found at depths much greater than 2 m (Detwiler et al., 2002; Fig. 1). During these periods, *N. succinea* densities are highest in nearshore sediments and rocky shoreline habitats.

Lakes that mix frequently (e.g. polymictic ones) typically experience greater phosphorus regeneration from sediments, and improvement

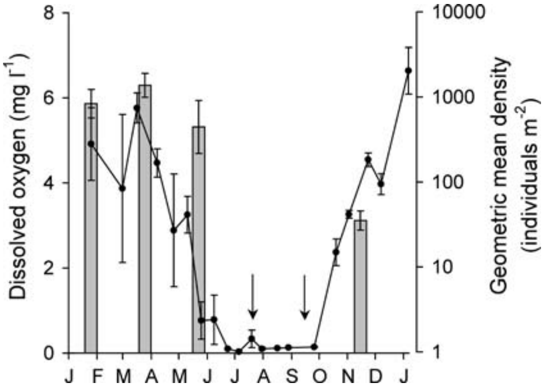

Fig. 1 Dissolved oxygen concentrations (line) in bottom waters (12 m) and densities of *N. succinea* (bars) in offshore sediments at 10 and 12 m in the Salton Sea, 1999. Dissolved oxygen concentrations represent the arithmetic mean of three mid-lake stations. *N. succinea* densities represent the geometric mean abundances at two stations (10 and 12 m depths) at three sampling transects. Error bars represent standard error (SE; $n = 3$ for dissolved oxygen and $n = 6$ for *N. succinea* densities). Arrows indicate dates where sampled *N. succinea* densities were zero. Data from Watts et al. (2001) and Detwiler et al. (2002)

in water conditions following reduced external loading is slow to develop (Welch & Cooke, 1995). In shallow lakes, larger volumes of the mixed layer and photic zone are in contact with the sediments, and such lakes may experience enhanced release of phosphorus from sediment re-suspended by wind-driven turbulence (Søndergaard et al., 1992). Additionally, in lakes that are exposed to high wind energy, thermal stratification tends to be temporary and bottom waters are frequently mixed into the upper waters, even during summer months (Osgood, 1988; Cooke et al., 1993). This allows a greater portion of phosphorus from the sediments to enter the photic zone than in lakes that remain stratified for long periods of time. This mixing provides phosphorus for algal populations and can therefore strongly affect lake trophic status and recovery.

The Salton Sea is a closed-basin, saline (41–45 g l^{-1}) lake located in the southwest corner of the United States. The lake was created in 1905–1907 when the Colorado River flooded the Salton basin for more than a year. It receives the majority (88%) of its freshwater inflow from agricultural and municipal wastewater (Watts et al., 2001). It is polymictic due to its shallowness (surface area = 980 km^2, mean depth = 8 m, maximum depth = 15 m) and high wind exposure. The development of a large phytoplankton biomass and the high water temperatures during spring and summer months (March–August) lead to widespread anoxia and the subsequent formation of hydrogen sulfide in bottom waters below about 10 m (Watts et al., 2001). During strong windstorms, the mixing of these anoxic, hydrogen sulfide-rich bottom waters into overlying water causes mass mortality of plankton, benthic macroinvertebrates, and fish (Detwiler et al., 2002; Riedel et al., 2002; Tiffany et al., 2002). From fall (September–October) to late winter (December–January), declining water temperatures and increasing oxygen concentrations due to increased mixing allow the recolonization of profundal sediments by macroinvertebrates (Detwiler et al., 2002).

The major sources of phosphorus inputs to the Salton Sea are from three rivers: the New, Alamo, and Whitewater rivers. The input of phosphorus, measured as total phosphorus (TP), to the Salton Sea in 1968–1969 was 0.68 g TP m^{-2} $year^{-1}$ (Bain et al., 1970). Since then, annual inputs of phosphorus have more than doubled (1.6 g TP m^{-2} $year^{-1}$ in 1997; J. M. Watts unpublished data), probably due to increased inputs from municipal sources. However, annual mean water column concentrations of TP measured in 1997–1998 do not differ much from those measured in 1968–1969 (0.069 and 0.095 mg l^{-1}, respectively; Holdren & Montaño, 2002). Direct comparison of these datasets is difficult due to incomplete information on sampling locations provided by Bain et al. (1970). The lack of change in average water column concentrations of TP when external inputs have more than doubled indicates that currently the sediments in the Salton Sea are acting as an effective sink for phosphorus.

The goals of this study were to quantify the contribution of phosphorus regeneration from the sediments to the annual inputs of phosphorus in the Salton Sea, and to quantify the contribution of *N. succinea* activity to this phosphorus regeneration from Salton Sea offshore sediments.

Methods

Field collections

Intact sediment cores were collected from sampling station number one (S-1), a reference sampling station used during a reconnaissance study of the biological limnology of the Salton Sea in 1997–1999 (see Watts et al., 2001 for map). This sampling station is located in the center of the northern basin of the lake and was chosen because it represents the typical sediment type (coarse silt) of the profundal region (≥10 m depth; Detwiler et al., 2002). Sediment cores were obtained by first collecting sediment using a modified Ekman box-corer ($15 \times 15 \times 50$ cm^3) and then sub-sampling box-core samples using acrylic cylinders. On each sampling date, approximately 100 l of Salton Sea water was collected from the lake surface for use in laboratory incubations.

N. succinea individuals were collected from the rocky shoreline habitat near Varner Harbor at the northeastern corner of the Sea. All individuals were immediately placed in filtered (Whatman GF/F, 0.6–0.7 μm), aerated Salton Sea water inside plastic containers for transport. Small (5×0.5 cm^2) glass tubes were added to each container as an artificial substratum, which helps to reduce stress and aggressive behavior in this species (D. Dexter & P. Detwiler, personal communication). All polychaetes were used in experiments within 48 h of collection.

Determination of sediment phosphorus regeneration rates

Six sediment cores were collected on each of two dates for determination of phosphorus regeneration rates under anoxic conditions: 29 September and 13 October 2000. These sediment cores were incubated inside an Anaerobe Systems Model 800 anaerobic chamber (Anaerobe Systems, Inc., Santa Clara, CA), which allowed water samples to be removed without exposure to oxygen. An incubator inside the anaerobic chamber maintained overlying water temperature.

Once inside the chamber, sediment cores were uncapped and the overlying water was removed and replaced with filtered Salton Sea water. Air stones were then placed in the overlying water approximately 10 cm above the sediment surface. This bubbling action circulated the overlying water and disrupted any concentration gradients of solutes that might have formed (Holdren & Armstrong, 1980). Water samples (~30 ml) were removed at 24 h intervals, stored in polypropylene screw-capped bottles, and immediately frozen (–20°C) until analyzed. Afterward, an equal volume of filtered Salton Sea water was added to each sediment core to maintain a constant water volume.

Sediment cores were collected on three dates for incubations with *N. succinea*: 20 January, 13 March, and 28 April 2001. Experiments conducted during January and March evaluated the effects of four levels of *N. succinea* density on phosphorus regeneration rates. Densities used were 0, 260, 1,040–1,070, and 1,890–1,940 individuals per m^2. These were achieved by adding 0, 1, 4, and 10 individuals, respectively, to each sediment core. The experiment conducted in April evaluated the effect of two densities of *N. succinea* on phosphorus regeneration rates from sediment cores: 0 and 1,890–1,940 individuals per m^2. Three replicate sediment cores for each *N. succinea* density were used. These densities are representative of those found in the profundal region during these times of year.

Water temperatures and dissolved oxygen concentrations measured in bottom waters (12 m depth) of the Salton Sea during the 1997–1999 reconnaissance study (Watts et al., 2001) were used to determine the conditions to be established in the overlying water for each experiment. Overlying water temperatures were maintained by incubating sediment cores inside a low-temperature incubator. Desired dissolved oxygen concentrations in the overlying water were obtained by bubbling air, nitrogen gas, or a combination of both into the overlying water through small-diameter (0.5 cm) tygon tubes and air stones located approximately 10 cm above the sediment surface. Each sediment core was assigned an individual air pump and/or nitrogen gas line, and the flow of either gas was regulated through stainless steel valves. After set-up, the appropriate gas/gas mixture was allowed to bubble in each sediment core for approximately 1 h. Dissolved oxygen concentrations were then measured, and adjustments to the gas flow in each sediment core were made each additional 0.5 h. This procedure was repeated until the concentrations were within 0.3–0.5 mg l^{-1} of those desired, which generally took 2.5–3 h. After 24 h, the appropriate number of polychaetes was added and the time was noted ($T = 0$ h). At 24 h intervals after $T = 0$, a water sample (~100–150 ml) was removed from each sediment core approximately 10 cm above the sediment surface using tygon tubing connected to a plastic syringe and stored as previously mentioned. An equal volume of filtered Salton Sea water was then added to each sediment core to maintain a constant water volume.

Sediment cores were incubated for 5 days (120 h) for all experiments, except the 28 April experiment, which was terminated after 3 days (72 h). At termination, each sediment core was sieved (350 μm), and all *N. succinea* individuals, as well as any other macroinvertebrates present, were recovered. After mortality was noted, each recovered polychaete was blotted dry, oven dried

(60°C) for 24 h, and weighed (Sartorius Analytic Balance, A 200 S) to the nearest 0.1 mg.

Phosphorus analyses, incubation conditions, and regeneration rate calculations

The ascorbic acid method of determining phosphate concentrations was used (APHA, 1998). Several phosphorus fractions were determined in each experiment: total phosphorus (TP), particulate phosphorus (PP), dissolved organic phosphorus (DOP), and soluble reactive phosphorus (SRP). Water samples were divided into two aliquots of equal volume. One aliquot was used for TP analysis, and the other was filtered (Whatman GF/F, 0.6–0.7 μm) and analyzed for total dissolved phosphorus (TDP) and SRP. Persulfate digestion was performed on water samples for TP and TDP analysis prior to measuring phosphate concentrations (APHA, 1998). PP and DOP concentrations were calculated by subtraction: PP = TP – TDP and DOP = TDP – SRP.

Water temperature and dissolved oxygen concentrations were measured in the overlying water every 24 h using a hand-held YSI-85 metre (Yellow Springs Instruments, Inc., Yellow Springs, OH). Water temperature was measured using a factory-calibrated thermistor (accurate to ±0.1°C), and dissolved oxygen concentration was measured using a rapid pulse oxygen probe (accurate to ±0.3 mg l^{-1}). The dissolved oxygen probe required daily calibration.

Sediment regeneration rates of each phosphorus fraction were determined for each sediment core using the standard flux equation:

$$F(\mathrm{mg\,P\,m^{-2}\,day^{-1}}) = \sum[(C_i - C_0)V]/A \cdot T$$

where F is the flux or regeneration rate of phosphorus, C_0 and C_i are phosphorus fraction concentrations (mg l^{-1}) at time 0 and time i, V is the volume (l) of water above the sediment inside the core tube, A is the sediment surface area (m^2), and T is total incubation time (days). This rate equation calculates the sum of the linear changes of phosphorus concentration in overlying water over the entire incubation period. These concentration changes were measured at each time point and were corrected for the dilution effect of replacing water lost due to daily sampling.

Determination of phosphorus excretion rates

Mass-specific excretion rates of phosphorus by *N. succinea* individuals were determined on three dates: 20 January, 13 March, and 28 April 2001. *N. succinea* individuals were grouped into three approximate size classes: 6–8 cm (large), 3–5 cm (medium), and 1–2 cm (small) in length. From each size class, 15 individuals were selected. Groups of five individuals from each size class were placed in 500 ml glass beakers containing 200 ml of filtered Salton Sea water (5 individuals × 3 replicate beakers = 15 individuals per size group). Five small (5×0.5 cm^2) glass tubes were added to each beaker as artificial substratum for each polychaete. Two glass beakers filled with filtered Salton Sea water only were used as controls.

To determine the time at which an increase in phosphorus concentration could be detected, water samples (~20 ml) were removed immediately after the polychaetes were added to each beaker ($T = 0$ h) and at $T = 2$, 4, 8, 10, 12, and 24 h for the 20 January experiment. For the two remaining experiments (13 March and 28 April), water samples were removed at $T = 0$ and 24 h only. Water that was removed through sampling was not replaced. However, due to the relatively low incubation temperatures used, loss due to evaporation was not significant. Water samples were carefully removed from the surface of each beaker to avoid any feces near the bottom.

For each excretion determination, water temperature and dissolved oxygen concentrations used in the corresponding sediment core incubation experiment were maintained and monitored in each beaker using previously described methods. The average change in phosphorus concentrations in control beakers was subtracted from the experimental beakers, and mass-specific excretion rates (μg P mg dry wt^{-1} h^{-1}) of dissolved phosphorus fractions (SRP and DOP) were calculated.

Mass-specific excretion rates of dissolved phosphorus fractions (SRP and DOP) were used to estimate the importance of excretion to the overall flux of phosphorus measured in intact core experiments. First, the *N. succinea* biomass density (mg dry wt m^{-2}) in each sediment core was multiplied by the appropriate excretion rate. This provides an estimate of the amount of phosphorus potentially regenerated in the sediment cores via excretion only (E). Second, this amount was divided by the phosphorus regeneration rate determined in each sediment core (R). This regeneration rate includes phosphorus regeneration via excretion and all other factors combined. The ratios (E/R) of SRP and DOP excreted to those regenerated in the incubation experiments were calculated for each sediment core for each experiment.

Phosphorus regeneration as a function of polychaete density

Laboratory-derived phosphorus regeneration rates and field estimates of *N. succinea* density were used to predict potential regeneration rates in the Salton Sea. Phosphorus regeneration rates were determined in this study and estimates of *N. succinea* biomass density come from the macroinvertebrate survey of Detwiler et al. (2002). The estimates employed were those measured in offshore sediments (10 and 12 m depths) on six dates in 1999. First, a mean SRP regeneration rate per mg *N. succinea* (μg SRP m^{-2} day^{-1} mg dry wt^{-1}) was calculated for each experiment. Second, a regeneration rate was chosen which was determined under laboratory conditions (e.g. temperature and dissolved oxygen concentration) that best represented those found in the Salton Sea for each survey date in 1999. Third, each *N. succinea* biomass density (mg dry wt m^{-2}) was multiplied by the appropriate SRP regeneration rate to obtain a lake-wide rate estimate for each survey date. For each survey date, lake-wide SRP regeneration rates corresponding to the maximum and mean *N. succinea* densities, as well as in the absence of polychaetes, were estimated. Maximum *N. succinea* density for a given survey date was defined as the highest station mean estimate.

Two limitations of these calculations may be noted. First, phosphorus regeneration rates were measured under conditions (temperature, dissolved oxygen concentration, *N. succinea* density) assumed to represent different seasonal conditions in the Salton Sea. Second, phosphorus regeneration rates measured by intact sediment core incubations provide a gross rather than net rate estimate, and the static condition of the incubations does not allow for additional input of organic matter to the sediment, nor does it allow for any affects of turbulence on phosphorus regeneration rates to be assessed.

Statistical analyses

For the 20 January and 13 March oxic experiments, the effect of *N. succinea* density on the regeneration rates of phosphorus fractions was analyzed using one-way analysis of variance (ANOVA). The effect of *N. succinea* density for the 28 April oxic experiment was analyzed using a two-sample *t*-test.

Results

Incubation conditions

In the saturated and reduced oxygen concentration experiments (20 January and 13 March, respectively), all polychaetes added to each sediment core immediately headed toward the sediment surface and began forming their characteristic U-shaped, mucus-lined burrows (average depth range: 2–15 cm). Approximately 2 h passed before all the polychaetes had completed burrow construction. Those along the edges of the core tube were also observed ventilating their burrows. As observed in other studies using *N. succinea*, the walls immediately surrounding these burrows were a lighter brown color as compared to the main sediment area, presumably due to oxidation of metals present. During the hypoxic condition experiment (28 April), all polychaetes added to the sediment cores headed toward the sediment surface but did not construct burrows at depth. Instead, the polychaetes constructed mucus linings around themselves with surficial sediment and remained on the sediment surface during the entire course of the experiment. Some ventilation activity was observed.

In all experiments, no mortality resulted during laboratory incubations. In addition, after sieving all sediment cores at the end of the incubations, no additional *N. succinea* other than those introduced were found. During the phosphorus excretion rate determinations, all *N. succinea* added to each beaker entered a glass tube and began to ventilate within it. Only small amounts of fecal material were observed at the bottom of each beaker, which indicates that 24 h was sufficient time to allow gut clearance.

Phosphorus regeneration rates

Regeneration rates varied with incubation condition and polychaete density. Under saturated oxygen concentrations (20 January), regeneration rates for all phosphorus fractions ranged from low to negative (Fig. 2a). Regeneration rates of all phosphorus fractions varied among *N. succinea* density treatments; however, differences were greatest for SRP and DOP between cores with maximum *N. succinea* density and all other

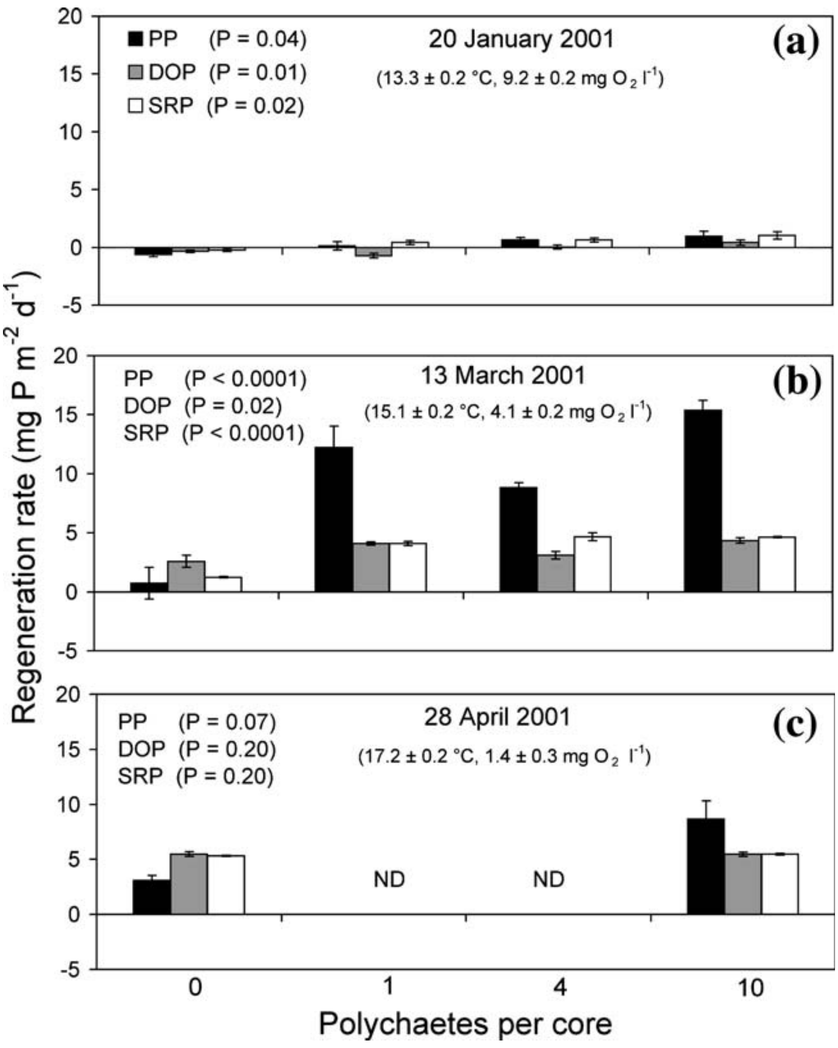

Fig. 2 Mean regeneration rates (±1 SE) of phosphorus fractions for intact core incubations for three sampling dates using representative abundances of *N. succinea* and conditions found in the Salton Sea. Overall mean (±1 standard deviation; SD) of water temperature and dissolved oxygen concentrations for each date are presented in parentheses. *P*-values are for one-way ANOVAs (**a** and **b**) and two-sample *t*-tests (**c**) ND = not determined

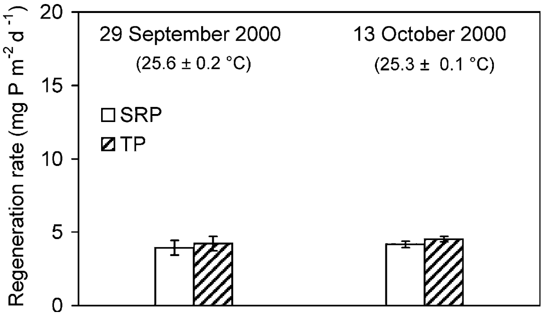

Fig. 3 Mean regeneration rates (± 1 SE) of phosphorus fractions for intact sediment cores incubated under anoxic conditions. Overall mean (±1 SD) of water temperature are presented in parentheses

density treatments (41–120% and 93–275% higher, respectively). Also, the total amount of phosphorus regenerated tended to increase with increasing *N. succinea* density.

Regeneration rates of all phosphorus fractions determined under reduced oxygen and hypoxic conditions (13 March and 28 April, respectively) were markedly higher than those measured under saturated oxygen concentrations (Fig. 2b, c). Under reduced oxygen concentrations, differences in regeneration rates were greatest between control (absence of *N. succinea*) and all other density treatments for PP and SRP fractions (Fig. 2b). Under hypoxic conditions, differences in regeneration rates between the two *N. succinea* densities were apparent for PP only (Fig. 2c). With the exception of control cores (absence of *N. succinea*), regeneration rates of SRP measured under reduced oxygen and hypoxic conditions were similar to those measured under anoxic conditions on both dates (Fig. 3).

SRP accounted for 92–94% of the phosphorus regenerated measured under anoxic conditions (mean ± 1 SE, $n = 6$; 3.9 ± 2.5 and 4.2 ± 1.1 mg m^{-2} day^{-1}, respectively; Fig. 3).

Phosphorus excretion rates

Changes in SRP and DOP concentrations in the 20 January experiment were measurable at each sampling time (2–24 h), and concentration increases were linear over the entire time interval (Swan, 2003). Therefore, 24 h is sufficient time for determining *N. succinea* phosphorus excretion rates using the described methods.

Excretion rates for SRP and DOP decreased with a decrease in dissolved oxygen concentration and increase in temperature, with SRP accounting for 71–80% of the total dissolved phosphorus excreted (Table 1). Mass specific excretion rates of SRP determined under saturated oxygen concentrations and hypoxia were similar (Table 1). Under reduced oxygen conditions, SRP excretion rates were 60–70% greater than those measured under the other two oxygen conditions. Excretion rates of DOP were similar between saturated and reduced oxygen concentrations, and lowest under hypoxic conditions (Table 1).

When the *E*/*R* ratio is ≥1, excretion contributes more to the total flux of phosphorus. If this ratio is < 1, excretion contributes less to the total flux of phosphorus from sediment. All *E*/*R* ratios were greater than one for SRP under saturated and reduced oxygen conditions, except in the cores with the lowest *N. succinea* density (Table 2). Also, *E*/*R* ratios for SRP were much larger under saturated than under reduced oxygen concentrations. The *E*/*R* ratio for SRP under hypoxic

Table 1 Mean mass-specific excretion rates (±1 SE) of SRP and DOP by *N. succinea* in the absence of sediment

Date	Excretion rate (×10^{-3} µg mg^{-1} dry wt h^{-1})		Percent of total TDP excreted		Temperature (°C)	Dissolved oxygen (mg l^{-1})
	SRP	DOP	SRP	DOP		
20 Jan 01	3.4 ± 0.2	1.3 ± 0.2	70.5	29.5	13.3 ± 0.2	9.3 ± 0.2
13 Mar 01	5.6 ± 0.2	1.6 ± 0.2	76.4	23.6	15.3 ± 0.2	4.3 ± 0.2
28 Apr 01	3.3 ± 0.1	0.9 ± 0.1	79.5	20.5	17.3 ± 0.2	1.6 ± 0.2

Percentage of total dissolved phosphorus (TDP = SRP + DOP) that SRP and DOP constituted in each rate determination is presented, along with overall mean (±1 SD) water temperature and dissolved oxygen concentrations maintained for each experiment conditions was very close to one (0.9; Table 2). The *E*/*R* ratios for DOP were greater than one at saturated oxygen concentrations and the highest *N. succinea* densities, as well as under hypoxic conditions (Table 2). The *E*/*R* ratios of DOP under reduced oxygen conditions were less than one for all *N. succinea* densities (Table 2).

Regeneration of phosphorus in the Salton Sea

Estimates of regeneration rates of SRP from Salton Sea sediments based on changes in *N. succinea* biomass vary seasonally (Fig. 4). The stimulation of SRP regeneration rates by *N. succinea* is greatest during spring, when *N. succinea* abundances are highest in offshore sediments and the water column is well-oxygenated. During March, a 65–80% increase in SRP regeneration was calculated for mean and maximum *N. succinea* densities, respectively. This stimulation declines rapidly by early summer when anoxia develops in bottom waters and *N. succinea* populations decline. Annual SRP regeneration rates were calculated by estimating the area under each curve presented in Fig. 4. Mean and maximum *N. succinea* densities are predicted to cause a 15–35% increase in the annual rate of SRP regeneration, respectively, relative to that estimated for sediments lacking *N. succinea* (1.27–1.59 vs. 1.08 g SRP m^{-2} year^{-1}).

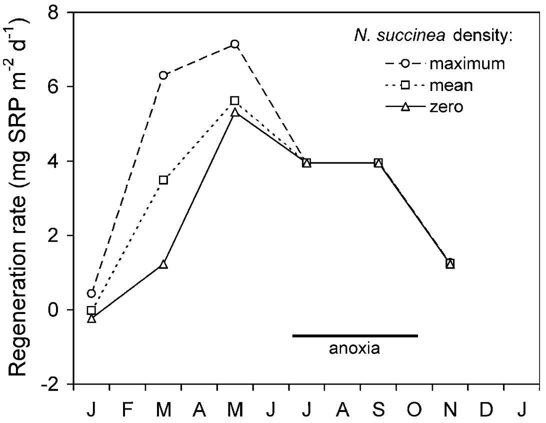

Fig. 4 Estimated SRP regeneration rate in the Salton Sea as a function of *N. succinea* densities during 1999. SRP regeneration rates were determined from intact sediment core incubations conducted in this study, and *N. succinea* densities in offshore sediments were determined from data in Detwiler et al. (2002). Solid bar indicates the time period when bottom waters are anoxic

Discussion

The role of oxygen

Phosphorus regeneration experiments were conducted at different times of the year, and factors such as organic matter content of the sediment, and gradients in pore water phosphorus concentrations most likely differed in sediment cores collected on each date. However, the focus of this study was on the comparison of phosphorus regeneration rates under temperatures, dissolved oxygen concentrations, and *N. succinea* densities typical in the Salton Sea. Except for the anoxic experiments, temperature differences between the *N. succinea* density experiments were small (13.3–17.2°C) and probably had a negligible effect on regeneration rates. In contrast, the influence of dissolved oxygen concentrations on the activities of *N. succinea* (e.g. burrow ventilation and excretion of phosphorus) within the sediments affected phosphorus regeneration rates.

The relatively small stimulatory effect of *N. succinea* on phosphorus regeneration rates under

Table 2 Ratios (*E*/*R*) of the estimated contribution of excretion (*E*) by *N. succinea* to total regeneration (*R*) of SRP and DOP determined in each sediment core incubation experiment

Date	No. of polychaetes per core	*E*/*R*	
		SRP	DOP
20 Jan 01	1	2.8 ± 2.1	–0.3 ± 0.1
	4	4.7 ± 0.5	1.8 ± 3.2
	10	5.1 ± 1.7	11.4 ± 8.03
13 Mar 01	1	0.4 ± 0.1	0.1 ± 0.02
	4	1.04 ± 0.1	0.4 ± 0.05
	10	1.5 ± 0.004	0.5 ± 0.03
28 Apr 01	10	0.9 ± 0.1	4.4 ± 0.3

Ratios are arithmetic mean (±1 SE)

saturated oxygen conditions can be explained by several mechanisms. It is widely accepted that oxic sediments effectively retain phosphorus, and upon exposure to hypoxic or anoxic conditions, this previously retained phosphorus is released (Boström et al., 1982; Roden & Edmonds, 1997). This redox-control of phosphorus within the sediments is thought to operate mainly through adsorption of phosphorus onto ferric hydroxide (FeOOH), whereby under reducing conditions, the reduction of Fe (III) to Fe (II) causes the dissolution of the ferric hydroxide and releases any adsorped phosphorus. This mechanism creates a "trap" for phosphorus within the upper layers of sediment.

Another possible mechanism for explaining the patterns observed under saturated oxygen conditions is differences in organic matter decomposition rates. The decomposition of organic matter has been determined to increase under exposure to oxygen (Kristensen et al., 1995; Prairie et al., 2001). This generally leads to increased pore water phosphorus concentrations by direct release of phosphorus from decomposed organic matter. However, the phosphorus "trap" in the upper layers of sediment may be sufficient to inhibit the upward diffusion of this phosphorus-enriched pore water. The upper layer (~5 cm) and areas around *N. succinea* burrows in each core were lighter in color than the surrounding sediment. If interpreted to indicate oxidation of iron compounds in the sediment, these lightly colored sediments qualitatively indicate the degree of oxygen penetration into the sediments under oxygen-saturated conditions.

N. succinea individuals actively draw water overlying the sediments through their burrows (Kristensen, 1983a), thereby exposing sediment surfaces to highly oxygenated overlying water. As a result, a large portion of phosphorus that may have been released via stimulated organic matter decomposition or pore water exchange remained "trapped" (e.g. adsorbed) in the upper sediment layers. The resulting decrease in the concentration gradient between pore water phosphorus and overlying water reduces phosphorus release from sediments (Holdren & Armstrong, 1980). The minimal phosphorus regeneration from Salton Sea sediments under saturated oxygen conditions most likely reflected a balance between the degree of phosphorus adsorption, the amount of labile organic matter present in the upper layers of sediment, and resulting pore water phosphorus gradients.

The overall increase in phosphorus regeneration rates under reduced oxygen conditions was most likely a result of reduced oxygen penetration into the sediments. As in the saturated oxygen experiment, the ventilation of burrows by *N. succinea* most likely increased the penetration of oxygen into the sediments and enhanced the decomposition of organic matter buried in sediments that would otherwise remain anoxic. However, the degree to which oxygen had penetrated into the sediment differed from that observed under saturated oxygen conditions. A striking, visible color change in these sediments was observed only immediately surrounding *N. succinea* burrow walls. Also, the layer of sediment that appeared oxidized was much thinner (~0.5 cm). This reduced penetration of oxygen may have reduced the effectiveness of the phosphorus–iron precipitation "trap" in mediating phosphorus release.

The reduction in oxygen concentrations may have also resulted in an increase in ventilating activity by *N. succinea*. In laboratory experiments, *N. succinea* was found to increase the volume of water pulled through their burrows as oxygen tension decreased (Kristensen, 1983b). This species typically inhabits sediments that are reducing in nature, and the burrows may quickly become hypoxic, even during short periods without ventilation (Kristensen, 1981). By increasing the duration of ventilation, *N. succinea* is able to maintain favorable oxygen concentrations within its burrow, as well as flush out any toxic hydrogen sulfide that may enter (Theede et al., 1973). Increased burrow ventilation also helps maintain a higher concentration gradient between pore water phosphorus and phosphorus concentrations in overlying water, thus enhancing molecular diffusion. Thus, in the present study, the increased burrow ventilation at the lower oxygen condition may explain the elevated PP regeneration rates relative to control cores without polychaetes. As other investigators have noted, increases in PP regeneration is thought to be due to re-suspended sediment (Guérin & Labroue, 1991).

The absence of a large effect of *N. succinea* density on phosphorus regeneration under hypoxic conditions can be explained by behavior differences. Under hypoxic conditions, *N. succinea* did not attempt to construct burrows but formed mucus tubes on the sediment surface in the sediment cores. Several individuals were observed ventilating these tubes, thereby suspending sediment into the overlying water. Other investigators noted an even more extreme response by *N. succinea* to hypoxic conditions: the construction of mucus tubes at the air–water interface (Reish & Richards, 1966). In addition to hypoxia, hydrogen sulfide is often present and may be responsible for some of these behavioral changes. While scuba diving in a fjord that experienced seasonal anoxia and high hydrogen sulfide in the bottom waters, Jørgensen (1980) observed individuals of *N. virens* and *N. diversicolor* (O. F. Müller) leaving their burrows and lying motionless on the sediment surface. Hydrogen sulfide concentrations increase when oxygen levels above the burrows are depleted, and the polychaetes are no longer capable of bringing in sufficient oxygen to oxidize the hydrogen sulfide (Miron & Kristensen, 1993). Although no measurements of hydrogen sulfide were made during this experiment, its strong odor was present while sieving sediment cores for macroinvertebrate counts after incubation. This was not observed during the other two experiments conducted under saturated and lowered oxygen concentrations. Hydrogen sulfide is present in high concentrations in bottom waters during late spring and summer periods in the Salton Sea. The lack of burrow construction by *N. succinea* can be expected to reduce this organism's importance in stimulating phosphorus regeneration and make it more available to predators.

Regeneration rates of SRP measured under anoxic conditions were similar to those measured under reduced oxygen conditions with *N. succinea* present, and slightly lower than those measured in the control cores under hypoxic conditions. This was surprising, given the fact that the water temperature differences between the anoxic experiments and all others were quite large (25.3–25.6°C vs. 13.3–17.2°C, respectively). In many lakes, regeneration rates of phosphorus are highest during, or just prior to the development of anoxia in water above the sediments. These results indicate that the activity of *N. succinea* stimulated regeneration rates of SRP to levels comparable to those measured under anoxic conditions. In this way, *N. succinea* may increase the time period during which relatively high rates of phosphorus will be released from Salton Sea sediments.

Phosphorus excretion rates

Phosphorus (SRP and DOP) excretion by *N. succinea* may help explain the patterns in sediment regeneration rates observed in this study. Numerous past studies have determined that excretion by benthic macroinvertebrates could account for a large portion of the phosphorus released from sediments in the laboratory (Gallepp, 1979; Granéli, 1979; Nalepa et al., 1980; Gardner et al., 1981; Fukuhara & Yasuda, 1985; Fukuhara & Sakamoto, 1987). Some of these calculations may be biased, however, due to varying methods of excretion rate determination. Large differences have been reported in phosphorus excretion rates, depending on incubation time, gut clearance, and the effects of crowding or antagonistic behavior between adults and juveniles (Gardner et al., 1981; Wilhelm et al., 1999; Devine & Vanni, 2002). Some of these factors are a simple function of organism size. Larger macroinvertebrates, such as *N. succinea*, generally have lower mass-specific excretion rates and may require longer incubation time intervals (e.g. 12–24 h) for determinations.

Changes in neither temperature nor dissolved oxygen concentrations had much effect on SRP excretion rates. Phosphorus excretion rates determined in this study for *N. succinea* (Table 1) were similar to some of those reported for tubificids (4.0–5.6 ng P mg dry wt^{-1} h^{-1}, 16°C; Nalepa et al., 1980), but were less than those for organisms with similar life modes such as chironomid larvae (27.6 ng P mg dry wt^{-1} h^{-1}, 20°C, cleared-gut; Gardner et al., 1981). Gardner et al. (1981) also found small differences in phosphorus excretion rates determined between 5°C and 20°C for tubificids and chironomid larvae.

Various mechanisms might explain the lack of an effect of lowered dissolved oxygen concentrations on phosphorus excretion rates. *N. succinea* can effectively regulate oxygen under lowered environmental oxygen tensions. When the ventilation patterns and oxygen uptake rates of three similar species of polychaetes (*Nereis virens*, *Nereis diversicolor* and *Nereis* (= *Neanthes*) *succinea*) were compared (Kristensen, 1983b), *N. succinea* was the best at regulating its oxygen uptake under a range of oxygen concentrations by increasing the amount of time spent ventilating.

In a study of the effects of dissolved oxygen concentrations on feeding behavior of *N. succinea* from the Salton Sea, lowered oxygen concentrations reduced feeding and under hypoxic conditions caused its cessation (Martin, 1974). In the study reported here, *N. succinea* individuals used in excretion rate determinations were initially kept in saturated oxygen conditions while acclimating to experimental temperatures and clearing their guts. Therefore, under natural conditions in the field, *N. succinea* phosphorus excretion rates under hypoxic conditions may be much lower than measured in this study due to reduced feeding.

Most attention in the literature has been placed on the measurement of SRP excretion rates by invertebrates. Very few studies report excretion rates of DOP, primarily because the bioavailability of this phosphorus fraction is relatively unknown (but see Björkman & Karl, 2003). Hargrave & Geen (1968) determined that 29–74% of the total dissolved phosphorus (TDP) excreted by several species of marine copepods consisted of DOP. Gardner et al. (1981) reported ranges of 15–24% and 30–38% of TDP as DOP from chironomid larvae and *Limnodrilus* spp., respectively. Fukuhara & Yasuda (1985) reported values between 10% and 45% of TDP excreted as DOP by various freshwater benthic invertebrates. The percentages of TDP excreted as DOP by *N. succinea* in the present study (20–30%) were similar to those found for these other organisms.

Importance of phosphorus excretion to sediment regeneration rates

Organisms that ventilate water through burrows are more likely to exchange excreted phosphorus with the overlying water (Matisoff & Wang, 1998). This exchange mechanism may override other physical and chemical processes that operate to reduce phosphorus regeneration from sediments. When exposed to low oxygen tensions in the laboratory (but not hypoxia), *N. succinea* increased the total volume of water ventilated through its burrows by increasing the total amount of time spent ventilating (Kristensen, 1983b). As oxygen tensions approached hypoxia, ventilation abruptly decreased. Approximately half of the *E*/*R* ratios calculated were equal to or greater than one. Since regeneration rates measured in sediment cores represent the net release of phosphorus, much of the phosphorus excreted may have not been directly released into the overlying water.

These results indicate that behavioral differences exhibited by *N. succinea* can be important in explaining the pattern of relative importance of excretion to overall regeneration of SRP from sediments. Other studies that investigate the importance of excretion by benthic macroinvertebrates relative to other processes involved in the regeneration of sediment phosphorus need to take into account the effects of varying environmental factors on the organisms present. In this study, excretion became less important to total flux of SRP as oxygen concentrations decreased, most likely due to interactions between the redox condition of the sediments, concentration gradients of SRP in pore waters, and behavioral changes by *N. succinea*.

Importance of sediment phosphorus regeneration in the Salton Sea

Comparing external loading to internal recycling of phosphorus assesses the relative importance of sediment phosphorus regeneration to a particular aquatic system. The methodology and assumptions employed may strongly affect the result. It is widely understood that phosphorus regeneration from sediments, as well as the abundances of organisms that may directly affect the regeneration rates of phosphorus, are likely to vary seasonally (Gamenick et al., 1996).

The estimated annual contribution of sediment phosphorus regeneration to the Salton Sea in this study is significant (Fig. 4). Although the sediments act as a sink for phosphorus over the long-term, a large percentage of phosphorus is potentially regenerated from the sediments. A recent study investigated the potential for phosphorus regeneration in the Salton Sea by using pore water profiles and calculating phosphorus diffusion rates (Schroeder et al., 2002). Their calculations indicated that sediment regeneration of phosphorus was an order of magnitude lower than external loading to the lake. However, estimates of phosphorus regeneration based on diffusion alone are not reliable in systems where organic loading, biota activity, and the potential for wind-driven resuspension of sediment are high (Søndergaard et al., 1992; Van Rees et al., 1996). The stimulation of sediment phosphorus regeneration rates by *N. succinea* is small but is highest during periods when the lake is frequently mixing (Watts et al., 2001). Phytoplankton populations are also maximal during this time of year (M. A. Tiffany, unpublished data). Therefore, when the water column is mixed, the movement of phosphorus into the photic zone is more likely to occur, and phosphorus regenerated from the sediments has strong potential for contributing to the overall production of the lake.

Sediment phosphorus regeneration: past and future

The population of *N. succinea* appears to have decreased since the survey conducted by Carpelan and Linsley in 1956 (Detwiler et al., 2002). The area-weighted standing crop of *N. succinea* in the Salton Sea was estimated to have been two orders of magnitude higher in 1956 than in 1999. There are several possible explanations for this apparent decrease. Watts et al. (2001) provide evidence for an historical increase in hydrogen sulfide concentrations and frequency of anoxia in the Salton Sea. Both of these changes were explained primarily by an increase in primary productivity leading to increased organic matter decomposition in bottom waters, as well as increases in sulfide concentration. Increased predation by tilapia (*Oreochromis mossambicus* Peters), which was not present in the Salton Sea until the late 1960s (Hoover & St. Amant, 1970), may also explain the apparent decline in *N. succinea*.

In the face of continued widespread anoxia and increases in salinity, *N. succinea* populations may decline and contribute less to phosphorus regeneration from sediments, although there would likely be an overall increase due to anoxic conditions. If restoration attempts succeed in maintaining better oxygen conditions or shortening the duration of anoxia during summer months, *N. succinea* populations may persist for longer periods throughout the year in offshore sediments. Thus, reductions in phosphorus regeneration from sediments by higher oxygen levels may be offset by the increased periods of stimulation due to *N. succinea* activity.

It is difficult to determine if sediment phosphorus regeneration rates were higher in the past than current estimates. Although external inputs of phosphorus have more than doubled since 1968–1969 (J. M. Watts, unpublished data; Holdren & Montaño, 2002), water column concentrations of phosphorus have changed little since the studies conducted by Carpelan (1958). Other indicators of trophic status, such as water clarity, as measured by Secchi disk depth, and chlorophyll *a* concentrations have changed little as well. This lack of change in measures of productivity, specifically in water column concentrations of phosphorus in the face of increased inputs, is typical of terminal water bodies. As there are no outlets in the Salton Sea, virtually all of the phosphorus that has entered the lake is present in either sediments or biota. However, what this may mean for future lake productivity in the Salton Sea cannot be ascertained by simply examining how much phosphorus has entered the lake. In order to predict the importance of the sediments as a source of phosphorus to the lake, knowledge of the mechanisms that stimulate the release of phosphorus, as well as what conditions regulate these mechanisms, is needed. This knowledge will be critical for predicting changes in lake productivity under reduced external nutrient inputs as well.

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