

Stratification, sulfide, worms, and decline of the Eared Grebe (*Podiceps nigricollis*) at the Salton Sea, California

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Abstract

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Over the last half century the Salton Sea has been an important migratory stopover site for the Eared Grebe (*Podiceps nigricollis*). However, in recent years there have been sporadic mass mortalities (*i.e.*, 150,000 in 1992) and a great reduction in the number of grebes visiting during the winter. We propose that a worsening food supply is causing the decline and that starvation may be a major cause of the unexplained mortalities. While at the Sea, grebes forage almost exclusively on a benthic polychaete, the pileworm (*Neanthes succinea*). This resident pileworm population has increasingly been subject to periodic crashes driven by exposure to anoxic, sulfide rich, hypolimnetic water following lake mixing events. A set of interlocking mechanisms seem to be operating. These involve, in particular, increasing lake salinity, weather events favoring lake stratification, and booms and busts in tilapia (*Oreochromis mossambicus* × *O. urolepis hornorum*) and plankton populations, including those of toxic cyanobacteria. In spring, Eared Grebes arrive from the Gulf of California and many arrive in need of food to fuel the remainder of their migration. When pileworms are scarce, many grebes are able to continue on toward their northern breeding grounds, but those that lack sufficient energy stores are forced to stay and may eventually perish. This analysis is surely incomplete, and definitive explanations of the excessive drinking and waterlogged plumage often exhibited by Eared Grebes during mass dieoffs have yet to be found.

Key words: *Neanthes succinea*, *Oreochromis*, tilapia, stratification, starvation, saline lakes, plankton, hydrogen sulfide, trophic cascade, migration, Gulf of California

Lament for a Dead Sea-Bird

*I grieve for grebes that wash ashore
To tread the dappled waves no more.*

*This little bird, that lately died,
Was wont to pedal through the tide,
His dumpy body, trim and pert,
To overbearing surf alert,
That braved, with no apparent care,
All onslaughts of both sea and air
When foam would fly and billows boil,
Succumbed to feather-clogging oil.**

*Each petal-fingered, leather hand
Is folded by a last command.*

His life's account is settled now.

His elfin bill and shallow brow

In dead disorder double back

On soggy plumes of grey and black.

He treads the dappled waves no more.

I grieve for grebes that wash ashore.

– Ralph A. Lewin

American Scientist 51:262a (1963)

* Had Dr. Lewin lived by the Salton Sea instead of the Pacific Ocean, this line might have read: *Succumbed to loss of pileworm oil, i.e., lipids.*

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Introduction

Adapted to exploit the food resources of inland saline lakes, the Eared Grebe (*Podiceps nigricollis* Brehm) has become the most abundant member of the family Podicipedidae (Jehl 2001). Most individuals of this species reside within the North American continent and are often associated with saline waterbodies along their migration routes (Cullen *et al.* 1999). In the north, Great Salt Lake, Utah, and Mono Lake, California, are important pre-migration staging areas, while the Salton Sea, California, and Gulf of California, Mexico, serve as southern wintering areas (Fig. 1). At these interior lakes, high salinities limit invertebrate composition to a few species that may attain very high densities in the absence of aquatic predators (Hammer 1986; Herbst 2001, 2006; Jehl 1994, 2001; Wurtsbaugh 1992). This abundance of forage permits grebes to accumulate the energy stores needed to migrate to and from their breeding grounds: typically fish-free freshwater lakes of the western United States and Canada (Jehl 1997; Cullen *et al.* 1999). The Eared Grebe's ability to capitalize on these seasonal invertebrate resources has facilitated a large continental population and wide breeding range (Jehl 2001).

Since its flooding in 1905, the Salton Sea, being close to the Gulf of California and the Colorado River Delta, has become one of the most important localities for waterbirds in the American Southwest (Shuford *et al.* 2000, 2002; Patten and Patten-Smith 2004). With regard to Eared Grebes, this lake has the dual distinction of being not only a heavily used wintering area and spring staging site but also the site of periodic mass mortality events. The greater Salton Basin has contained a large lake, off and on, with water present during most of the last 1300 years (Waters 1983; Smith 1999; Patten and Smith-Patten, 2004). Its use by grebes likely did not intensify until introduction of a polychaete, the pileworm (*Neanthes succinea* Frey and Leuckart), into the Salton Sea in the 1930s (Jehl and McKernan 2002). The majority of grebes using the Sea stay for only a short period between January and March as they make their way north to breed. Several weeks of feeding on these pileworms is sufficient to meet energy demands of the next leg of migration (Jehl and McKernan 2002). However, in the 1990s unusual Eared Grebe mortality events, specific to the Salton Sea, brought into question the overall value of this stopover site to the continental population. One particularly large die-off of 150,000 grebes in the winter of 1991-92 stimulated intensive investigations of possible factors responsible for this loss (Meteyer *et al.* 2004). While no single factor was identified as the major cause of mortality, much has been learned about the epidemiology of these events. Since then, new research on the Salton Sea has led to a greater understanding of physical, chemical and biological phenomena in this unique terminal lake.

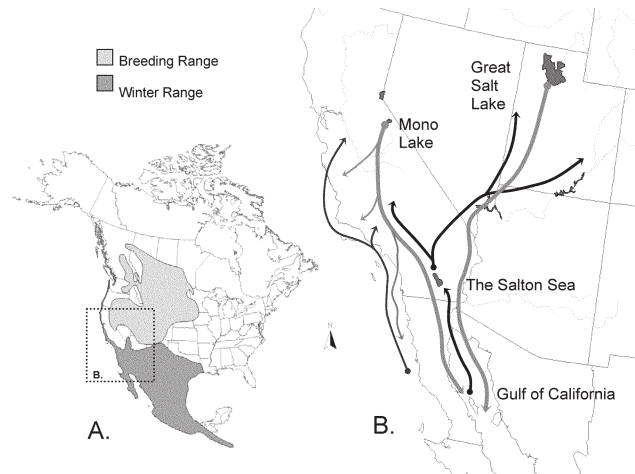


Figure 1.—Eared Grebe range in North America (A) after Cullen *et al.* (1999) and major staging areas/migration routes between summer and winter habitats (B) based on Jehl (1996) and Jehl *et al.* (1999, 2003).

The objectives of the present study are to summarize existing information on recently declining numbers and large periodic die-offs of Eared Grebes at the Salton Sea and to propose how these may have resulted from a set of interconnected, fundamentally limnological phenomena. Recent research has documented large changes in populations of fish, pileworms, and plankton driven by increasing salinity, extreme weather events, and more frequent upwelling of sulfide-rich bottom waters. Declining use of the Salton Sea by grebes may be due to a change in migratory patterns driven by diminished pileworm abundance. Furthermore, the large periodic die-offs of grebes may be due to starvation and possibly cyanobacterial toxins. Given current Salton Sea restoration efforts, we also discuss what components of a future Salton Sea are important for the North American Eared Grebe population.

Data sources

This review is primarily a synthesis of published or previously available information, but also presents some new data. Sources of information and methods of data collection and analysis are summarized as follows.

Eared Grebe surveys

Documentation of Eared Grebe presence, abundance, and distribution provides an understanding of their habitat preferences and the timing of population movements. Grebe use of the Salton Sea has been well documented through two separate survey efforts. From 1986-1999 monthly aerial surveys were used to obtain grebe numbers during peak periods of migration (Jehl and McKernan 2002). These were whole-sea

surveys using two observers flying at 85-105 km h⁻¹ and at an altitude of 100-200 m. From 1999 to 2005 monthly land-based surveys conducted by the Salton Sea Wildlife Disease Program were used to identify trends in grebe numbers at the Sea. These data were collected as point counts from 20-27 locations along the shoreline using 10×50 binoculars and a 20-60 power spotting scope. Due to the large area covered, each monthly survey required 2-3 days. It is difficult to adequately compare results from the two census methods to one another without cross-checks, but because of the consistency with which the surveys were conducted we believe they are both sufficient for identifying strong trends.

For the Gulf of California, the primary overwintering area of the grebe, only sparse information has been published on abundance (Jehl 1988; Jehl and McKernan 2002), movements (Jehl 1988, Jehl 1993; Jehl *et al.* 1999) and on mortality events (Jehl and Bond 1983; Nishikawa *et al.* 1984; Jehl 1996; Jehl *et al.* 2002). These references, specifically those documenting mortality events, identify some years in which the Gulf of California has been less than suitable for the wintering grebes.

Data on Eared Grebe abundance in North America have been obtained through the Breeding Bird Survey (BBS) database, coordinated by the U.S. Geological Survey and Canadian Wildlife Service. This is an annual survey conducted on over 2,900 routes, of which 107 were deemed consistently reliable for use in generating a survey wide Eared Grebe trend for the years 1983–2005. Sauer *et al.* (1997) provides details on the methods used to generate this trend. Briefly, each route covers 39.4 km with three minute point counts made every 0.8 km of all birds seen and heard within 0.4 km of the route. An index of abundance, generated from these data, provides a trend estimate for the continental population. There are many biases associated with the BBS, some of which are more common with waterbirds and in areas of limited accessibility (see Sauer *et al.* 1997); however, with 107 routes consistently meeting the criteria for inclusion we believe the results are useful if interpreted with caution.

Eared Grebe mortality

A record of wintering Eared Grebe mortality has been compiled for the purpose of identifying trends. Data for the Salton Sea come from the National Wildlife Health Center epizootic database and have been cross-checked with unpublished records at the Sonny Bono Salton Sea National Wildlife Refuge. Included are carcass retrievals and estimates of total mortality for undiagnosed or open investigations involving Eared Grebes recovered from the Salton Sea area during the period from 1980 to 2004. Descriptive reports and studies of past mortality events have been scoured for any identifying patterns. Jehl (1996), Friend (2002), Franson and Rocke (2003) and Meteyer *et al.* (2004) provide detailed accounts

of past die-offs at the Salton Sea. Likewise, Nishikawa *et al.* (1984), Jehl and Bond (1983), and Jehl *et al.* (2002) provide insight on winter mortality in the Gulf of California.

Plankton Sampling

Detailed study of the abundance and composition of Salton Sea phyto- and zooplankton was carried out during 1997-1999 (Tiffany *et al.* 2002; Tiffany *et al.* 2007a,b). After noting, in following years, dramatic changes in the plankton, we decided to sample it again on two dates – Apr 27 and May 4 – in the spring of 2005, with the same protocols used in 1997-1999. Sampling was carried out at a single mid-lake station (S-1) on Apr 27 and at three mid-lake stations (S-1, S-2, S-3) on May 4. Precise locations and details of methods are as described in Tiffany *et al.* (2002, 2007a) and Watts *et al.* (2001) and are summarized below.

At each station water samples for chlorophyll *a* and phytoplankton analysis were taken from depth strata 0-3, 3-6 and 6-9 m and composited. Separate sub-samples were taken for chlorophyll *a* analysis and phytoplankton enumeration. Samples for chlorophyll *a* analysis were filtered through GF/C filter paper within 24 h, then extracted and measured via the trichromatic method. Samples for phytoplankton counts were preserved in 1% Lugol's solution and processed using standard inverted microscope methodology. Identifications were made to the species level whenever possible. Mean cell or colony biovolume was estimated for each species. These estimates were used to calculate total biovolume densities for each major taxon and for total phytoplankton on each date.

Densities of planktonic pileworm larvae were determined as in Tiffany *et al.* (2002). Briefly, samples were taken at 2 m depth intervals from 0.5 to 10.5 m at each station, preserved in formalin and counted at 40× with a modified Sedgewick- Rafter cell. An arithmetic mean over all depths was determined for each station and date.

For data on numerical densities, biovolume densities, and chlorophyll *a* concentrations, geometric means and their standard error factors were calculated for the May 4 data.

Population trends and mass mortalities

Winter migrants vs. continental population size

Many Eared Grebes stay at the Salton Sea throughout the winter, but many more simply stop over to “refuel” during spring migration. Here they feed almost exclusively on the pileworm (Jehl and McKernan 2002) which unlike other Salton Sea macroinvertebrates remains abundant during the winter (Detweiler *et al.* 2002). Jehl and McKernan (2002) report seeing “[Eared Grebe] gizzards from the Sea...packed

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with hundreds or thousands of worm teeth.” The hard, amber-brown, pileworm mandibles (Fig. 2) are often abundant in gizzards of grebes at the Salton Sea and were first identified in several gizzards by D. Dexter (pers. comm., San Diego State University), in 1989. She observed that, aside from their own finer feathers, which Eared Grebes frequently ingest for unknown reasons, pileworm mandibles and setae were virtually the only prey remains in the gizzards. Mandibles, head capsules, or other hard parts of other invertebrates present (e.g., amphipods, waterboatmen, brine flies) were not observed in her microscopic examination. Quast (1961) presents a regression analysis for pileworm wet weight on mandible length; mandible lengths of 1 mm and 2 mm correspond to pileworms weighing roughly 10 mg and 80 mg, respectively.

The lake’s potential as a migration stopover point is best demonstrated by an estimated 3.5 million grebes having been documented during an aerial survey in March 1988 (Jehl and McKernan 2002). At roughly 98% of the continental population, that may have been an extraordinary year. However, for most years, significant numbers of grebes visit during some portion of the non-breeding season (Table 1). With such a large proportion of the population periodically making use of the Salton Sea, it is important to understand the degree of dependence they have on this resource.

Standardized counts at the Salton Sea indicate year-to-year variability during 1983-2005 in maximum numbers of grebes seen there (Fig. 3). Within this period, two patterns are apparent. First, there was a post-1988 dip in numbers which persisted into the early 1990s, followed by a slight recovery in the mid-1990s. Second, there was a post-1998 decline in numbers that was initially gradual and then precipitous, post-2001. This post-1998 decline is also evident in numbers of grebes tallied during the Christmas Bird Count (CBC) (Fig. 11 in Hurlbert *et al.* 2007). CBC data have limited value for documenting grebe trends at the Sea since they come from two census circles that include only small portions of the northern and southern ends of the lake and the counts are conducted around a fixed date, whereas grebes occur over the entire Sea and timing of their migration can vary tremendously from year to year (Jehl and McKernan 2002). Despite these deficiencies a post-1998 dip in grebe numbers at the Salton Sea is apparent in the results of this mid-winter survey.

There is no indication that the great reduction in numbers at this wintering area is a reflection of the continental population. Indeed, Breeding Bird Survey (BBS) data, using the methods of Sauer *et al.* (1997), documents an increase of 160 percent in the index of abundance for the North American Eared Grebe population over the period 1983-2005 (Fig. 3). Since the beginning of the BBS (1967-2005) the Eared Grebe population is estimated to have increased by 5.4 percent per

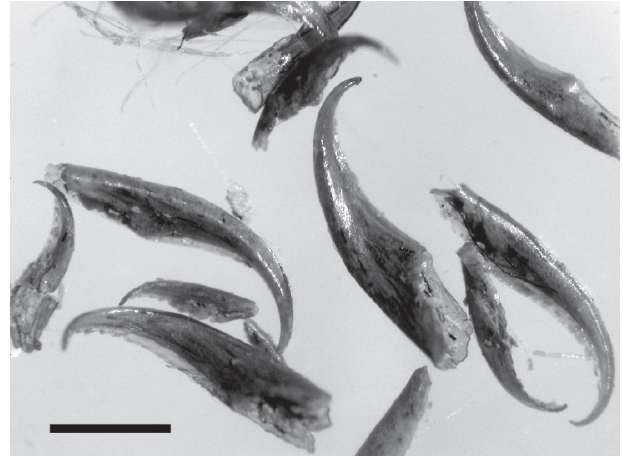


Figure 2.—Photograph of *Neanthes* jaws from the gizzard of an Eared Grebe. Scale bar is 1mm.

year ($p < 0.025$, 95% CI = 0.8 – 9.9). This increasing trend in the BBS index appears to have been sustained even through the post-1998 decline at the Sea (Fig. 3).

Other more direct, if less systematic, information on the grebe population continent wide gives no evidence of recent decreases in the North American population (J. Jehl, unpublished data.). It has been argued that the BBS is inadequate for documenting Eared Grebe population numbers (Cullen *et al.* 1999; Jehl *et al.* 2002). A strong upward trend in the BBS index could have, for example, resulted from BBS routes not being selected to cover the major grebe breeding grounds or from the grebes shifting their distribution in response to large scale climatic change, such as the two large droughts the western U.S. has experienced during the past 25 years. Drying up of major breeding sites, which may have been poorly represented in the BBS because of their inaccessibility, could have caused grebe numbers to increase on less preferred wetlands that *were* well-represented in the BBS.

For purpose of the present analysis, the main import of the BBS data on the Eared Grebe is that there is no indication of a downward trend in continent-wide grebe numbers over the last decade. Thus, the reduced numbers seen at the Salton Sea must be attributed to a smaller proportion of the North American population making use of this migration site, and explanations for the decline must be looked for at the Sea itself.

Investigations into major mortality events

As evidenced by records of avian mortality maintained by Sonny Bono Salton Sea National Wildlife Refuge and the National Wildlife Health Center Epizootic Database, migrating and wintering Eared Grebes have periodically encountered

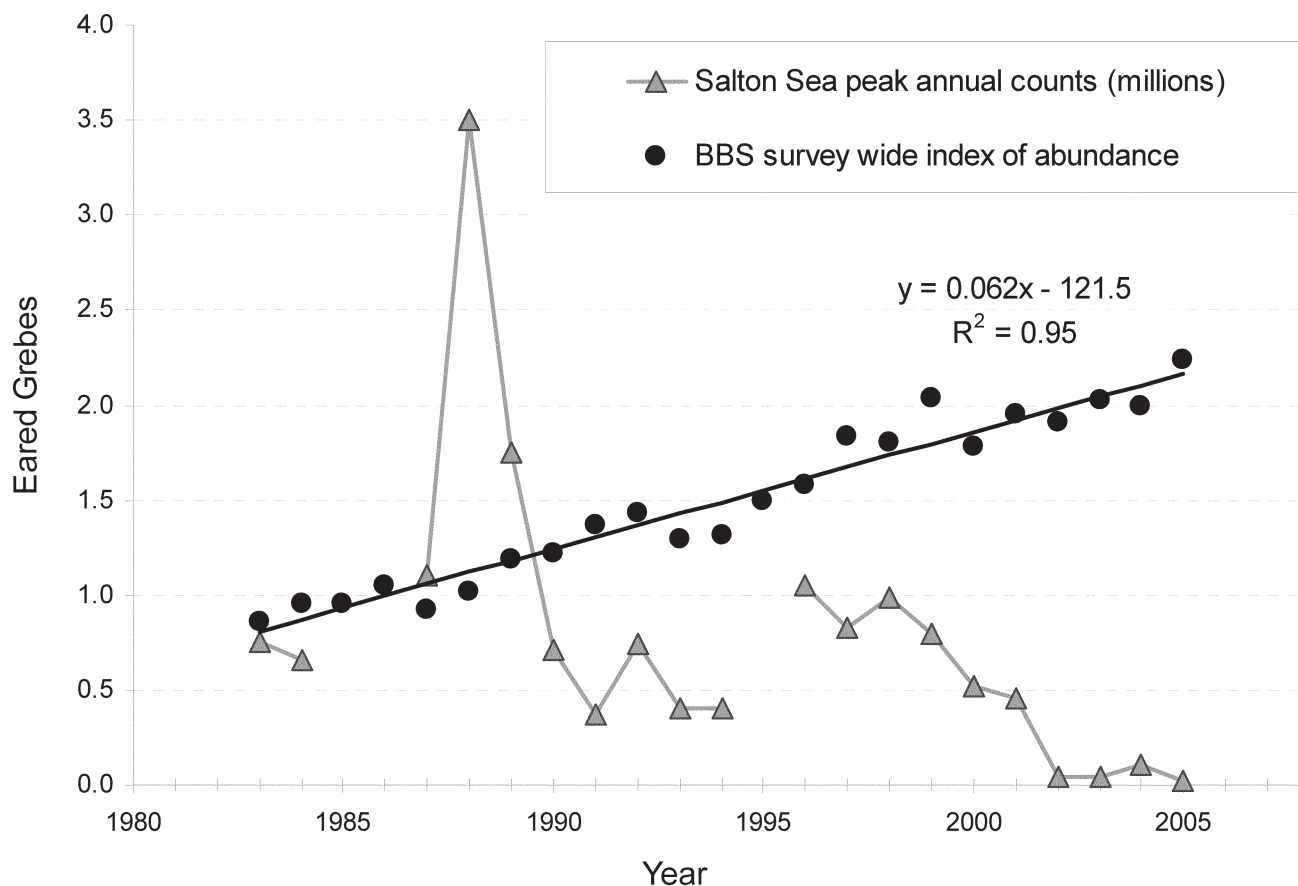


Figure 3.—Annual peak number of Eared Grebes at the Salton Sea, 1983-2005, and Breeding Bird Survey index of grebe abundance, 1983-2003.

less than suitable conditions while at the Salton Sea. Along with frequent cases of avian cholera, large-scale Eared Grebe mortality of undetermined causes has occurred at the Salton Sea at least five times with no discernable pattern (Table 1). Additionally, Jehl (1996) recounts the events of an additional large die-off during the winter of 1987-88 in which grebes exhibited clinical signs similar to those described below. It is also important to note that there have been two very large mortality events reported for the Gulf of California (Jehl and Bond 1983; Nishikawa *et al.* 1984; Jehl *et al.* 2002). A better understanding of these mortality events provides insight into the diminished grebe use of this important migration destination.

Observations of sick grebes at the Salton Sea during 1991-92 established an etiological profile that has since been useful in identifying subsequent outbreaks of this “unidentified eared grebe disease.” Unusual behaviors described by Jehl (1996) and Meteyer *et al.* (2004) characterize afflicted grebes as preening excessively, with many individuals disheveled and wet. They were often found congregating near freshwater inflows where they frantically gulped water or hauled out

on shore. Prior to death, birds were typically lethargic and unresponsive to disturbance or predation and died without signs of paralysis or other neurological impairment. The physical condition of specimen birds indicated that many had suffered a prolonged wasting away with 40 percent also bearing wounds likely inflicted by opportunistic gulls (Meteyer *et al.* 2004). Low body weight (ca. 237 g; Jehl 1996), atrophied musculature, and little to no fat reserves suggested the possible influence of chronic disease, low level exposure to contaminants, or simply starvation.

Because the 1991-92 event and later, smaller mortality events involving Eared Grebes are believed to be unique to the Salton Sea area, characteristics of this ecosystem were scrutinized in an attempt to identify environmental factors responsible for these grebe mortalities. Toxicology and pathology studies coordinated by the National Wildlife Health Center in Madison, Wisconsin, looked for evidence of contaminants and disease (Franson and Rocke 2003; Meteyer *et al.* 2004). Concentrations of metals and of organochlorine, organophosphorus, and other pesticides in the water and sediments of the Salton Sea were measured and compared to

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Table 1.—Summary of information regarding Eared Grebe migration through the Salton Sea region, known mortality events throughout their winter habitat, and Sea Surface Temperature (SST) anomalies in the Gulf of California.

Winter	Migration		Mortality					ENSO			
	Maximum Estimated Birds ^(1,2) (x 1000)	Peak Month	Salton Sea carcass counts ^(3,4) (x1000)	Specimen Diagnoses ⁽³⁾					Estimated total mortality ⁽³⁾ (x 1000)	Specimen birds average weights (grams)	Gulf of California Average SST Anomalies ⁽⁵⁾ (°C) (+) El Niño (-) La Niña
				avian cholera	salmonella	parasitism	trauma	Inconclusive			
1982-83	755		0.02						>25* ^(6,7)	200 g ⁽⁶⁾	+ 2.0 §
1983-84	660										+ 1.5
1984-85	no est.										- 0.5
1985-86	no est.										+ 1.0
1986-87	1,100	Mar									+ 0.5
1987-88	3,500	Mar	0.01								0
1988-89	1,750	Mar						>100 ⁽⁷⁾		342 g ⁽⁷⁾	- 2.5
1989-90	715	Mar						<0.6			- 0.5
1990-91	375	Feb						<0.1			0
1991-92	740	Jan	43.34	+	-	-	+	+	155	237 g ⁽⁷⁾	+ 0.75
1992-93	400	Jan									+ 0.75
1993-94	400	Jan	15.67	+	-	-	-	+	20		0
1994-95	no est.			-	+	+	-	+	<2	310 g ⁽⁷⁾	+ 0.75
1995-96	1,050	Feb									+ 0.75
1996-97	829	Feb	2.44	-	-	-	-	+	no est.		- 0.75
1997-98	984	Mar	3.45	+	+	-	-	+	>400* ⁽⁹⁾	178 g ⁽⁹⁾	+ 1.75
1998-99	800	Apr	0.72	+	-	-	-	-	no est.		- 1.25
1999-2000	525	Feb	3.73	+	+	-	-	+	no est.		- 1.25
2000-01	454	Feb	0.39	+	+	-	-	-	no est.		+ 0.5 §
2001-02	42										- 0.5 §
2002-03	45	Nov	2.97	-	-	-	-	+	no est.	Fig. 3 ⁽¹⁰⁾	+ 1.0 §
2003-04	101‡	Mar	0.08	+	-	-	-	-	no est.		+ 0.5 §
2004-05	20‡	Mar									0 §

* value from the Gulf of California, § <http://www.cpc.ncep.noaa.gov/products/GODAS/> (monthly plots of global X-Y Sea Surface Temperature data, Jan.–Feb.), ‡ whole Sea values estimated by Jehl 141,000 and 47,500 for 2003-04 and 2004-05 respectively, ¹ Jehl and McKernan 2002 (1982-1999); ² Salton Sea Authority records (2000-2005); ³ USGS National Wildlife Health Center, Epizootic Database; ⁴ Sonny Bono Salton Sea National Wildlife Refuge Files; ⁵ Lavin *et al.* 2003; ⁶ Jehl and Bond 1983; ⁷ Jehl 1996; ⁸ Meteyer *et al.* 2004; ⁹ Jehl *et al.* 2002; ¹⁰ Franson *et al.* 2004

concentrations in invertebrate prey and grebe tissue samples. Healthy, sick and dead grebes were examined for parasites and bacterial and viral pathogens. Despite this exhaustive testing and the finding of a few cases of avian cholera and salmonellosis, no single agent was identified as a dominant or principal cause of death for these birds, and no contaminant, including selenium, was identified in the Salton Sea environment that could explain such mass mortality. Selenium, a frequent concern for waterbird populations at the Salton Sea, was found to be elevated in specimen grebes (Meteyer *et al.* 2004), but only at levels that may cause chronic long-term health and reproductive impairment rather than acute toxicity (Fairbrother and Fowles 1990). Selenium, at the concentrations observed in grebe tissue, has the potential to affect immune suppression systems (Fairbrother and Fowles 1990). Meteyer *et al.* (2004) suggested that some unidentified interactive effects or contaminant-related immune suppression may be responsible.

Another line of investigation, into the role of algal toxins, has revealed the presence of several toxin producing organisms at the Salton Sea, periodically in very high densities (Reifel *et al.* 2002; Carmichael and Li 2006). While sick grebes have not been noted to exhibit clinical signs normally associated with exposure to algal toxins, Carmichael and Li (2006) did find levels of microcystins, a class of cyanobacterial toxins, in tissues from specimen grebes that could cause acute lethal toxicity. Possible roles of algal blooms will be discussed later.

Evidence of starvation

Past investigations have explored the role of disease, contaminants and toxins, but little to no attention has been given to the potential role of starvation. Influence of this factor was suggested by the low body mass of specimen birds during the 1991-92 and 2002-03 mortality events. Grebes collected 23 February to 10 April 1992 were underweight during this period in which losses were estimated to be over 150,000 (Meteyer *et al.* 2004). Differences in mass existed between the 15 specimen grebes testing positive for cholera (mean mass of 298 g) and the 35 testing negative (242 g). The latter were characterized as dying of undetermined causes. Since avian cholera kills quickly, those birds diagnosed with cholera also provide a good indication of body mass when initially exposed to *Pasturella multocida*. While a mean mass of 298 g falls within the low end of a range considered healthy for wintering grebes (mean \pm SD, 320 \pm 39 g) reported by Jehl (1997), those grebes that died of undetermined causes, with a mean mass of 242 g, were clearly underweight. These values suggest that birds could not obtain food and eventually died in an emaciated condition. Some of these birds contracted the bacterium *P. multocida*, possibly ending their starvation prematurely. Since no additional disease or toxin could be linked to these birds (Meteyer *et al.* 2004) it is plausible

that the majority starved to death. Unfortunately, there is not enough known to say whether they starved from a lack of pileworms or if another condition prevented them from foraging effectively.

Continuing to use 320 g as a benchmark body mass and considering data from Franson and Rocke (2003), we can make inferences about the condition of Eared Grebes at the Sea through the winter of 2002-03 (Fig. 4). Weights of twenty birds collected as control specimens in January were variable but healthy for wintering birds (mean \pm SD, 352 \pm 63 g). By April, a period by which most Eared Grebes would typically be on their way back north, heading toward their breeding grounds, the 103 specimen birds were consistently underweight (mean \pm SD, 200 \pm 27 g), whether dead, sick, or collected as apparently healthy control birds. The poor condition of these birds is even more apparent considering that late winter grebes at the Salton Sea average much higher mass (mean \pm SD, 384 \pm 45g) prior to migration (Jehl 1997). In dissecting these birds it was clear that they had not accumulated the fat reserves or conditioned their muscles sufficiently to finish their spring migration (T. Anderson, pers. observation). Of 145 specimen birds salvaged or collected that winter, none tested positive for viral or bacterial diseases, nor were any toxicants identified as a problem (Franson and Rocke 2003). These findings corroborate the idea that underweight grebes are unable to attempt migration, even if there is no compromise in their health from disease or contaminant stressors. Only when migrating birds have sufficient energy stored do they have the option of continuing north to breed. Those that lack adequate fat and muscle may not be able to achieve flight and will be forced to stay and attempt to find food.

Stressors such as starvation are also likely to directly affect functions of the immune system (Bonneaud *et al.* 2003). A weakened immune system resulting from stressful energy expenditures, such as conditioning for flight or migration itself, can make individuals more susceptible to pathogens, parasites or toxins (Sheldon and Verhulst 1996). In a starvation scenario at the Salton Sea, immune functions may be similarly compromised. Weakened birds, arriving after a physically demanding flight, will be more vulnerable to many diseases, parasites, and predators. In such situations birds will die from a combination of factors and tests for specific causes of mortality become inconclusive. Past investigations into grebe mortality events have often identified multiple causes of mortality (Table 1). The uncertain diagnoses and inconclusive nature of these investigations are indirect support for the idea that starvation may have been an underlying cause of mortality.

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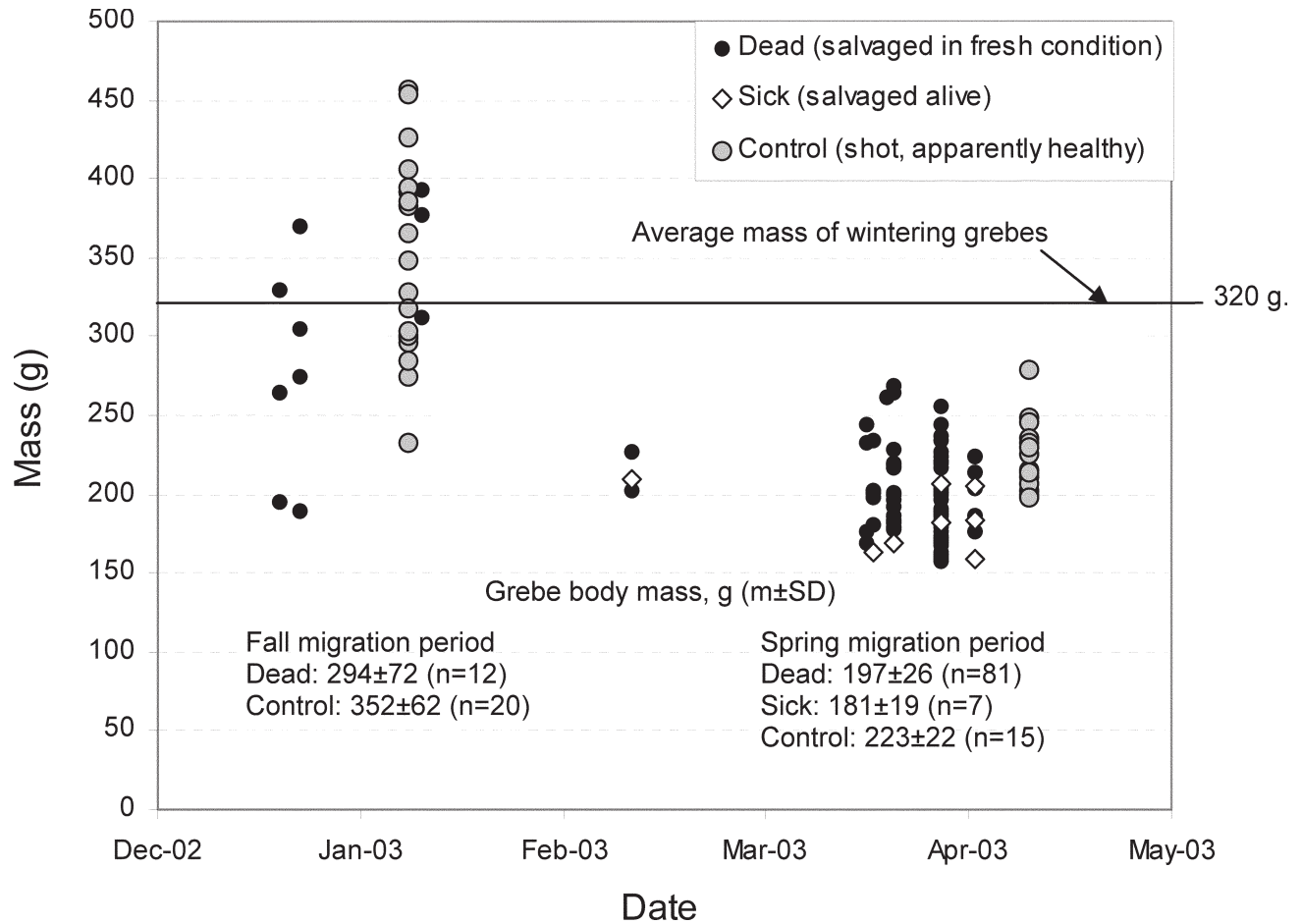


Figure 4.-Mass of specimen Eared Grebes during the 2002-03 mortality event (data from Franson and Rocke 2003). Average mass of wintering grebes, 320 g, from Jehl (1997).

Stratification induced starvation: the hypothesis

We believe the fundamental factor driving the observed decline in grebe use of the Salton Sea has been both gradual and episodic reductions the pileworm population. This polychaete has long been the most abundant macroinvertebrate at the Salton Sea, occurring at mean densities of 100 to >1000 individuals per m² over much of the Sea's bottom during at least the winter months (Carpelan and Linsley 1961; Detwiler *et al.* 2002). Adult pileworms range up to 35 mm in length. They likely are very nutritious given their almost complete lack of hard parts and their gamete-laden condition when swarming in surface waters (Neuhoff 1979). Other benthic invertebrates present are much smaller, occur in generally lower densities, and are found only in very shallow waters (Detwiler *et al.* 2002). The only exception would be water boatmen (*Trichocorixa reticulata* Guérin-Ménéville) which on various occasions in recent decades greatly increased in near-shore waters following crashes in fish populations

(Sahagun 1989; N. Niver, Salton City, pers. comm.; pers. observ. authors).

Anoxia and sulfide production

A number of interconnected phenomena and mechanisms are suspected to have been responsible at various times for reduced pileworm abundance, usually via production of anoxic conditions with high sulfide levels (Fig. 5). Sulfide is generated in bottom waters, accumulates during periods of anoxia and can then be delivered to the rest of the water column by mixing or upwelling events driven by wind (Watts *et al.* 2001, Tiffany *et al.* 2007c). Production of hydrogen sulfide results in part from bacterial decomposition of sulfhydryl-containing proteins in organic detritus consisting principally of dead planktonic organisms. But the very high levels of sulfide (>20 mg l⁻¹; Tiffany *et al.* 2007c) that can accumulate in Salton Sea bottom waters derive from an additional microbial process, direct reduction of sulfate ion to sulfide by sulfate-reducing bacteria (Goldhaber and Kaplan

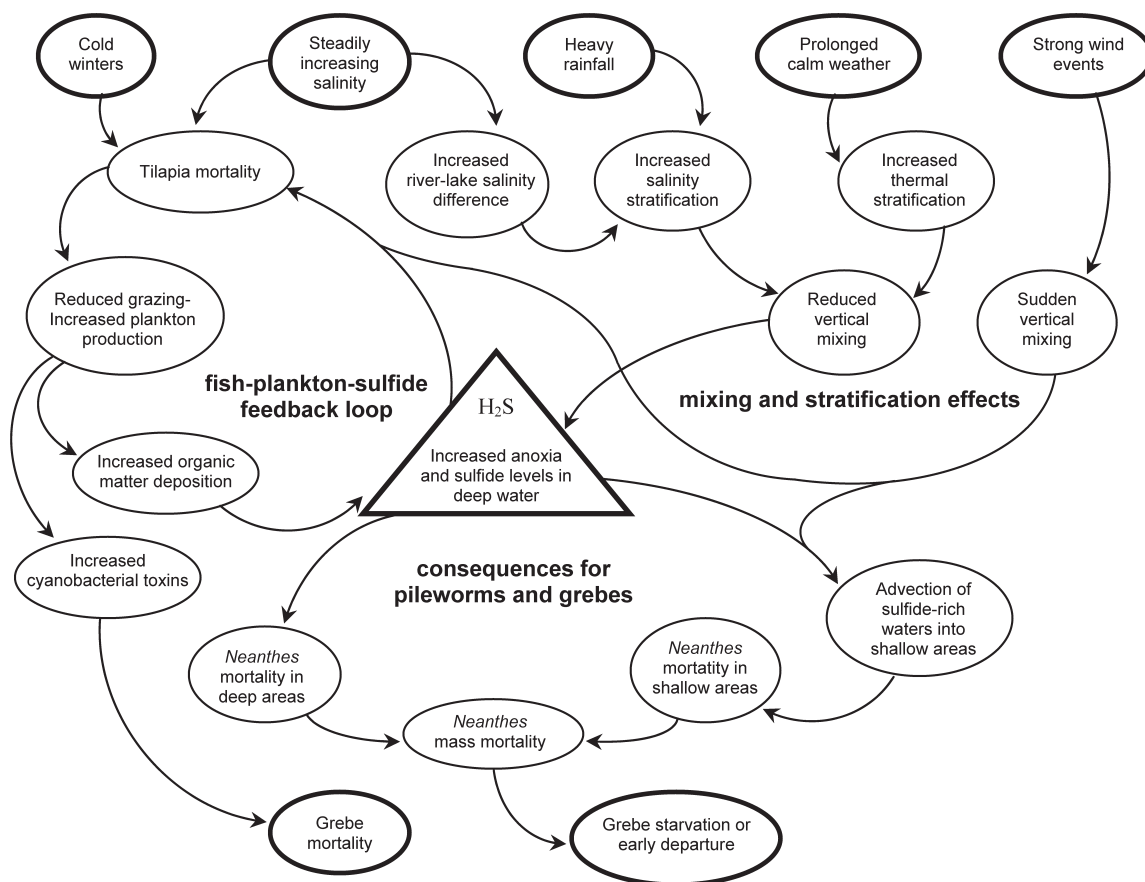


Figure 5.-Postulated mechanisms for effects of limnological phenomena on grebe numbers at the Salton Sea, California.

1974). Sulfide ions will react with molecular oxygen, if available, to produce sulfate ions, or, in its absence, simply start accumulating. In response to prolonged anoxia and accumulating sulfide, and perhaps ammonia, all obligately aerobic organisms, such as the pileworm, living in or on bottom sediments die or are driven away, perhaps upward in the water column.

So long as the lake remains stratified, sulfide levels will increase in bottom waters without directly affecting organisms in the upper part of the water column. The rate of increase in sulfide levels will be a function of water temperature and rate of arrival of organic detritus in bottom waters.

Upwelling or mixing events can deliver high levels of sulfide to surface waters and shoreline habitats, causing mass mortalities of organisms there, including the planktonic larvae of the pileworm as well as the benthic juveniles and adults that often abound in coarse barnacle shell substrates in protected, shallow water areas (Detwiler *et al.* 2002). The frequency, spatial extent, and seasonal timing of such mixing events will be determined by many factors (Fig. 5).

We now discuss how all these factors may have operated in the recent past. In some cases we can argue on principle the likelihood of a particular phenomenon having a role in this system. In other cases we show a close association between particular physical events and the behavior of pileworm, fish, or Eared Grebe populations.

Changes in the pileworm population

Information on pileworm abundance at the Salton Sea is sparse. Year-round samplings were carried out only in 1956 (Carpelan and Linsley 1961) and 1999 (Detwiler *et al.* 2002), and spatially extensive, one-time samplings were carried out in April 2004 and March 2005 (Dexter *et al.* 2007). Abundance in the fall (September-November) were possibly about two orders of magnitude lower in 1999 than in 1956 (Detweiler *et al.* 2002). In April 2004, densities at 2 m deep stations were similar to those in April 1999, but those at 6 m and 10 m were greatly reduced compared to 1999. In March 2005, the pileworm population was close to zero. A sampling of 74 stations at depths ranging from 1 m to 10 m turned up only a single worm. From the odor and appearance

of surface waters and bottom sediments on March 14, 2005, it was evident that sulfide-rich bottom waters had been mixed to the surface only a short time earlier (M.F. Moreau, pers. comm.). Not only had the pileworm population been killed off but so had essentially all other macroinvertebrates (barnacles, amphipods) normally present in shallow water areas.

As evidenced by these surveys, the historical seasonal pattern has been for the pileworm to disappear in the spring from deeper waters as they become anoxic under the influence of rising water temperatures and reduced mixing of the water column. There is some evidence that oxygen conditions in 1956 were better than in 1999 (Watts *et al.* 2001; Detwiler *et al.* 2002). It was also clear that anoxic conditions set in earlier in 2004 and 2005 than in 1999 (Dexter *et al.* 2007).

Stratification and mixing regimes

What secular or episodic changes in the lake's mixing regime might have occurred and to what extent to the detriment of the pileworms? Several simple and straightforward scenarios can be envisaged, even if tests of these hypotheses against hard data on pileworms or Eared Grebes are not possible.

Historic increase in salinity

When freshwater flows enter a salt lake they will tend to create strong salinity gradients in the water column. A layer of freshened lakewater will be created that overlies more saline lower strata. The resultant vertical density gradient will inhibit mixing and favor development of anoxia in bottom waters. The degree to which this occurs will be a function of the salinity differential between stream inflows and lakewater, of inflow volume relative to dimensions of the receiving portion of the lake, and of wind, currents and other factors. Evidence of freshened surface layers and a density-stabilized water column have been found at least occasionally in the southern portion of the Salton Sea, even tens of kilometers from the mouths of its main inflows, the New and Alamo rivers (Arnal 1961; Parsons 1986; Watts *et al.* 2001; Reifel *et al.* 2007).

While the salinity of the Salton Sea has increased in a somewhat irregular fashion over the last half century, from about 35 g l⁻¹ to 45 g l⁻¹, salinity of the main inflows, the New and Alamo rivers, has remained roughly constant at ~ 3 g l⁻¹ (Tostrud 1997; Cohen *et al.* 1999; Hurlbert *et al.* 2007). We can use these numbers to examine how this historic increase in the salinity differential between inflows and lakewater might have influenced mixing regimes by calculating the classical measure of water column stability (Idso 1973) for a hypothetical 8 m isothermal water column. Assume that inflows at 3 g l⁻¹ salinity mix with lakewater in the ratio 1:4 to reduce the salinity of the top meter to 28.6 g l⁻¹ (in the case of lakewater initially at 35 g l⁻¹) or 36.6 g l⁻¹ (in the case

of lakewater initially at 45 g l⁻¹). In the first case, stability of the 8 m water column would be 0.0364 g-cm cm⁻² and in the second it would be 0.0574 g-cm cm⁻². This 58 percent increase in resistance of the water column to vertical mixing suggests that under certain conditions some variable portion of the southern end of the lake should be experiencing more prolonged periods of water column stratification and anoxic bottom waters than was the case half a century ago. The magnitude of this change and its areal extent cannot be estimated easily, but this increased water column stability could have influenced many aspects of the hydrodynamics, biogeochemistry, and foodweb of the lake in addition to the pileworm population.

The increasing salinity could also have deleterious effects on the pileworm population in other ways. For instance, although laboratory experiments suggests that adult pileworms are capable of surviving extended periods in salinities up to 70 g l⁻¹, the upper limit for successful reproduction has been estimated to be 45-50 g l⁻¹ (Kuhl and Oglesby, 1979). As the current salinity flirts with this threshold, conditions are undoubtedly more stressful for this species which is marine in origin. Nevertheless, the pileworm was abundant in shallow (2 m) waters in April 2004 (Dexter *et al.* 2007), so the 1999-2002 crash in grebe numbers is not reasonably attributed to a *salinity*-induced crash in the pileworm population. The absence of pileworms in deeper (> 2 m) waters in April 2004 and at all depths in March 2005 thus must have been due to other factors.

Wind, rain and polymixis

The annual mixing regime of the Salton Sea is an uncommon type known as discontinuous warm polymictic (*sensu* Lewis, 1983). Mixing of the full water column in deep waters does occur during the warmer two-thirds of the year but only sporadically at intervals ranging from several days to several weeks (Watts *et al.* 2001). Were the lake several meters deeper, it would probably develop a persistent stratification lasting the duration of the warm season and be classified as a warm monomictic lake. Were it several meters shallower it would probably experience complete mixing of the water column at least every few days during the warm season and be classified as a continuous warm polymictic lake (Lewis 1983).

A distinctive feature of discontinuous warm polymictic lakes is that the warm season mixing regime for their bottom waters will vary greatly from year to year. It will be highly dependent on the frequency, strength and duration of wind events. To a lesser extent it will be influenced by unusual cold spells which cool surface waters and thereby induce convective circulation of the water column. If the lake has high salinity, the seasonal regime of rainfall events may influence the mix-

ing regime by producing salinity gradients in surface layers that temporarily inhibit mixing.

When bottom waters of such a lake become anoxic and accumulate high levels of sulfide, as happens at the Salton Sea, each major mixing event has the potential to kill off large numbers of organisms in the upper part of the water column and in shallow water areas. Large year to year variations in the health and abundance of the Salton Sea pileworm population are thus to be expected, quite independently of any long term trends in the nature of the system.

While only the limited data already cited exists on year to year changes in the pileworm population, we have for the period 1998-2006 excellent information on year to year variation in summer and fall mixing events that bring sulfide-rich bottom waters to the surface. These events lead to formation of tiny crystals in oxic surface waters, where sulfide first is oxidized to sulfate ion which then combines with calcium and precipitates out as gypsum (Watts *et al.* 2001; Tiffany *et al.* 2007c). These crystals reflect solar radiation giving a strong signal captured by satellite imaging systems. In true color imagery, these gypsum blooms show up as light yellow-green patches that sometimes occupy most of the lake's surface. Analyzing such imagery, Tiffany *et al.* (2007c: Fig. 7) found that, reflecting the irregularity of the polymictic mixing regime, the timing of gypsum blooms varied greatly from year to year. More importantly, their frequency and size both were much greater during 2003-2006 when grebe numbers were low, than during 1998-2001 when grebe numbers were high (Fig. 3). We infer that, consistent with our brief field observations in the springs of 2004 and 2005, pileworms were more thoroughly eliminated by sulfide events in this latter period than in the earlier one, and that Eared Grebe numbers responded accordingly.

When sulfide events occur repeatedly and extensively during the summer and early fall, these could so reduce the pileworm population that even if it were to increase a hundred-fold by the time the migrating grebes arrived, it would be too sparse a food supply for grebes to survive on. In the late fall and winter when vertical mixing is aided by cooling, convective circulation, and a generally isothermal water column, the water at all depths, and surface sediments, are well-oxygenated (Watts *et al.* 2001; Holdren and Montano 2002). These conditions are favorable to rapid development of pileworm populations that would then be available to Eared Grebes. However, the *absolute* increase in pileworm biomass would depend on the numbers of pileworms and larvae still alive in late fall.

Fish-plankton-sulfide feedback loop

We believe the set of mechanisms shown on the left side of Fig. 5 played a major role in causing the crashes in grebe

numbers at the Salton Sea in both the late 1980s and the early 2000s (Fig. 3), including the die-off of 150,000 grebes in 1992. It proposes that the population of the omnivorous tilapia (*Oreochromis mossambicus* Peters × *O. urolepis hornorum* (Trewavas)) is greatly reduced by unusually cold weather in winter, by periodic sulfide events, by increased salinity or by combinations of these. This results in reduced grazing by tilapia on phytoplankton, increased plankton densities, and increased precipitation of organic matter into bottom waters and onto lake sediments. That in turn favors more rapid deoxygenation and faster build up of sulfide in bottom waters, increasing the severity of sulfide poisoning of both fish and pileworms when future mixing events occur. There is considerable circumstantial evidence of the operation of these mechanisms.

Tilapia die-offs

Since the 1970s, tilapia usually has been the most abundant fish in the Salton Sea and hence often the most abundant component of fish kills when these have been observed (Riedel *et al.* 2002; Caskey *et al.* 2007; Hurlbert *et al.* 2007). Having evolved in freshwaters of southern Africa, it has also been more susceptible to the effects of low winter water temperatures (*e.g.*, 12-15 °C) than the other fish in the Salton Sea.

Two major die-offs of tilapia have been documented during the period (1983-2005) for which we present data on grebe abundance. Unusual periods of prolonged below-freezing air temperatures in the winters of 1986-1990 along with an increase in salinity from 40 g l⁻¹ to 43 g l⁻¹ during roughly the same period apparently brought the tilapia population down close to zero (Hurlbert *et al.* 2007). No information was gathered on pileworm or plankton populations at that time, but between 1988 and 1991 our annual estimates of peak Eared Grebe numbers declined by 89 percent (Fig. 3).

The second major die-off of tilapia began in 1996 and took place more gradually over the following five years. It was a consequence of poor tilapia reproduction or recruitment in combination with frequent, massive sulfide-caused kills of adult tilapia (Caskey *et al.* 2002; Hurlbert *et al.* 2007). Indeed, in 1999 the tilapia population was large and *seemed* healthy – until it was determined that it consisted solely of the 1995 year class. By 2003 all the other fish in the lake had also disappeared. There was some recruitment of tilapia during 2003-2006, enough to occasionally bring fishermen and pelicans back to the lake. But there have also been periodic massive fish kills, consisting solely of tilapia, and the population remains below its abundance in 1999 (J. Crayon, pers. comm.). Between 1996 and 2002, our data shows that peak Eared Grebe numbers observed at the Salton Sea declined by 96 percent and has remained low in subsequent years at least through 2005.

Increases in phytoplankton

Tilapia die-offs apparently created conditions conducive to even further tilapia die-offs as well as reductions in pileworm abundance. Production and accumulation of sulfide should be strongly dependent on the amount of organic detritus that sinks to the bottom waters and lake bed. That detritus is primarily planktonic in origin in this macrophyte-free lake.

Following the most recent tilapia die-off, there was a tremendous increase in mid-lake phytoplankton abundance and, we presume, rates of delivery of organic matter to the sediments (Table 2). In April-May 2005, chlorophyll *a* levels were 3.3 times and phytoplankton biovolume densities 6.8 times greater than they averaged in April-May 1998 and 1999. This tilapia is omnivorous, feeding on phytoplankton, zooplankton, benthos and detritus (Mironova 1969; Maitipe and DeSilva 1985), and its grazing greatly reduced both phytoplankton and zooplankton abundance in a 1990 Salton Sea microcosm experiment (Hart *et al.* 1998; M. González, unpubl. data).

The difference between those two estimates of change probably reflects the selective grazing by tilapia on larger phytoplankters and, hence, their greater response following decline of the tilapia population. Phytoplankton biovolume density values do not include the contribution of cells < 5 μm in diameter or length (see *Phytoplankton sampling*), while chl-*a* values do. The abundance of large ciliates (*Condylostoma* spp., *Favella* sp.), but not small ones, also increased over the 1997-1999 period as the adult tilapia population was declining (Tiffany *et al.* 2007b).

Changes in species composition of the phytoplankton between 1998-99 and 2005 were dramatic, and some may have further reflected the advantage to large forms occasioned by the tilapia crash (Table 2). Dinoflagellates became strongly dominant, largely as a result of a large dinoflagellate (*Gonyaulax grindleyi*) that was not even detected in the springs of 1998 and 1999. Three genera of filamentous cyanobacteria (*Arthrospira*, *Oscillatoria*, *Geitlerinema*) not detected at all in the mid-lake plankton in 1997-1999 had also become very abundant by 2005. If it was a crash of the tilapia population that caused these shifts in composition, the changes likely occurred prior to 2005. There is some evidence for that. Carmichael and Li (2006) recorded cyanobacterial genera *Geitlerinema*, *Lyngbya*, *Merismopedia*, *Oscillatoria*, and *Synechococcus* as being “dominant” phytoplankters in the Salton Sea during the period November 1999 to April 2001. They provided no information on actual densities, however, and all their samples were collected nearshore and almost all in the vicinity of the freshwater inflows to the Sea. Earlier, Wood *et al.* (2002) had found, in samples of nearshore waters, and epilithic and epipelagic assemblages, all these cyanobacterial genera (except *Merismopedia*) plus an additional five genera.

Among the diatoms, *Thalassionema* sp. was the most abundant species in 1998-99 but had disappeared by 2005 (Table 2). The abundance of two smaller species – *Nitzschia frustulum* and *Ceratoneis closterium* – greatly increased over this time period to dominate that group. A benthic diatom, *Pleurosigma ambrosianum*, which would have been especially vulnerable to increased sulfide concentrations and was often found in the plankton during windy periods in 1998-99 (Tiffany *et al.* 2007a), was not found at all in 2005.

The planktonic larvae of the pileworm were effectively absent in April-May 2005, *i.e.*, at least >99.9 percent less abundant than in 1998-99 (Table 2). That is consistent with our observation that the benthic juvenile and adult portions of that population had been wiped out prior to mid-March 2005 by sulfide events.

We have surmised that reduced grazing by tilapia caused the large post-1999 increase in phytoplankton and, hence, increased severity of sulfide events and pileworm mortality. If correct, then similar sequelae may have followed the tilapia crash of the late 1980s.

Role of algal toxins

While we believe that elimination of its main prey, the pileworm, has been the major cause of the Eared Grebe's difficulties, there is the possibility that toxic algae have played a subsidiary role. They may have increased following tilapia declines. Though many toxic or potentially toxic algae and cyanobacteria have been found in the Salton Sea, no firm evidence of their role in any mortality event exists.

In 1992 following the largest die-off of Eared Grebes, we suggested that algal toxins may have been the responsible agent (S. Hurlbert, as cited by Reifel *et al.* 2002). In the 1990 Salton Sea microcosm experiment, we had observed that the toxic prymnesiophyte *Prymnesium* sp. developed much higher densities in tanks at 48 g l⁻¹ salinity than those at 39 g l⁻¹ (Gonzalez *et al.* 2007). *Prymnesium parvum* produces hemolytic toxins and is known world-wide for causing fish kills in aquaculture facilities and reservoirs (Shilo 1981; Moestrup 1994; Kullman 2005). This species was never recorded from the Salton Sea until February 2006, when we found it at densities up to 82,000 ml⁻¹ (Tiffany *et al.* 2007d). It probably had become abundant earlier but no plankton monitoring was conducted between 1999 and 2005.

In 1994, extracts of a Salton Sea water sample dominated by *Gonyaulax grindleyi* showed high toxicity to mice (K. Steidinger, D.J. Faulkner, R. Dickey, unpublished data, as cited by Reifel *et al.* 2002). This species is known to produce yessotoxins in marine environments (Reifel *et al.* 2002). It was not observed during our 1998-99 springtime monitoring of the plankton but was present during 2005. If vulnerable to tilapia grazing, it may have been abundant in 1994 and

Table 2.—Comparison of springtime plankton abundance and composition at mid-lake Salton Sea stations, 1998-1999 versus 2005. Values given are geometric means. Numbers in parentheses represent the bounds for the geometric means \times/\div standard deviation factors. Descriptor names are given in a companion paper (Tiffany *et al.* 2007a).

Sampling Date →	1998		1999		2005	
	24-Apr	22-May	25-Apr	10-May	27-Apr	4-May
Number of stations sampled	1	3	3	3	1	3
<i>Total phytoplankton abundance (geometric means)</i>						
Chlorophyll <i>a</i> ($\mu\text{g l}^{-1}$)	40.2	27.5 (25.1-30.1)	32.6 (29.8-35.5)	26.0 (23.8-28.3)	118	92.5 (71.2-120)
Biovolume density ($\text{mm}^3 \text{l}^{-1}$)	16.4	2.8 (2.3-3.4)	2.7 (2.0-3.7)	3.0 (2.3-3.9)	48.9	35.5 (25.8-48.8)
<i>Numerical densities of individual taxa^a (no. ml⁻¹) -and- Biovolume densities of major taxa ($\text{mm}^3 \text{l}^{-1}$, in bold)</i>						
Cyanobacteria (blue-green 'algae')	0.00	0.00	0.00	0.00	2.46	2.32
<i>Arthrospira</i> sp. (260 μm)	0	0	0	0	143	76.3
<i>Oscillatoria</i> sp. (72 μm)	0	0	0	0	899	1,540
<i>Geitlerinema</i> sp. (54 μm)	0	0	0	0	17,600	30,200
Dinophyceae (dinoflagellates)	11.50	1.60	0.28	0.19	42.9	29.0
<i>Gyrodinium uncatenum</i> (39 μm)	594	50	7	13	0	0.1
<i>Gymnodinium</i> sp. 1 (27 μm)	80	21.7	5	0	4	0.3
<i>Heterocapsa niei</i> (21 μm)	345	290	0	5	396	199
<i>Prorocentrum minimum</i> (18 μm)	10	12.3	7	3.3	0	0
<i>Oxyrrhis marina</i> (22 μm)	0	2.5	11	2.2	0.7	10.1
<i>Gonyaulax grindleyi</i> (48 μm)	0	0	0	0	956	656
<i>Scrippsiella</i> sp. (30 μm)	0.5	42	0	0	0	2.9
<i>Oblea</i> sp. (25 μm)	6	0.5	0	0	3.6	80.3
small dinoflagellates (14 μm)	112	9.9	5	5	5.3	10
Bacillariophyceae (diatoms)	0.23	0.85	1.34	2.11	3.3	3.8
<i>Thalassionema</i> sp. (54 μm)	234	1,950	1,630	4,890	0	0
<i>Chaetoceros muelleri</i> (7 μm)	0	0	0	16	0.7	0
<i>Cyclotella</i> spp. (9 μm)	88	354	34	1,571	415	511
<i>Pleurosigma ambrosianum</i> (73 μm)	55	3.9	340	15	0	0
<i>Nitzschia frustulum</i> (9 μm)	1,060	540	0	3.3	3,300	3,840
<i>Ceratoneis closterium</i> (17 μm)	56	57	112	794	27,900	34,300
Chlorophyceae (green algae)	0.01	0.01	0.53	0.24	0.00	0.00
<i>Oocystis</i> sp. (17 μm)	1.0	4	33	12	1.0	0.4
<i>Crucigenia rectangularis</i> (14 μm)	19.7	4	1,300	1,060	0	0.3
Other algal classes	4.65	0.38	0.55	0.52	0.23	0.44
<i>Pleurochrysis pseudoroscoffensis</i> (10 μm)	101	0	5	690	7.6	22.1
Cryptomonads (10 μm)	18,500	1,570	1,630	1,060	900	1,750
All other algal taxa	13.9	10.9	0.6	3	1.3	8.6
Metazooplankton						
<i>Neanthes succinea</i> larvae (no. l ⁻¹)	15.4	7.2 (6.0-8.5)	6.2 (4.2-9.1)	3.7 (3.5-3.9)	0.005	0.000

^a Values in parentheses following species and genera are greatest linear axial dimensions of the phytoplankter.

2005 because the tilapia populations were small, still unrecovered from the crashes of the late 1980s and early 2000s, respectively (Hurlbert *et al.* 2007).

In 1997, the large raphidophyte *Chattonella marina* (Subrahmanyam) Y. Hara et Chihara, known to be responsible for large fish kills in marine environments, was first detected at the Salton Sea, achieving peak densities on the order of 500 cells ml⁻¹ (Tiffany *et al.* 2001, 2007a). Tilapia collected from the Sea at the height of the bloom of this species showed evidence of damage to gill lamellae.

Toxic cyanobacteria have not been given much consideration until the recent studies by Carmichael and Li (2006). Epipelagic and epilithic mats of cyanobacteria are sometimes conspicuous in shallow waters at the Sea (Carpelan 1961; Wood *et al.* 2002). Wave action and light reduction by dense phytoplankton greatly restrict the distribution, abundance, and contribution to lake primary production of these mats, however. Also, until our 2005 monitoring (Table 2), representation of cyanobacteria in the midlake phytoplankton seemed restricted to coccoid unicells such as *Synechococcus* (Carpelan 1961; Wood *et al.* 2002; Tiffany *et al.* 2007a).

Increases in post-1999 phytoplankton densities likely have further reduced, by increased shading, the extent and importance of benthic cyanobacterial mats. But with cyanobacteria now abundant in the phytoplankton, the potential role of cyanobacterial toxins is increased.

Carmichael and Li (2006) reported that some tissues collected from Eared Grebes found dead at the Salton Sea in 1992-1994 and 1999-2001 had concentrations of the cyanotoxin microcystin high enough to cause acute toxicity. Low levels of microcystin were found to be produced by lab cultures of *Synechococcus*, *Oscillatoria*, *Gloecapsa*, *Phormidium*, *Aphanothece*, and *Lyngbya*, but raw water samples contained microcystin concentrations that were “generally less than those needed to cause acute lethal toxicity from ingestion of bloom samples by mammals” (Carmichael and Li 2006). Sick grebes were observed drinking copious amounts of water near freshwater inflows during past die-offs which might explain the high microcystin levels in tissue samples, but the cause of this excessive drinking behavior remains a question. Furthermore, if algal toxins are directly affecting Eared Grebe survival, uptake may also occur via its diet. Testing of pileworms for presence of microcystin is to be desired. Testing of grebe feathers, which could vector toxins to grebes during preening (Reifel *et al.* 2002), is desirable also.

Carmichael and Li (2006) cautioned that lowering of the salinity of the Salton Sea might favor cyanobacteria genera, such as *Microcystis* or *Anabaena*, that produce higher levels of microcystins. More likely, however, is that by improving conditions for tilapia, a lowered salinity would favor its

increase and reduce phytoplankton densities and those of filamentous cyanobacteria in particular.

Role of dissolved organic matter

Phytoplankton abundance may favor not only high levels of sulfide and toxic algae but also high levels of dissolved organic matter (DOM). Reifel *et al.* (2002) summarized much circumstantial evidence suggesting that by lowering surface tension, high DOM levels could allow penetration of water through the natural spacing of barbs on feathers, resulting in loss of insulation and death by hypothermia. Diving birds, such as grebes, would be particularly affected. While this may explain the wet, disheveled appearance of sick grebes, death by hypothermia would be too rapid to account for the low body weights discussed earlier. Further studies of effects of DOM on waterproofing are desirable. Water-logged Ruddy Ducks (*Oxyura jamaicensis* Wilson), the only other abundant diving bird at the Salton Sea, have not been observed, but these doubtless differ from Eared Grebes in feather structure and behavior in numerous ways.

A prerequisite to starvation at the Salton Sea

For Eared Grebes the absence of pileworms at the Salton Sea diminishes the utility of this lake from an important “refueling” site to simply a migration stopover point, a place to rest between long overnight flights. Without this food resource there is no reason to stay for any extended period. There are simply no other abundant macroinvertebrates in the lake, at least when fish are present in any numbers (Detwiler *et al.* 2002).

It is important to recognize that pileworm availability and the grebes’ need for this resource are not always coinciding. The post-1998 decrease in grebe use of the Salton Sea included only two winters (1999-2000 and 2002-03) in which large numbers of grebes died (Table 1). Insufficient forage at the Sea may decrease the number of grebes making a prolonged stop at the lake but will not always result in starvation events. During some years, absence of the pileworm may not be detrimental to migrating grebes. Provided they are in excellent condition, grebes departing the Gulf of California should be able to not only reach the Salton Sea but, if necessary, continue much further northward without depleting their energy stores. It is when there is reduced prey availability in the Gulf of California that a stop at the Sea may be essential to fuel the remaining migration. During the two years in which severe grebe mortality was recognized at the Gulf of California, the region was considered to be experiencing strong El Niño Southern Oscillation (ENSO) cycles, and mortality was attributed to starvation (Jehl *et al.* 2002). Changes in primary productivity and the uncoupling

of predator-prey relationships in the Gulf of California have been well documented during ENSO years (e.g., Valdez-Holguin and Lara-Lara 1987; Sanchez-Velasco *et al.* 2002). In the most severe years, those with sea surface temperature anomalies at or exceeding 2 °C, Eared Grebes may find prey so sparse that they are unable to fly in search of better resources, eventually perishing from starvation (see Jehl *et al.* 2002). If the birds are able to get airborne, the closest and historically most bountiful cache of food is the Salton Sea. Being geographically close yet disconnected to oceanic cycles, the Sea can serve as a reliable emergency food source for wintering grebes. However, in the absence of pileworms there is little food for grebes and the lake becomes a place to go and die. There is insufficient information to investigate the potential of Salton Sea mortality events corresponding to years with large sea surface temperature anomalies in the Gulf (Table 1), but in theory they should be highly linked.

An unusual case and an earlier prediction

If our interpretation of these foodweb dynamics is correct, it is a situation that departs from our usual expectations about certain fish-bird interactions. In the introduction we pointed out the importance of fish-free waterbodies as Eared Grebe feeding and breeding areas. Fish and invertebrate-eating waterbirds are often in competition with each other, and removal of fish from ponds and lakes by natural factors, such as high salinity or periodic desiccation, or by human intervention, almost always results in increased abundance of both large zooplankters, macroinvertebrates, and birds that feed on them (e.g., Swanson and Nelson 1970; Hurlbert *et al.* 1972; G. Andersson *et al.* 1978; Eriksson 1979, 1983; G. Andersson 1981; Hurlbert and Mulla 1981; A. Andersson 1982; Hurlbert *et al.* 1986; Winfield and Winfield 1994; Hart *et al.* 1998).

A different scenario seems to have happened at least twice at the Salton Sea: the tilapia and other fish populations crashed, the pileworm population then crashed, and the number of Eared Grebes using the Sea declined. In a microcosm experiment, this tilapia species was observed to greatly reduce both *Trichocorixa* and *Gammarus* populations (Hart *et al.* 1998). Pileworms were not present in that experiment, but their population probably would have been similarly affected, by tilapia feeding on both the planktonic larvae and benthic adults. Thus it has been predicted that by the time Salton Sea salinity gets up to 60 g l⁻¹ the fish populations will have crashed and “[r]elease from fish predation will result in large increases in invertebrate biomass...[and] the consequences for invertebrate-eating waterbirds would be positive” (Hart *et al.* 1998). That may yet happen, as 60 g l⁻¹ is still many years away, and when invertebrate predators in the Salton Sea such as *Apocyclops dimorphus* Kiefer and *Trichocorixa*

reticulata disappear, brine shrimp (*Artemia franciscana* Kellogg) may become abundant, as brineflies (Ephydriidae) also might (Hammer 1986; Herbst 1999, 2006; Hammer and Hurlbert 1992). What was not considered, however, is the importance of sulfide events or the role of the omnivorous tilapia in keeping phytoplankton populations low. Thus, it was not anticipated that the ecosystem might pass through an intermediate state where the most abundant macroinvertebrate might decrease in abundance concurrently with tilapia.

Conclusion

For Eared Grebes, the value of the Salton Sea is contingent on food availability. During most years they can bypass the lake en route to their breeding grounds, but in other years it may be an indispensable food source for overwintering grebes and spring migrants. As the lake continues to evolve, becoming a waterbody less suitable for tilapia and pileworms, we should also expect further diminishing use of this lake by Eared Grebes. It would benefit the continental Eared Grebe population if the Salton Sea were less prone to stratification, had less input of nutrients, and remained capable of supporting tilapia and pileworm populations. These considerations should continue to be addressed as the State and Federal governments develop ecosystem restoration plans for the Salton Sea.

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