A synthesis of our knowledge of the biological limnology of the Salton Sea

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Benthos

Our understanding of the Salton Sea benthic ecosystem in its present condition is limited. The only quantitative sampling of the Salton Sea benthos was done during the 1950s (Walker, 1961) which sampled invertebrate species found in lake sediments over a 28 month period and included studies on the marine polychaete worm *Neanthes succinea* and the barnacle *Balanus amphitrite*. The report also includes comments on some of the meiobenthos. With the exception of recent mostly unpublished studies by SDSU students and faculty, the Walker report remains the only substantive database on sediment-dwelling invertebrates at the Sea.

There are no studies in the scientific or gray literature of the benthic communities associated with the rocky substrates, barnacle shell sand, or connected lagoons within the Salton Sea.

Neanthes succinea was identified as the most important benthic organism in the Salton Sea food chain (Walker 1961). *N. succinea* was most abundant on mud at a depth of 15-25 feet, had intermediate densities in shallow water, and was least abundant in deeper water. Adults were not present in sediments deeper than 9 m (56% of total bottom area) during the summer months, a loss attributed to anoxia. Polychaete biomass ranged from 8 to 40 grams/m^2 with an estimated biomass of 13.2 million kg for the entire sea. *Neanthes succinea* was the key species linking detrital food chains to fish and birds. Benthic feeders forage on *N. succinea* living in mud, but the polychaete's cryptic benthic habitat is not easily exploited by fish predators. However, the reproductive stages of the worm, called heteronereids, swarm all year round providing easy access for fish and birds that feed in the water column. Some predation on *Neanthes* occurs between dusk and dawn when heteronereids are present in the plankton. Stomach content analysis of Salton Sea eared grebes shows *Neanthes* to be a major food item (D. Dexter, personal observations).

Spawning occurred every month with peaks in spring and fall, and heteronereids declined to low numbers during winter (effect of cold temperature) and summer (reduced oxygen availability). More recent studies on salinity tolerance suggest that *N. succinea* will not be able to reproduce at salinities exceeding 50‰ (Hanson 1972, Kuhl and Olgesby 1979), a level which is rapidly approaching in the Salton Sea. If this conclusion is correct, and *Neanthes succinea* is lost from the sea, an immediate and major decline of most fish species will follow.

Most of the abundant benthic invertebrate species known to be present in the Salton Sea have a wide geographic distribution, and have been studied at other locations. *Neanthes succinea* has an extensive geographical distribution occurring in temperate estuarine habitats of both the eastern Pacific Ocean and eastern Atlantic (Hartman 1968). It is a non-selective substrate feeder (Fong 1987). An analysis of its carbon budget indicated that it can take up substantial amounts of dissolved amino acids and assimilate carbon from plant detritus, as well as consume bacteria and microorganisms associated with sediments thereby utilizing all the components of the detrital system (Cammen 1980). Tenore (1982) found no significant difference in specific growth rates at several densities but noted that food transfer rates varied with salinity. Important differences in various organic components (glycogen, lipid and proteins) occurred before and after spawning, with highest food value just prior to spawning (Neuhoff 1979 a, b). Reish (1954) suggested that predation is higher on female heteronereids which are much slower swimmers than spawning males.

Another benthic species of marine origin is *Balanus* which has a worldwide distribution in warm temperate and tropical waters (Flowerdew 1985). Simmons (1957) found this species living in field salinities of 78‰. The Salton Sea population is considered by many as the subspecies *saltonensis* , however, Flowerdew (1985) and Raimondi (1992) concluded that there was no significant genetic difference between this subspecies and the subspecies *amphitrite*, in contrast to the findings of Sixtus (1978) who observed that the Salton Sea population had decreased heterogeneity and reduced polymorphism compared to the population in San Diego Bay.

The Walker report (1961) indicated that the growth rate of the Salton Sea *Balanus* population during the coldest months was less than 10% of the summer growth rate, during which time sexual maturity was achieved within 30 days from time of settlement. Reproduction occurred year round, although it was very limited during colder temperatures. Therefore, several generations are produced each year, and the availability of hard substrates limits the adult population. Adult barnacles were seldom consumed by fish, but naupliar larvae were a food source for the croaker *Bairdiella icistius*. The report suggested that uptake of detritus by *Balanaus* reduces the food availability to *Neanthes* and thus reduces food transfer from the benthos to the corvina *Cynoscion xanthus*.

There are 3 more recent studies on the Salton Sea barnacle population. Vittor (1968) noted that declines in adult seasonal abundance are due to increased temperature and reduced oxygen levels. Survival rates are higher, and life expectancy longer, for juveniles recruiting during the winter versus those recruitment in the spring. Survival rate was very low for barnacles recruiting during conditions of low salinity (19‰). He concluded that crowding and competition for space were the most important factors controlling population abundance.

The effects of abiotic factors on the physiology of *B. amphitrite* have been investigated. Sixtus (1978) studied the thermal tolerance of *B. amphitrite* and concluded that the Salton Sea population was more tolerant of short-term temperature changes than the San Diego Bay population. In microcosm experiments using Salton Sea water adjusted to different salinities, Simpson and Hurlbert (1998) found a negative correlation between shell growth and salinity. Shell growth was slowest at 63 g/L and barnacles reached their largest size at 48 g/L. He also investigated the force needed to break barnacle shells and concluded that shell strength declined steadily as salinity increased from 39g/L.

Another organism, the corixid insect *Trichocorixa reticulata*, is common found swimming at the surface of the water in protected embayments and isolated pools at the fringe of the lake, where salinity is usually higher than the main body of the lake. Its distribution, prevents its categorization as either a planktonic or benthic organism. *T. reticulata* has been found in salinities ranging from 0 to 190‰ (Balling and Resh 1984). It is distributed in the Caribbean Islands, the southern U.S., and from Peru north along the west coast of Americas to Arcata, California (Balling and Resh 1984). In tropical regions this species reproduces continuously, and in colder regions 2-3 generations are produced yearly (Balling and Resh 1984).

Since the Walker (1961) study, at least 6 species of organisms have been found to be abundant in the Salton Sea benthos (D. Dexter, personal observations). The most abundant is an amphipod, *Gammarus mucronatus*. This species lives in algal mats, and is also found among living barnacles, in the barnacle sand along the shoreline, and within the soft sediments of the lake. *G. mucronatus* has been shown to be a food item of eared grebes and is presumably available to other bird species that feed in shallow water. At night, the amphipod is free swimming in the water column at night during mating and so becomes available to fish. It was probably introduced into the Salton Sea in 1957 (Barnard and Gray 1968).

The amphipod *Gammarus mucronatus* occurs from the Gulf of St Lawrence south to Florida and along the Gulf to Texas inhabiting intertidal brackish, estuarine, coastal areas, and hypersaline lagoons, mostly within muddy areas, and is often associated with seagrasses or green algae (Barnard and Gray 1968; Hedgpeth 1967). Its life history has been studied in warm temperate estuarine habitats (Fredette and Diaz 1986a, b) and in cold temperate salt marshes (Borowsky 1980, LaFrance and Ruber 1985). Developmental time is faster during periods of warm temperature when sexual maturity can be attained in 2 weeks, and several cohorts are produced yearly (Fredette and Diaz 1986b). It is not very specialized in its food habits, feeding on bacteria, a variety of microeukaryotes, macroalgae, invertebrates, and detritus (Smith et al. 1982, Zimmerman et al. 1979, Hart et al. 1998, Simpson et al. 1998). If this species is abundant in the soft sediment, it would also be a major food chain link between the detritus and fish, as well as resident and migratory bird species which feed in shallow water at the sea.

There also is an unidentified corophiid amphipod that lives in muddy tubes on submerged rocks. This species has a patchy distribution, and we only have a few preserved specimens. We have no knowledge on the biology of this species, and until sufficient specimens are available for taxonomic identification by a specialist, its status will remain unknown. However, it is likely to be a known species of marine amphipod rather than a new species.

The densities of two species of macroscopic green alga alternate seasonally on shoreline rocks at the south end (Red Hill Marina, Obsidian Butte) of the Salton Sea. In 1990 *Chaetomorpha* sp. was abundant from May to November, while *Enteromorpha* sp. was abundant from December through April (D. Dexter, personal observations). They provide important habitat for invertebrates, and, in addition to detritus, are major food sources for *Gammarus* and *Neanthes*. These macroscopic algae presumably are fed upon by some birds. Predaceous fish feed on corixids, amphipods and polychaetes.

A small harpacticoid copepod *Cletocamptus deitersi* (Dexter 1995) is very abundant among algae and detrital debris on rocks and is also present in the mud. *C. deitersi* is a cosmopolitan species, present on 4 continents, and was maintained in culture in Salton Sea water adjusted to various salinities for 120 days. Successful reproduction occurred in cultures from 0.5 to 80 g/L, but few individuals survived at higher salinities (Dexter 1995). Harpacticoid copepods are used as food for fish larvae in aquaculture and so are of potential importance for juvenile fish (Hicks and Coull 1983).

The adult forms of amphipods, polychaetes, corixids, and possibly algae and barnacles provide food for fish and birds that forage on the bottom; their reproductive stages provide food for fish that feed in the water column and at the surface. Because there are such a small number of species in the food chain, physical and chemical changes have the potential for destabilizing the food base and, as a consequence, posing problems for reproduction and survival of fish and wildlife.

Collections of benthic sediments during the Walker (1961) study were analyzed by various scientists for meiofauna. The most detailed study was that of Arnal (1958) who examined the foraminifera. He found 20 species, including 3 species of *Thecamoebina,* and 4 new species, all of which he illustrated. Soule (1957) verified the presence of two bryozoan species *Nolella blakei* and*Victorella pavida* in the Salton Sea. The Walker report also notes the presence of unidentified amoeba, radiolarians, ciliates, ostracods, and the nematode *Spilophorella* in the blue green algal mats.

More recently, microcosm experiments conducted at SDSU. have revealed the presence of other meiofaunal organisms in the sediments collected from the Salton Sea. Species found included the ciliates *Condylostoma* sp. and *Fabrea salina*, the foraminiferan *Quinqueloculina* sp., a textularin foraminifer, two species of nematodes belonging to the Family Monhysteridae, and one nematode species belonging to the Family Plectidae (Simpson et al. 1998). The harpacticoid *Nitocra dubia* has also been observed in mud, although it has not been collected since 1983 (S. Hurlbert, personal communication).

Phytoplankton

The photosynthetic algae of any water body form the base of the food chain. In the Salton Sea the abundance of algae is very high due to nutrient inputs from agricultural and municipal wastewaters. At times the Secchi disc reading, which gives an indication of the amount of algae in the water, is as little as about a half a meter. The quantity of algae is not the only important feature of the phytoplankton of this lake. The species present are also significant as some algal species can produce toxins (Tables 1, 2).

Two surveys of the algae in the Salton Sea were completed decades ago when the salinity of the lake was near to that of sea water. There are no phycological reports in the scientific or gray literature for the Sea at its present salinity, which is 25% higher than that of sea water. Carpelan (1961) reported on the density of algae in surface samples at a shore station and a station three miles offshore over a period of 18 months in 1955-1956. He found that the dominant algal species at that time were diatoms, dinoflagellates and a non-motile green algal species which he thought might be *Westella botryoides*. There was no mention of any taxon which might be a raphidophyte at that time. The diatom species he found to be most abundant were *Cyclotella* (he thought close to *C. caspia*), *Nitzschia longissima* (which we now know to be *Cylindrotheca closterium*), and *Thalassionema nitzschioides*. The dinoflagellates he encountered most frequently were a *Prorocentrum* species (which he identified as *Exuviella compressa*) and *Glenodinium* sp. (which we now are calling *Heterocapsa niei).*

The USDI (1970) studied the lake in 1968-1969 and again found that dinoflagellates and diatoms predominated, but in addition two "motile green algae" had become extremely important. No description of these taxa was given, but it is possible that one or both may have been *Chattonella* cf. *marina*, a raphidophyte. This taxon appears green in color and has two flagella and has been found in high abundance in the 1997-1998 sampling effort by San Diego

State University researchers. The dinoflagellates they recorded by USDI (1970) were *Cachonina niei* (now *Heterocapsa niei*), *Exuviella* sp.(*Prorocentrum*) and a dinoflagellate which they identified as *Gyrodinium resplendens*, now found to be a prominent member of the plankton. This latter species could be the same *Gyrodinium* presently found in the lake and identified by Karen Steidinger of the Florida Marine Research Institute as *Gyrodinium uncatenum*. A *Peridinium* sp. was fairly common and is likely to be *Scrippsiella trochoidea*, now also relatively abundant in the lake. They also found the diatoms to be abundant at times and to be composed of the same species that were found in the earlier study with the addition of a *Nitzschia* sp. that could have been *Tryblionella punctata*, unfortunately again no description was given of this species.

A sampling effort was begun in January 1997 to determine the species composition and abundances of the phytoplankton now present in the Sea. This effort continues to the present day. Some of the same species found in the previous studies were found to be still present in the plankton. New taxa have been found in the lake, some of which may be critically affecting the ecosystem.

The diatoms have barely changed since the salinity was near that of sea water. The prominent diatom species are *Thalassionema nitzschioides*, *Cyclotella* sp., *Pleurosigma salinarum*, and two newly reported species *Chaetoceros muelleri*. and a nitzschioid species which we think may be *Tryblionella punctata* .

The dinoflagellates are *Gyrodinium uncatenum*, *Heterocapsa niei*, *Scrippsiella trochoidea*, *Prorocentrum minimum*, *Gonyaulax grindleyi* and a *Gonyaulax* which is probably *G. spinifera*. Several heterotrophic (nonphotosynthetic) dinoflagellates have been found, *Oblea* sp. and a small dinoflagellate yet to be identified. At times the dinoflagellates became so abundant as to color the water a "coffee" brown.

In addition to these groups a raphidophyte, *Chattonella* cf. *marina*, became very abundant in the plankton in the summer of both 1997 and 1998. This species may prove to be extremely toxic to fish in the lake and may be the cause of the "green tides" frequently observed in the summer months. Flagellates such as *Cryptomonas* sp. and *Chroomonas* sp. were nearly always abundant, although of small size and relative biovolume. An unidentified coccolithophore has been detected in the plankton in small numbers as well as other haptophytes, *Prymnesium* sp. and *Chrysochromulina* sp. A euglenoid, *Eutreptia lanowii*, has been found in fairly large numbers at times. On one sampling date in 1998 a green algal species, *Crucigenia rectangularis*, became very abundant.

In general the diatoms and dinoflagellates co-dominated in the plankton with the superimposition of an abundance of the raphidophyte *Chattonella* in the warm months. Cryptomonads, although plentiful are small and contributed little to the biovolume. In the winter a large diatom, *Pleurosigma salinarum*, was the most important diatom both in number and in biovolume and may have been able to remain in the water column due to the mixing that occurred at that time. In the summer the marine planktonic diatom, *Thalassionema nitzschioides* was by far the dominant diatom. The most numerous dinoflagellate in the winter was *Heterocapsa niei*. *Gyrodinium uncatenum* was present in fairly high density all year especially in the spring, and in the summer *Gonyaulax grindleyi* became an important member of the phytoplankton.

Toxic Algae

Not much is known about the toxicity of the algal species found in the Salton Sea. Only three reports (Carpelan 1961, USDI 1970, Gonzalez et. al. , in preparation) have provided substantive information on the algae of the Salton Sea. Various dinoflagellate species are likely to be toxic (see Table 2). Recurring major mortality events in the eared grebe occur during the winter and early spring at the Salton Sea (Table 3), and major fish kills are common. A highly toxic extract was obtained from a May 1994 phytoplankton sample dominated by an unarmored gymnodinoid dinoflagellate (see below). Also, a "*Pfiesteria*-like" organism was reported from 1997 samples.

During the 1992 eared grebe mortality event, where 150,000 birds were found dead over a several month period, extensive studies were done by the National Wildlife Health Center to determine the cause of death (NWHC, 1992). Forty-six eared grebes from the Salton Sea and, as a control group, six grebes from Camp Pendelton, California were examined. Avian cholera and avian botulism were found in a small number of individuals, but this finding was not considered to be significant. Of the individuals who died of undetermined causes, brain sodium and cholinesterase levels were within normal range, and no significant viruses or bacteria were isolated. The most common findings in these birds were pulmonary edema and erythrophagocytosis of the liver and spleen. Many were emaciated. A conference sponsored by the Fish and Wildlife Service pertaining to the 1992 mortality event was held in San Diego, California in July 1992 (Audet 1992). At the conference, it was reported that endrin, organophosphate pesticides, and salt toxicosis had been ruled out as causes of the dieoff. The Fish and Wildlife Service also held a conference in response to the 1994 mortality event (USFWS, 1994, Steffeck, 1994). Organochlorine, organophosphorus and carbamate insecticides, botulism, and salt toxicosis were all ruled out as causes of the dieoff. Some contaminants (e.g. selenium, mercury, chromium) were found in individuals from both the 1992 and 1994 events, but all were below lethal levels.

Several algal species are especially abundant during the winter when the grebe mortality events take place. An armored dinoflagellate, *Heterocapsa niei*, is often the dominant algal species. At least one species of *Heterocapsa* is known to be toxic to other microorganisms (Uchida et. al. 1995, Kamiyama et. al. 1997), and to bivalves (Matsuyama et. al. 1995, Matsuyama et. al. 1997)(Table2). *Gyrodinium uncatenum* and several species of *Gymnodinium* have also been observed at these times. Some species of both *Gymnodinium* and *Gyrodinium* are known to produce toxins (Jones et. al. 1982, Seki et. al. 1995, Oshima et. al. 1987). Algal toxins have been responsible for mortality events involving birds (Fritz et. al. 1992, Beltran et. al. 1997, Henriksen et. al. 1997), fish (Burkholder et. al. 1995, Burkholder et. al. 1992) and marine mammals (Geraci et. al. 1989) in marine systems and are a likely culprit in the grebe mortality events.

In May and June of 1997, a raphidophyte determined to be *Chattonella* cf. *marina* was confirmed in the Salton Sea and formed a conspicuous 'green tide'. State Park personnel at the Sea have observed such periodic green tides for years, and it is possible that the abundant but unidentified "motile green flagellates" reported in 1968-1969 (USDI, 1970) were also *Chattonella*. This species is known to cause major fish kills in Japan (Endo et al. 1992) and Tasmania (Hallegraeff et al. 1997). Studies of *C. marina* shows that it produces neurotoxins such as breve toxins (Onoue et al. 1990; Ahmed, M. et al. 1995) as well as superoxide radicals which are injurious to fish gills (Tanaka et al. 1994). Scanning electron microscopy of gills of tilapia collected in Salton Sea 'green tide' areas showed swollen gill filaments of the same sort seen in fish from *C. marina* blooms off Japan (Endo et al., 1992); secondary lamellae were locally fused and filament tips were extremely swollen and club-shaped (Boris Kuperman and Victoria Matey, pers. comm.).

Certain cyanobacteria are well-known as producers of toxic blooms, especially in fresh-water systems. It is unlikely they cause problems at the Salton Sea, however. There have never been reports of planktonic cyanobacterial blooms at the lake. Earlier studies (Carpelan 1961, USDI 1970) found planktonic cyanobacteria to be so scarce that they did not bother to give estimates of their abundance. Over many years of qualitative examination of Salton Sea samples, we have never observed a sample where cyanobacteria were dominant in terms of biomass, though small coccoid forms sometimes have moderate densities.

In May of 1994, a huge plankton bloom was observed in progress, and samples were taken at the southern end of the lake for analysis. Dr. Karen Steidinger (Florida Marine Research Institute) determined these samples to be dominated by an unarmoured gymnodinioid dinoflagellate, possibly a *Gyrodinium* or *Gymnodinium*, with some *Gonyaulax grindleyi* also present. Extracts of the mixture were tested for toxicity using mouse bioassay. The extracts tested positive, and from the results, we concluded that we were probably dealing with an organic water-soluble toxin that had been produced by one of the dinoflagellates.

Zooplankton

The sole quantitative zooplankton study of the Salton Sea prior to 1997 was performed by Carpelan (1961) in 1954-1956 when the lake had approximately the salinity of sea water (34 g/l). The species he documented were a rotifer, a copepod, and the planktonic larvae of a barnacle and a polychaete worm.

Carpelan found that the most numerous zooplankton species was the rotifer *Brachionus plicatilis*. There seemed to be two forms of this rotifer. The "summer form" was the larger, averaging about 200 μm x 120 μm. The "winter form" was 150 μm x 90 μm. He found maximum abundances of this taxon in the late summer of 1954 of 1283 per liter at his sampling site located three miles offshore. He did not observe any males during his study.

The copepod, which Carpelan identified as *Cyclops dimorphus,* was present only in the summer months. The maximum found in 1955 was 535 per liter. It disappeared in the winter months and was not detected from February to May of 1955 or 1956. He felt that the copepod was feeding on the phytoplankton.

Other common zooplankton species Carpelan found were the larvae of some benthic species, a polychaete worm and a barnacle. The barnacle larvae of *Balanus amphitrite saltonensis* had two forms in the plankton, the naupliar and the cypris stage. Both of these were in higher abundance near the shore where the adult sessile forms are found. A spring and a fall peak of abundance was observed. The larvae of the polychaete worm, *Neanthes succinea*, were found nearly throughout the year with a few collections that had no worm larvae in July through September. This he attributed to the lack of oxygen at depth during these months.

The salinity of the Salton Sea in the 1990s has reached at least 46 g/l. The survey of zooplankton by San Diego State University in 1997-1998 has shown some of the same species are still present in the Salton Sea that were documented by Carpelan at the lower salinity (see also Dexter, 1993). There is at least one abundant new species of rotifer present and we have discovered that ciliates also have an important role in the zooplankton community.

The metazooplankters fall into two groups, those that are abundant in the summer and those that are abundant in the winter. The summer zooplankton in 1997 was dominated by two species, a rotifer in the genus *Brachionus* and a copepod now correctly identified as *Apocyclops dengizicus* (Dexter 1993). The average size of the *Brachionus* by measurement of 20 random individuals was 150 µm in April 1998 and 130 µm in July 1998. This implies that we have the species *B. rotundiformis* as it is in the size range of the small S-type *B. plicatilis* which has been assigned this new name (Segers 1995, Gómez and Serra 1995) The much larger size of the "summer form" of rotifer in the 1955 survey (200 µm) may mean that two rotifers in the genus *Brachionus* were present in 1955, *B. plicatilis* and *B. rotundiformis*. In our samples no *B. rotundiformis* were detected in January 1997. It then showed up in small numbers in the following months and had a great increase in April and May. The maximum abundance occurred in August, after which the numbers steadily declined. The copepod followed somewhat the same trend with a sharp increase in early June declining gradually thereafter, suggesting the copepod may be preying on the rotifer. At least a few specimens of *A. dengizicus* were found on every sampling date although the numbers were much reduced in the winter months.

In 1997 we found a great abundance of another rotifer, *Synchaeta* sp., in the winter zooplankton. This rotifer was not reported to be present in the lake by Carpelan but was observed in our microcosm study (Hart et al. 1998) and has come to be an important member of the plankton community. It declined in the summer as *Brachionus* increased in abundance and was not detected at all in samples from June through October. It appeared again in November in large numbers. There were months in early spring and late fall when both rotifers were present in the plankton. It would appear that each of these two rotifers species spend at least some time in resting stages in the sediments.

Two larval forms were also common in the winter zooplankton in 1997, the barnacle, *Balanus amphitrite saltonensis*, and the polychaete worm, *Neanthes succinea*. The presence in the plankton of these larvae indicates that these two taxa are still reproducing successfully in the increased salinity of the present day Salton Sea. Barnacle larvae were found in greatest abundance in January through April. The polychaete worm larvae had a peak of abundance in March declined in the summer and appeared to be increasing again in November.

A Microcosm Experiment

To assess likely future changes in the lake a 15-month microcosm experiment was undertaken in 1990-1992 in 312 L tanks at San Diego State University. This examined the effect on plankton, benthos, nekton, and nutrient levels of five experimentally manipulated salinity levels (30, 39, 48, 57, and 65 g/L). Salinity levels were created by starting with Salton Sea water diluted to 30 g/L and adding four different salts in proportions designed to yield ionic compositions expected as the Salton Sea increases in salinity. At two salinities (39 and 57 g/L) microcosms were also set up each having one small (8 g) tilapia (*Oreochromis mossambicus*) in order to assess the influence of this fish on the system. That stocking rate is equivalent to approximately 130 kg/ha, a rather low standing stock for a eutrophic lake. Four tanks were set up at each salinity-fish treatment combination. Each tank was inoculated not only with the organisms in the original Salton Sea water but also with organisms collected from other water bodies of varied salinities (1-270 g/L) in the Salton Sea region. Each tank also was provided with Salton Sea sediments.

Detailed results of this experiment are reported in (González et al. 1998, in prepn, Hart et al. 1998, Simpson and Hurlbert 1998, and Simpson et al. 1998). Some of the more salient findings may be summarized as follows:

The amphipod *Gammarus mucronatus* was the dominant invertebrate at the two lowest salinities but did poorly at the higher salinities, probably reflecting direct negative physiological effects of salinity on its survival and reproduction. *Gammarus* is a voracious omnivore, and its responses to salinity generated many of the other strong salinity effects observed. Its scarcity at high salinities was associated with increased abundance of algal mats, brinefly larvae (*Ephydra riparia*), water boatmen (*Trichocorixa reticulata*), brineshrimp (*Artemia franciscana*), an harpacticoid copepod (*Cletocamptus deitersi*), and certain nematodes. Total metazoan biomass decreased with increasing salinities, but total protozoan biomass usually was similar for all salinities. Except when *Artemia* was abundant, the protozooplankton biovolume greatly exceeded biovolume of the other truly planktonic metazoans (*Apocyclops dengizicus*, rotifers, larvae of *Balanus amphitrite*). This may be typical of salt lakes.

At 65 g/L high densities of *Artemia* appeared to cause reduced phytoplankton densities and primary production which in turn were associated with decreased particulate N and P levels in the water column, increased diatom-rich benthic algal mats and reduced concentrations in the water column of dissolved Si, orthophosphate and dissolved organic P.

Effects of salinity on the taxonomic composition of the diverse phytoplankton were numerous and complex. Cyanobacteria, chlorophytes, diatoms, dinoflagellates, and haptophytes were the dominant groups. At 65 g/L diatoms (8 genera) and prasinophytes (*Tetraselmis* sp.) were little affected by *Artemia* grazing while all other major algal taxa were markedly reduced. A haptophyte, *Prymnesium* sp., became exceedingly abundant at 48 and 57 g/L, where it achieved densities up to 10^6 per ml and constituted 60-80 percent of the total phytoplankton biovolume during the latter third of the experiment. This genus has been known to cause fish kills in estuaries and in aquaculture operations in various parts of the world.

Responses of these microecosystems to the presence of tilapia were equally dramatic, and suggestive of the role tilapia plays in the Salton Sea foodweb. This fish is an omnivore capable of feeding on phyto- and zooplankton, nekton, phyto- and zoobenthos, and detritus. The larger invertebrates (*Gammarus, Trichocorixa*) were greatly reduced in abundance. These reductions were accompanied by large increases in certain copepods, rotifers, and ciliates, and in the abundance of benthic and attached algae. Total zooplankton biovolume, total phytoplankton biovolume, and total N and total P in the water column were all greatly reduced by tilapia. This suggested that a commercial harvest of this fast-growing fish could remove enough nutrients to be of help in reversing the Sea's highly eutrophic condition. Tilapia caused large changes in phytoplankton composition as well. At 39 g/L, it shifted a diatom and chlorophyte dominated system to a *Prymnesium* and chlorophyte dominated system. At 57 g/L, it shifted a strongly *Prymnesium* dominated system to one where *Prymnesium*, chlorophytes, cyanobacteria, dinoflagellates, and diatoms were co-dominants.

Virtually all species in these microecosystems have wide salinity tolerances and maintained larger or smaller populations across the whole 30 to 65 g/L salinity range tested. Each species can be presumed to have experienced direct physiological effects of the salinity manipulation. It seems likely, however, that most of the major effects documented were due primarily and most proximately not to salinity itself but rather to alteration in the array of predators, grazers, competitors, or nutrient conditions each species encountered. The appearance, disappearance, or marked change in abundance of a single functionally important species directly affected by salinity - such as *Gammarus* or tilapia - may shift the system into a radically different state. Such a change of state at the Salton Sea might be predicted each time that salinity reaches the tolerance threshold of one of the dominant invertebrate or fish species present.

Table 1. Planktonic algae recorded from the Salton Sea (C - Carpelan 1961, U - USDI 1970, P -unpublished observations, and G- Gonzalez et al. 1998 from 312 L outdoor microcosms established with Salton Sea water). The microcosm experiment of Gonzalez et al. (1998) used experimental salinities of 30, 39, 48, 57, and 65g/L; the salinity value given is that at which density was maximal. For other studies the salinity value is that of the Salton Sea at the time the samples were taken.

Taxon	Ref.	Density (cells/ml)	Salinity (g/L)
Cyanobacteria			
Lyngbya spp.	C	--	35
Gomphosphaeria lacustris	C		35
Anabaena spiroides	G	7,000	30
Anabaena sp.	G	40,000	30
Oscillatoria sp.	G	200,000	30
Romeria sp.	G	200,000	57
Spirulina major	G	80,000	57
Chlorophyceae			
Chlamydomonas sp.	G	500,000	30
Oocystis sp.	C		35
	G	300,000	
Crucigenia rectangularis	C		35
Motile green A	U	5,100	37
Motile green B	U	10,000	37
Westella botryoides ?	C	160,000	37
Euglenophyceae			
Eutreptia lanowii	C	1,300	35
Eutreptia sp.	U	500	37
Prasinophyceae			
Tetraselmis sp.	G	20,000	39
Cryptophyceae			
Cryptomonas sp.	C	--	35
	G	9,000	39
Chroomonas sp.	G	4,000	57
Dinophyceae			
Amphidinium kofoidii	C	--	35
Peridinium trochoideum	C	--	35
	G	4,000	39
Peridinium sp.	U	4,600	37
Gonyaulax sp.	C	--	35
(=*Alexandrium*?)	G	2,000	48
Gonyaulax grindleyi	P	--	44
Gymnodinium spp.	P	--	44
Heterocapsa niei	C	100,000	35
	U	89,000	37
	G	6,000	30
Prorocentrum minimum	C	--	35
Prorocentrum compressa	C	63,000	35
Prorocentrum sp.	U	25,000	37
	G	20,000	48
Gyrodinium resplendens	U	9,400	37
Gyrodinium uncatenum	U	--	
Gyrodinium cf. *instrictum*	P	--	46
Dinophyceae (cont.)			
Oxyrrhis marina	G	4,000	65
	P	--	46
Scrippsiella sp.	P	--	46
Oblea sp.	P	--	46
Pfiesteria sp.?	P	--	46
Prymnesiophyceae			
Pleurochrysis sp.?	G	10,000	39
Prymnesium sp.	G	1,000,000	57
Chrysochromulina sp.	P	--	46
Chrysophyceae			
Dinobryon sp.	G, P	--	46
Synuraphyceae			
Synura sp.?	G, P	--	46
Ebridaceae			
Hermesinum adriaticum	C	450	35
Bacillariophyceae			
Tablularia sp.	C	--	35
Navicula sp.	C	--	35
Gyrosigma spp.	C	--	35
Pleurosigma sp nov.	C	375	35
	U	4,400	37
	G	200	65
Opephora sp.	G	2,000	39
Amphora spp.	G	500	65
Cylindrotheca closterium	C	56,000	35
	U	540	37
	G	200,000	39
	P	--	46
Nitzschia spp.	U	11,000	37
	G	1,000	39
Thalassionema nitzschioides	C	9,000	35
	U	22,000	37
	G	1,000	57
Cyclotella spp.	C	53,000	35
	U	3,800	37
Mastogloia pumilla	G	6,000	39
	G	700	65
Chaetoceros muelleri	P	--	46
Fallacia pygmea	P	--	46
Diploneis sp.	P	--	46
Brachysira aponina	P	--	46
Raphidophyceae			

Gymnodinium sanguineum	G	3,000	30	*Chattonella* cf.*subsalsa*	P	1,490	46

Table 2. Algae found in the Sea that are known to be toxic elsewhere or are closely related to toxic species.

	SPECIES FOUND IN SS	CLOSELY RELATED TOXIC SPECIES	TOXIN PRODUCED	SPECIES AFFECTED	REFERENCE
DINOPHYCEAE					
Gonyaulax spp.	*Gonyaulax cf. spinifera*	*G. catenella*			Hall, et. al., 1990
	G. grindleyi				
Gymnodinium spp.		*G. breve*	brevetoxin and metabolites	fish, mollusk, humans	Husain et. al., 1996
			8 toxins	fish	Shimizu, 1989
	unidentified Gymnodinioid		brevetoxin	humans	Hallegraeff, et. al., 1995
		G. cf. mikimotoi (=G. nagasakiense)	hemolysins	fish & invertebrates	Hallegraeff, 1993
			gymnodimine,	fish	Seki, et. al., 1995
			causes NSP		
			PSP toxins	humans	Hallegraeff, 1989
		G. catenatum	saxitoxin, PSP	humans	Hall, et. al., 1990
			PSP toxins	humans	Hallegraeff, 1995
Gyrodinium spp.	*G. resplendens*			fish, invertebrates	Tangen, 1977
	G. uncatenum	*G. aureolum*		fish (salmon)	Jones, et. al., 1982
	G. sanguineum			fish	Shimizu, 1989
				fish	Hallegraeff, 1993
Heterocapsa spp.		*H. circularisquama*	cell surface protein	bivalves	Matsuyama et. al., 1997
	H. niei		cell surface protein	tintinnids	Kamiyama & Arima, 1997
		Heterocapsa sp.	cell surface protein	oysters	Matsuyama et. al., 1995
			cell surface protein	*Gyrodinium* sp.	Uchida et. al., 1995
Pfiesteria spp.	Pfiesteria-like organism	*P. piscicida*	neurotoxin	fish, crabs, scallops	Burkholder, et. al., 1995a
			exotoxin; neurotoxin	fish, crabs, scallops	Burkholder, et. al., 1995b
Prorocentrum spp.	*P. minimum*	*P. minimum*	neurotoxin	humans, fish?	Grzebyk, 1997
				humans	Stonik, 1994
RAPHIDOPHYCEAE					
Chattonella spp.	*C. cf. marina*	*C. marina*	brevetoxin	fish	Endo, et. al., 1992
			superoxide radicals		
		C. antiqua		fish	Hallegraeff, et. al., 1995
PRYMNESIOPHYCEAE					
Prymnesium spp.	*Prymnesium* sp.	*P. calathiferum*	unknown	fish	Moestrup & Thomsen
		P. parvum	hemolytic compounds	fish	Moestrup & Thomsen
Chrysochromulina spp.	*Chrysochromulina* sp.	*C. leadbeateri*	not isolated	fish	Moestrup & Thomsen
		C. polylepis	hemolytic compounds	fish, invertebrates	

Table 3. List of the major mortality events of eared grebes at the Salton Sea. In most cases, the cause of death is unknown.

Date	Number Dead	Reference
Jan-Mar 1989	>40,000	Jehl, 1996
1992	150,000	USFWS, 1996
Feb-Mar 1994	2,100	Jehl, 1996; USFWS, 1996
Jan-Apr 1995	2,000	Jehl, 1996; NWHC
Mar-97	2,441	NWHC
Dec-97	2,645	NWHC

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