Hydrobiologia (2007) 576:185–203
DOI 10.1007/s10750-006-0301-2

SALINE WATER

Population dynamics, distribution, and growth rate of tilapia (*Oreochromis mossambicus*) in the Salton Sea, California, with notes on bairdiella (*Bairdiella icistia*) and orangemouth corvina (*Cynoscion xanthulus*)

Lucille L. Caskey · Ralf R. Riedel ·
Barry Costa-Pierce · John Butler ·
Stuart H. Hurlbert

Abstract The Salton Sea is a highly saline lake that has long supported sportfishery and large populations of fish-eating birds. A study was initiated in 1999 to assess the status of orangemouth corvina (*Cynoscion xanthulus*), bairdiella (*Bairdiella icistia*) and tilapia (*Oreochromis mossambicus* × *O. urolepis*). Multimesh (50 × 2 m) gillnets were set at nine stations in 1999, ten stations in 2000 and six stations in 2002. These stations were sampled every two months in 1999, every three months in 2000 and once in 2002. *O. mossambicus* was the most abundant of the four species, with a maximum mean catch per unit effort (CPUE) 13.8 kg net^{-1} h^{-1} or 29.9 fish net^{-1} h^{-1} being observed at the river mouth stations in August 1999. From spring to summer, tilapia CPUE increased at nearshore and river mouth stations and decreased at pelagic stations, apparently reflecting migration away from midlake areas in response to anoxia or hypoxia caused by periodic springtime overturn events in deep waters. Tilapia catches in nearshore, river mouth and pelagic habitats were 83 and 60% males in 1999 and 2000, respectively. Tilapia catches in rivers in August 1999 averaged only 6% male. During 1999–2000, the tilapia population consisted essentially of only the 1995 and 2000 year classes. Harsh conditions at the Salton Sea have led to erratic reproduction and survival rates and unstable age structures for its resident fishes. Massive parasite infestations of fry and physiological stressors such as anoxia, high sulfide levels, high salinity and high and low temperatures are potential causes of the irregular recruitment and periodic dieoffs of tilapia. The abundance of all fish species declined over the years of study. Between 1999 and 2002, the late summer mean CPUEs for tilapia, bairdiella and orangemouth corvina at four nearshore stations dropped from 16 fish to 0.02 fish, from 4.7 fish net to 0.23 fish, and from 0.08 fish to 0.02 fish, respectively. During 2000–2003, parallel declines occurred in estimated numbers of adult fish involved in mass mortality events at the Sea. The boom-and-bust dynamics of tilapia and other fish populations in the Sea have major consequences for fish-eating bird populations, for other

---

Guest Editor: John M. Melack
Saline Waters and their Biota

L. L. Caskey (✉) · R. R. Riedel · S. H. Hurlbert
Department of Biology and Center for Inland Waters,
San Diego State University, San Diego, CA 92182,
USA
e-mail: lucyandjohncaskey@yahoo.com

B. Costa-Pierce
Mississippi-Alabama Sea Grant College Consortium
(MASGC), Ocean Springs, MS 39566, USA

J. Butler
8604 La Jolla Shores Dr., NOAA Fisheries, La Jolla,
CA 92037, USA

components of the ecosystem, and for the recreational value of the lake.

Keywords Saline lake · Age · Growth · Fish die-offs · Fishery · Sulfide · Anoxia

Introduction

This article documents the population dynamics of an exotic fish, the Mozambique tilapia (*Oreochromis mossambicus* (Peters)), in the Salton Sea, a large (980 km^2), saline, closed basin lake in the Colorado Desert of southern California (Fig. 1). Maximum depth of the lake is 15 m and its mean depth is 8 m. Large areas at its northern and southern ends are shallow (<2 m). Fed mainly by agricultural wastewaters since its accidental formation in 1905–1907, its salinity increased from 3.5 g l^{-1} in 1905 to 41–44 g l^{-1} during the 1990s (Cohen et al., 1999; Watts et al., 2001). Mean water column water temperature ranges from a minimum of 13–15°C in winter to a maximum of 31–34°C in summer (Fig. 2a; Watts et al., 2001; Holdren & Montaño, 2002). During the spring and summer, the water column is thermally stratified most of the time, and the bottom waters become anoxic. Periodically, after strong wind, the entire lake becomes briefly oxygen deficient as anoxic bottom waters, and the organic matter, sulfide and microbial heterotrophs in them, are mixed into the surface waters (Fig. 2b).

Historical changes in the fish fauna of the Salton Sea have been large (Walker, 1961; Riedel & Costa-Pierce, 2001; Hurlbert et al., 2007). Carp (*Cyprinus carpio*), bonytail (*Gila robusta*), humpback sucker (*Xyrauchen texanus*), rainbow trout (*Salmo gairdneri*), striped mullet (*Mugil cephalus*), and desert pupfish (*Cyprinodon macularius*) were washed into the Salton Sea when it was created by flood flows from the Colorado River (Walker, 1961), but by 1929 the carp had disappeared and many of the other freshwater species had declined as the salinity of the lake rose. Since 1929, more than 30 species of marine fish have been introduced, of which only bairdiella (*Bairdiella icistia* (Jordan and Gilbert)), sargo (*Anisotremus davidsonii* (Steindachner)), orangemouth corvina (*Cynoscion xanthulus* (Jordan and Gilbert)) and longjaw mudsucker (*Gillichthys mirabilis* (Cooper)) survived.

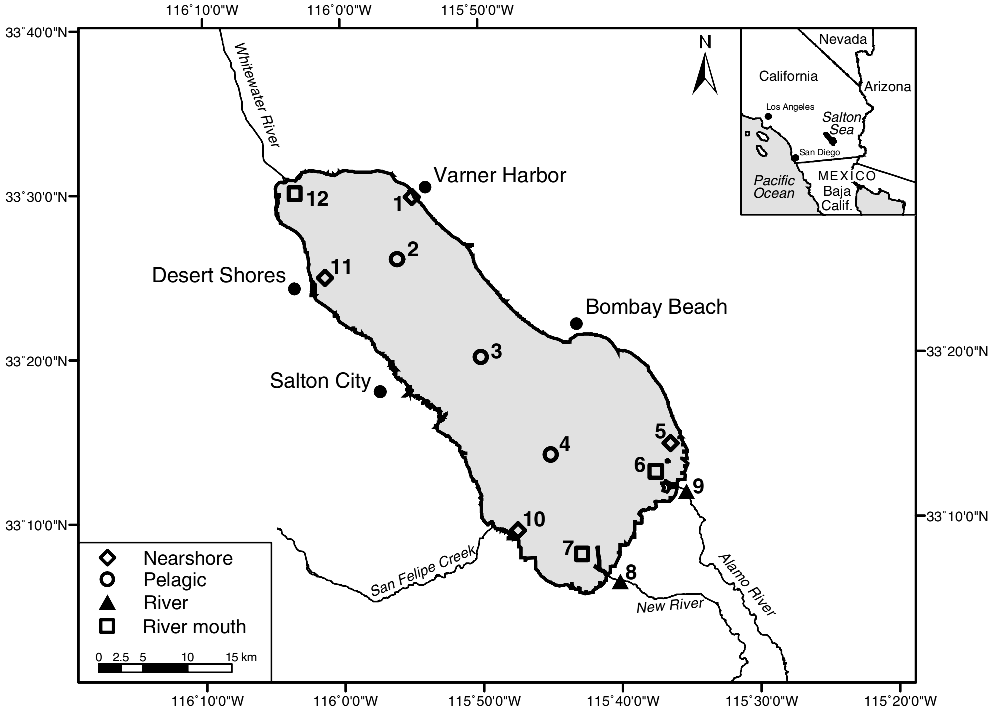

Fig. 1 Location of the sampling stations within the Salton Sea

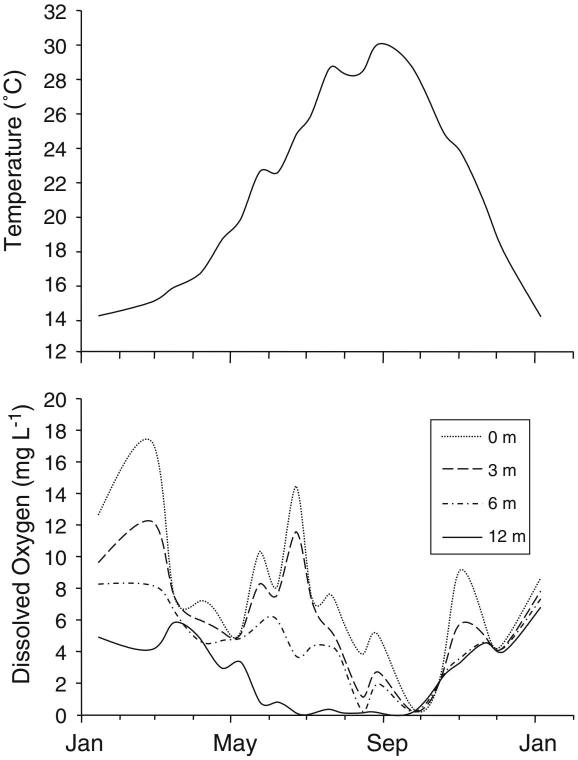

Fig. 2 Mean temperature (Top) over entire water column and dissolved oxygen patterns (Bottom) at four depths during 1999; adapted from Watts et al. (2001)

Tilapia likely escaped to the Salton Sea in the 1960s from a tropical fish farm (St. Amant, 1966) and from irrigation canals where they had been stocked to control vegetation (Costa-Pierce & Doyle, 1997). We will refer to these fish as *O. mossambicus* (or simply tilapia), although they are genetically distinguishable from *O. mossambicus* and may be a hybrid of *O. mossambicus* and *O. urolepis hornorum* (Costa-Pierce & Doyle, 1997). *O . mossambicus* is an adaptable species that can survive and reproduce in a wide variety of salinity and dissolved oxygen conditions. It can reproduce at young ages and small sizes and devote energy towards reproduction or it can mature at larger sizes after allocating more energy towards growth when young (Noakes & Balon, 1982).

Tilapia was first caught in the Salton Sea by gill nets and sportsfishermen in 1975, was the most abundant fish (38–67%, by number) caught in multipanel gill net surveys carried out by the California Department of Fish and Game during 1979–1983 (Hurlbert et al., 2007), and was the most abundant fish at the outset of this study in 1998–1999. It has been a major element of the sportfishery, there being no legal catch limit for it as there is for other species, and was being considered for a possible future fishmeal fishery (Gonzalez et al., 1998; Riedel et al., 2001; Moreau et al., 2007). Despite its abundance, or perhaps in part as a consequence of it, dieoffs of millions of fish have occurred in recent years (Hurlbert et al., 2007). The combined effects of fluctuations in temperatures and dissolved oxygen levels, high salinity, toxic algal blooms and parasite infestation may play a role in these periodic dieoffs.

Tilapia has multiple large influences on this lake ecosystem. It has for some decades been important as a sport fish, as food for fish eating birds, and, since the 1990s, as an occasional vector of botulism to white and brown pelicans (Friend, 2002). It is an opportunistic feeder, capable of feeding on phytoplankton, zooplankton, benthos and detritus (Bowen, 1980; Maitipe & DeSilva, 1985; R. Riedel, unpubl. data). An experiment with Salton Sea microecosystems showed that at realistic densities, tilapia caused large reductions in amphipod and corixid populations, increases in certain harpacticoid, rotifer, nematode, and ciliate populations, increased periphyton abundance and decreased phytoplankton abundance (Hart et al., 1998; Simpson et al., 1998; M. Gonzalez, unpubl. data). In six months, tilapia grazing and growth reduced total phosphorus and total nitrogen levels in the microecosystem water columns by roughly 60 and 35%, respectively, suggesting the potential for sustained tilapia harvesting for eutrophication reversal in the Salton Sea (Gonzalez et al., 1998).

The analyses and interpretations reported here for tilapia supersede earlier preliminary ones (Costa-Pierce & Riedel, 2000; Riedel et al., 2002) and also document the crash of tilapia and other fish populations in this lake during the period 2000–2003.

Methods

Sampling regime

Fishes were collected in river, nearshore, river mouth and pelagic habitats using 50 × 2 m, multi-panel (stretched mesh sizes of 1, 2, 7, 10, and 12.5 cm) gillnets. Nets were set at nine stations in 1999, 10 stations in 2000 and at six stations in 2002 (Fig. 1, Table 1). Sampling dates were: February 7–14, April 4–13, May 24–31, August 2–17, October 2–23 and December 1–6, 1999; April 15–21, July 27–August 1, October 12–21, November 30–December 4, 2000; and September 2–3, 2002. During each sampling period, two bottom and two surface gillnets were set at each station greater than 2 m deep. At stations less than 2 m deep, the two gillnets spanned the water column. Soak time varied from 1 to 30 h depending on weather and net saturation times. In nearshore areas during the summer, we decreased soak time because of the high volume of fish that were being caught. After collection, all fishes were sexed, weighed to the nearest 0.1 g and measured to the nearest mm for total length. For each station, on each date, pairs of sagittal otoliths were removed from up to 30 fish of each species for age estimation.

This information was supplemented by detailed records on fish kills kept by Salton Sea Authority wildlife biologists during 1999–2003.

Age determination and validation

An otolith was placed in a fingerbowl with distilled water and examined under a dissecting microscope using a 16× objective, and reflected light and opaque zones were counted by two individuals. If counts of opaque zones differed for the two counters by one or more, those estimates of age were removed from analysis. The frequency of zone deposition within the otolith was determined using Marginal Increment Analysis (MIA) (Barnes & Foreman, 1994; Caskey, 2002). Age was estimated as the total number of opaque zones within an otolith divided by the number of opaque zones deposited per year. MIA of tilapia otoliths revealed that annuli were probably deposited once each year and that the opaque zone was deposited between April and August of each year (Caskey, 2002). Those conclusions were based on counts of daily growth increments within the margin of the otolith (Caskey, 2002) as well as on the pattern of otolith deposition observed over the two years of sampling.

Annual growth rates were calculated using the Von Bertanlanffy growth function (VBGF). The VBGF describes the growth of individual fish over their lifespan. The VBGF is commonly used in fisheries biology, and VBGFs for tilapia of various systems have been calculated (Weyl & Hecht, 1998; Bruton & Boltt, 1975; Hecht, 1980).

The VBGF is:

$$L_t = L_\infty\left(1 - e^{-K(t-t_0)}\right) \tag{1}$$

Table 1 Location and characteristics of stations sampled during 1999, 2000 and 2002

Sampling stations	Year	Habitat type	GPS coordinates		Leadline depth (m)		No. of gillnets	
			Lat.	Long.	Surface	Bottom	Surface	Bottom
1. Northeast	99,00,02	Nearshore	33°29.80′	115°54.90′	< 2	5–7[a]	2	2[b]
2. North Basin	99,00	Pelagic	33°26.00′	115°56.00′	< 2	>12	2	2
3. Center	99,00	Pelagic	33°20.00′	115°50.00′	< 2	>12	2	2
4. South Basin	99,00	Pelagic	33°14.00′	115°45.00′	< 2	>12	2	2
5. Southeast	99,00,02	Nearshore	33°14.60′	115°36.30′	< 2	5–7[a]	2	2[b]
6. Alamo River	99,00,02	River mouth	33°12.90′	115°37.40′	< 2		2	
7. New River	99,00,02	River mouth	33°08.00′	115°41.60′	< 2		2	
8. New River	99	River	33°07.80′	115°41.60′	< 2		2	
9. Alamo River	99	River	33°12.40′	115°37.00′	< 2		2	
10. Southwest	00	Nearshore	33°09.00′	115°48.00′	< 2		2	
11 Northwest	00,02	Nearshore	33°24.00′	116°03.00′	< 2		2	
12. Whitewater River	00,02	River mouth	33°29.00′	116°04.00′	< 2		2	

[a] Bottom gillnets in 1999 only as location moved slightly inshore to a depth of less than 2 m in 2000

[b] Bottom gillnets were used in 1999 only

where L_t is predicted length at time t, L_∞ is mean asymptotic length predicted by the equation, K describes the rate at which L_∞ is approached, t is age at time t, and t_0 is the age at which fish length is zero. Using Systat 8.0$^{\text{TM}}$, the parameters (L_∞, K, t_0) for the VBGF for tilapia were calculated using least squares estimates and the Gauss–Newton method for non-linear equation fitting. Parameters were estimated using mean total length at age and age quantified as age class (0+, 1+, 2+, etc.) rather than as actual age. While this is common practice, it will generally yield lower estimates for K than would be obtained if actual ages could be used. Age classes that contained fewer than ten fish were eliminated from this analysis.

Analysis of abundance data

Catch per unit effort (CPUE), calculated on the basis of both biomass and numbers of individuals, was used to examine spatial and temporal distribution patterns of tilapia. CPUE in number of individuals was also used to assess changes in bairdiella and orangemouth corvina populations in the Salton Sea between 1999 and 2002. As the basic datum, CPUE (individuals or biomass per net per hour) was calculated for the combined catch of the two nets at each depth at each station during each sampling period. Since distributions of CPUE were non-normal and had heterogeneous variances, CPUEs were log transformed prior to statistical analysis. Prior to log transformation, a constant (k) value of 0.017 individuals was added to each numerical CPUE datum, and a constant of 0.007 g was added to each biomass CPUE datum, to avoid having any zeros in the datasets. These constants represent the smallest possible non-zero value obtainable, given the sampling regime and reporting units used. The k value was calculated by dividing the smallest non-zero number of tilapia caught (1) or the weight of the smallest tilapia caught (0.4 g), by 60 h, i.e., the longest soak duration (30 h) times 2 nets^{-1}station. Ideally, each soak duration would be the same, so that CPUE values of zero for different stations and dates would be equivalent; however, due to large differences in CPUE among habitats and thus saturation times, as well as weather considerations, soak times varied from 1 to 30 h.

Differences among habitats in mean tilapia CPUE for each sampling period were assessed using a one-way analysis of variance (ANOVA). Separate analyses were carried out for surface and bottom nets.

Spatial and temporal variations in sex ratio of tilapia were assessed. For each station, the total proportion of tilapia that was male was arcsine transformed and mean sex ratio estimated for each habitat. Differences among habitats were assessed with date-by-date one-way ANOVAs using stations as replicates.

Results

Age and size structure of the tilapia population

MIA indicated that tilapia that had three, four, and five annuli on the otolith were three, four and five years old. An initial analysis (Costa-Pierce & Riedel, 2000) had suggested that the Salton Sea tilapia population in 1999 was comprised of mostly 1+ year-old-fish (i.e., fish produced in 1998), but it later was determined that these fish represented the 1995 cohort (Riedel & Costa-Pierce, 2001; Riedel et al., 2002).

The great majority of tilapia caught were from the 1995 and 2000 year classes, and the 1996, 1997, 1998 and 1999 year classes were scarce (Fig. 3).

On each sampling date between February 1999 and April 2000, the 1995-year class comprised more than 90% of the total tilapia aged. Between July and December 2000, the 2000-year class constituted 25–39% of fish aged. During the entirety of 1999–2000, only 78 individuals from the 1996, 1997, 1998, and 1999-year classes were observed while 1695 individuals from the 1995-year class were observed.

We also found a restricted length-frequency distribution (Fig. 4). Between February 1999 and April 2000, over 95% of the tilapia catch on each sampling date was 25–35 cm in total length. A higher incidence of small tilapia were observed in July 2000, when 60% of the total catch were

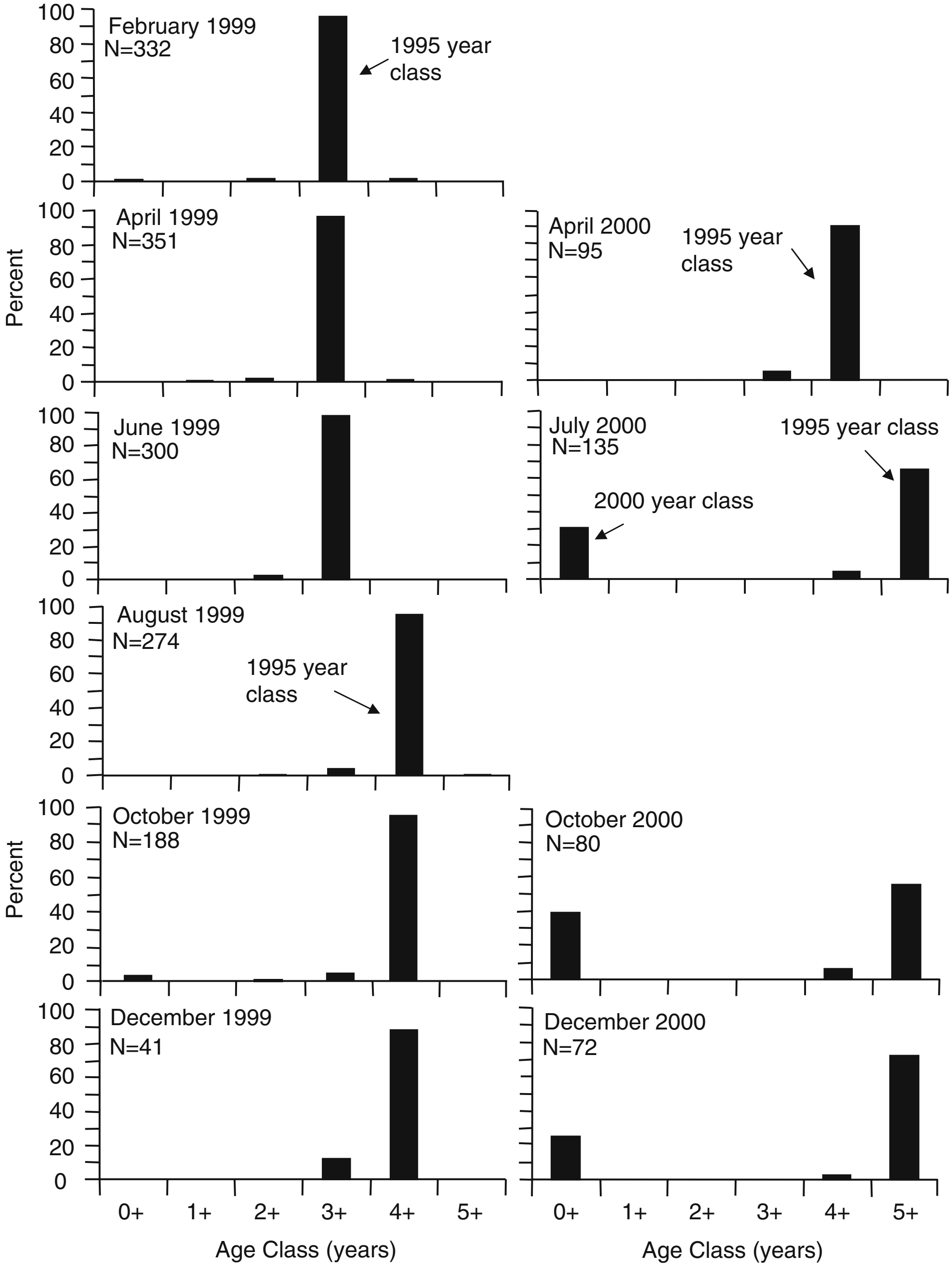

Fig. 3 Age-frequency distribution of tilapia by sampling period. *N* = number of individuals aged

young-of-the-year tilapia 4–15 cm in total length. In both October and December of 2000, these young-of-the-year tilapia were larger, ranging between 12 cm and 17 cm in total length and comprised 25% of tilapia caught. In contrast, individuals less than 20 cm comprised less than 2% of the catch on all dates in 1999. These changes reflected a decrease in dominance of the 1995-year class and successful recruitment of young-of-the-year tilapia beginning in July 2000.

Spawning appeared to be successful in both years, but capture of young-of-the-year in 1999

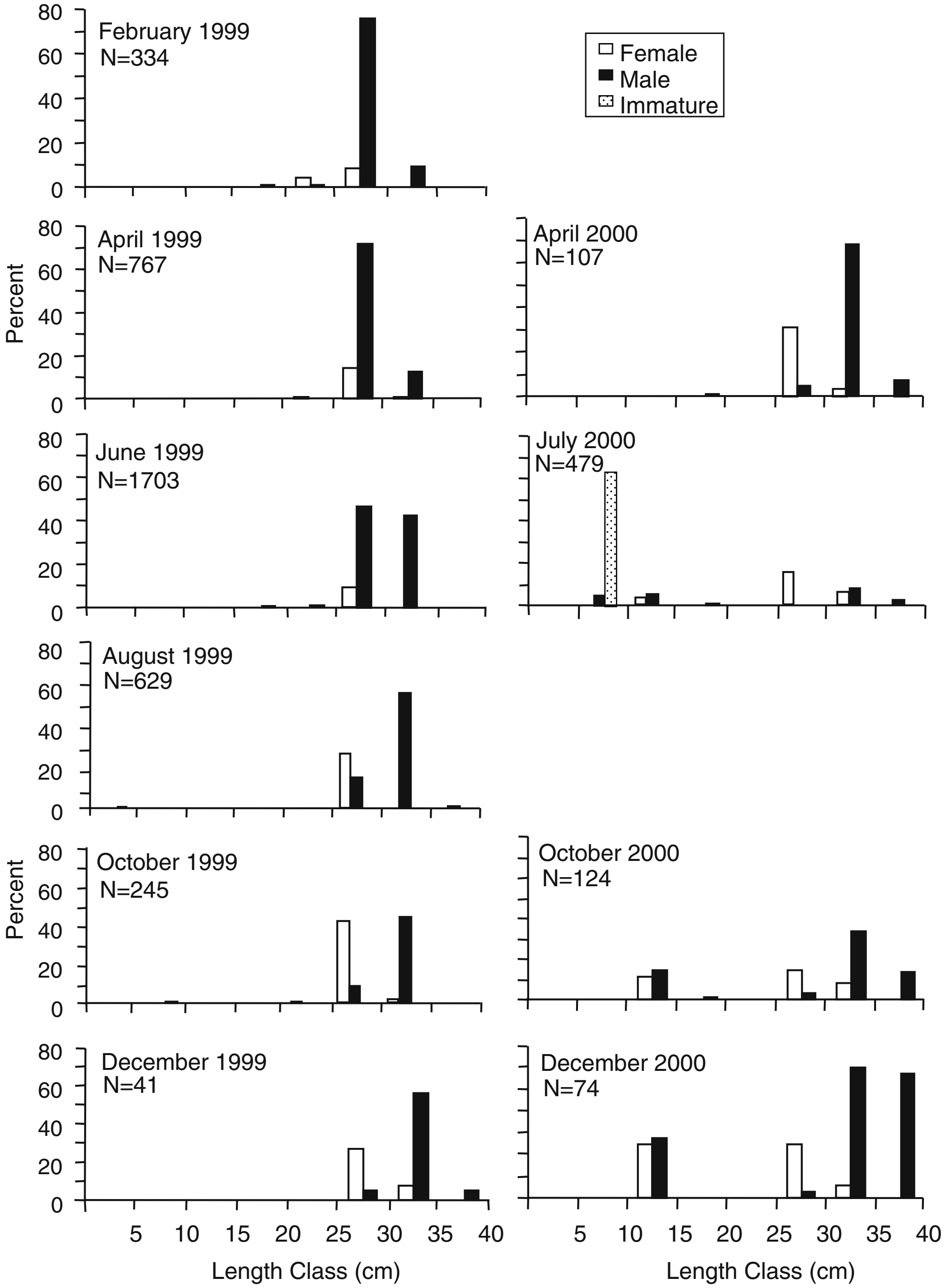

Fig. 4 Length-frequency distribution of tilapia by sampling period. *N* = number of individuals measured

was reduced relative to 2000. During 1999 and 2000, very small young-of-the-year tilapia were observed in the shallow areas of the Salton Sea, and fry were often observed in the mouths of captured brooding females from June to October. However, these young-of-the-year were rarely observed in catches between June 1999 and April 2000.

Spatial and seasonal abundance patterns

Catch per unit effort of tilapia varied markedly among habitats, seasons and years at the Salton Sea. This variation presumably reflected corresponding variation in both abundance and catchability of tilapia. CPUEs were generally greatest at nearshore and river mouth and lowest at river and pelagic stations (Figs. 5, 6). Highest mean CPUEs for river mouth and nearshore habitats were 29.9 and 21.7 fish net^{-1} h^{-1}, respectively, while the highest mean CPUEs for pelagic and riverine habitats were only 1.3 and 0.40 fish net^{-1} h^{-1}, respectively. It appears that river mouth and nearshore areas represent the preferred environment for tilapia in the Salton Sea.

In spring, CPUE increased in the nearshore and river mouth habitats at the same time it declined in the pelagic habitat (Figs. 5, 6). Mean CPUE in 1999 in the river mouth habitat increased from 0.4 fish net^{-1} h^{-1} in February to 29.9 fish net^{-1} h^{-1} in August, with a similar change occurring in the nearshore environment. Over the same period, mean CPUE for the pelagic habitat decreased from 0.6 fish net^{-1} h^{-1} to less than 0.1 fish net^{-1} h^{-1}. The screen of a sonar depth finder mounted on the sampling vessel also indirectly demonstrated the shift. In warm months, although large numbers of unidentified fishes were detected in shallow waters, these fishes disappeared when depth exceeded ca. 4–6 m. Tilapia, as well as other fishes, appeared to

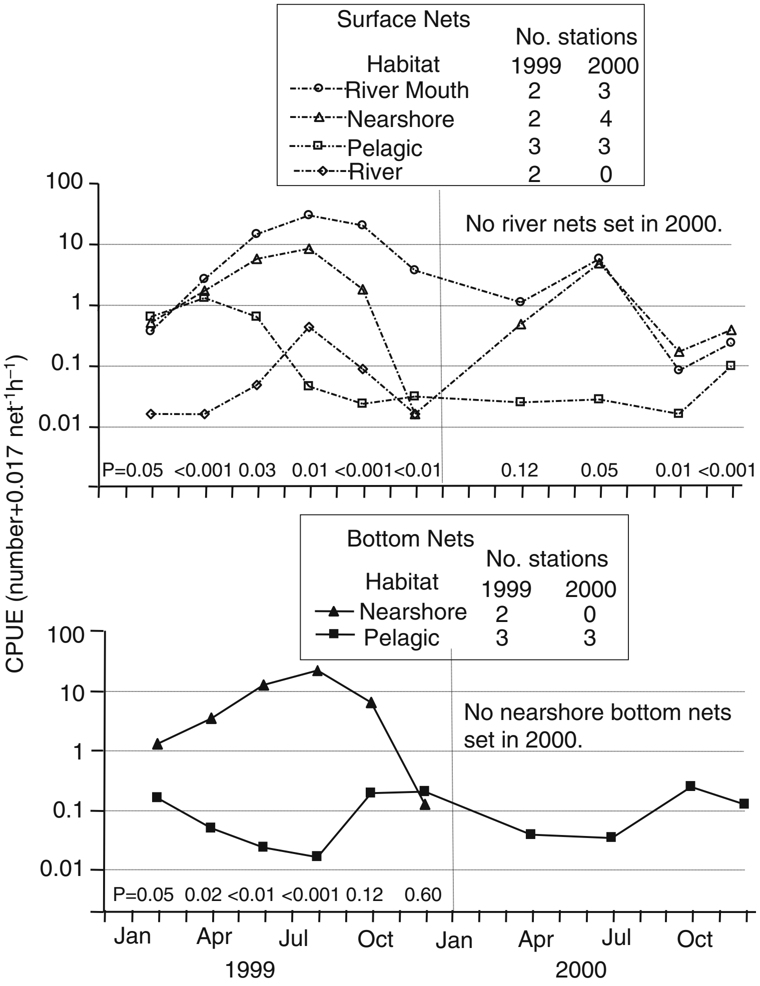

Fig. 5 Geometric mean number of individuals caught per unit effort by habitat type, net depth and sampling period. *P* values are for one-way ANOVAs for differences among habitat types

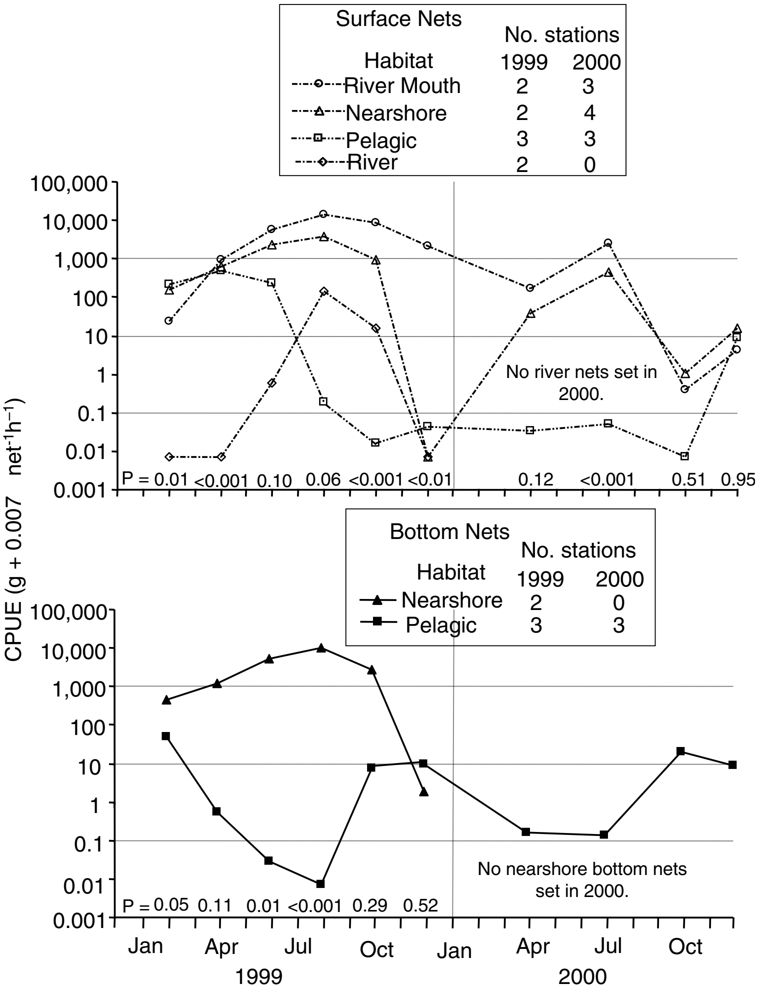

Fig. 6 Geometric mean biomass caught per unit effort by habitat type, net depth and sampling period. *P* values are for one-way ANOVAs for differences among habitat types

migrate from the pelagic areas to the nearshore and river mouth habitat in the spring.

Declines during 1999–2003

CPUE for bairdiella and tilapia declined between 1999 and 2002, while corvina showed a less clear pattern. Figure 7 shows CPUEs for all nearshore and river mouth stations that were monitored in late summer during at least two of the three years (1999, 2000, 2002). It also shows a dotted line representing mean CPUE calculated only for those four river mouth and nearshore stations monitored in each of the three years. For tilapia, this mean CPUE was 15.9 fish net^{-1} h^{-1} in 1999, 6.6 fish net^{-1} h^{-1} in 2000, and 0.025 fish net^{-1} h^{-1} in 2002. Tilapia appeared almost nonexistent at all stations sampled in August 2002. Nets were set at three nearshore and three river mouth stations for 3–1/2 h, but only four tilapia were caught. Local fisherman report that fishing for tilapia has been poor since 2001.

A similar decline was observed in bairdiella (Fig. 7). Mean late summer CPUE at the four stations was 4.7 fish net^{-1} h^{-1} in 1999, 6.3 fish net^{-1}h^{-1} in 2000, and 0.23 fish net^{-1} h^{-1} in 2002. Mean CPUE for orangemouth corvina at these stations was 0.080 fish net^{-1} h^{-1} in 1999, 0.0095 fish net^{-1} h^{-1} in 2000, and 0.024 fish net^{-1} h^{-1} in 2002. An exceptionally high CPUE in 1999 of 2.0 fish net^{-1}h^{-1} for the Alamo River mouth represented a catch of five fish in two nets set for 1 h.

Decline of bairdiella and tilapia during 2000–2003 was also strongly indicated by a decrease in

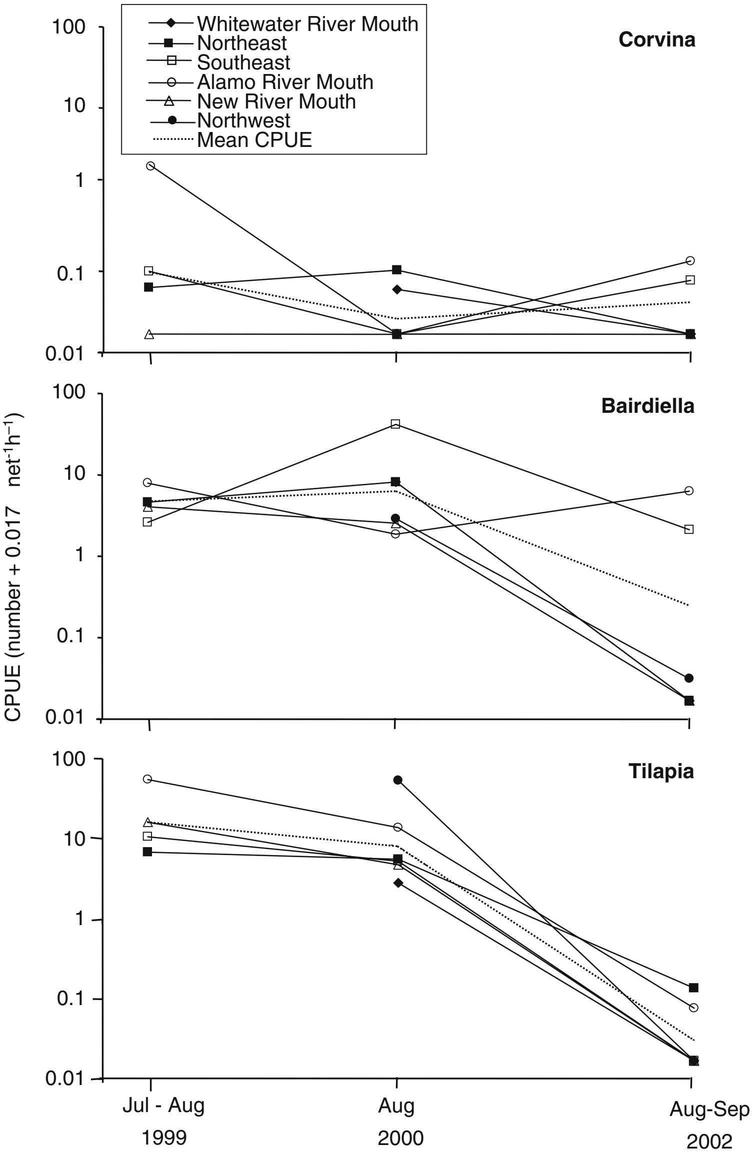

Fig. 7 Change in capture per unit effort in late summer for three species during the period 1999–2002. Geometric means connected by the dashed line are based only on those four stations (1, 5, 6, 7: Table 1) sampled in each of the three years

the frequency of major fish kills (Table 2; Hurlbert et al., 2005). During those years, Salton Sea Authority wildlife biologists Tahni Johnson and Tom Anderson (personal communication) made rough estimates of the numbers and sizes of fish in any kill of adult fish observed on the Sea. At least the larger numbers in Table 2 represent kills occurring on multiple dates and at multiple points in the lake. Forty-eight events were reported over the four years. If we assume the occurrence of those events was similar from one year to another, then these kill data may be taken as rough indices of how the actual population sizes of these species changed over this period. These fish kill data and the gillnetting CPUE data all suggest a shift from tilapia being the most abundant fish in the lake in 1999–2000 to bairdiella being the dominant species in 2002–2003.

Tilapia growth rate

The estimated VBGF suggests that Salton Sea tilapia grow fast. Although tilapia samples included only one year class for a majority of

Table 2 Estimated numbers of fish found dead in fish kills during 2000–2003 (data from T. Anderson, Salton Sea Authority, and Hurlbert et al., 2007)

Species	Year			
	2000	2001	2002	2003
Tilapia	13,922,200	9,113,020	74,910	12
Bairdiella	319,100	11,859,010	256,000	11,000
Orangemouth Corvina	1,200	24,800	2,150	600
Sargo	0	31,400	0	0

sampling periods, mean total length could be estimated directly for five age classes during the two-year sampling effort (Fig. 8). Mean total length was estimated for three-year-old tilapia over the first three sampling periods, for four-year-old tilapia over the next four sampling periods, and for five-year-old tilapia over the final three sampling periods. When fish were available, lengths from the 1996- and 1997-year classes were used to estimate length for the two-year-old-age class. Mean total length for the three-year-old 1995-year class may have been overestimated, because tilapia were sampled from the second half of its fourth year of growth. Similarly, mean total length may have been underestimated for the five year old 1995 age class that was only sampled for the first half of its sixth year of growth. The estimated VBGF parameters should be viewed with caution, as they are based primarily on the 1995 and 2000 year classes and may not accurately represent growth for the missing age or year classes.

Salton Sea tilapia grew fast when compared with *O. mossambicus* from other systems, as suggested by our estimate of the Brody growth coefficient (*K*) of 0.84 (Fig. 9). Using reported or calculated mean total length and age information in published reports, we estimated *K* values ranging between 0.31 and 0.93 for *O. mossambicus* populations in South Africa and Mozambique. Estimates of *K* for *O. mossambicus* from various other natural systems ranged from 0.20 to 0.64 (Riedel et al., 2002). Mean total length at age, as well as the growth coefficient, for tilapia from the Salton Sea were generally greater than those for tilapia in other systems. (This analysis of tilapia growth differs from a preliminary one (Riedel & Costa-Pierce, 2001; Riedel et al., 2002) that reported a lower value for *K* (0.54) but contained technical errors.)

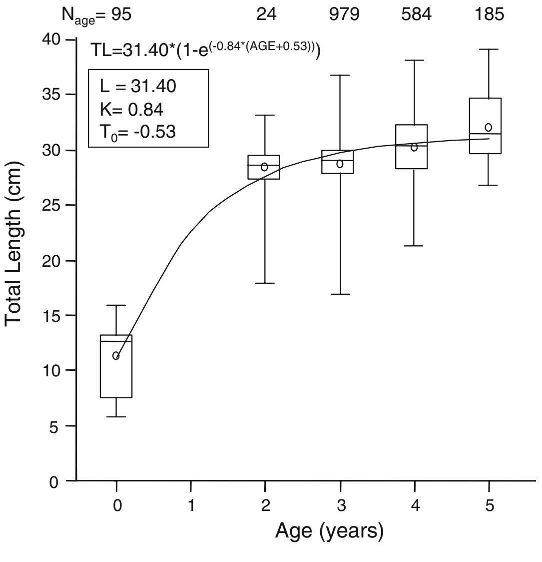

Fig. 8 The estimated VBGF and observed mean total length (TL) at age for tilapia collected over a two-year period. Shown are mean (O), median(-), bounds for the first and third quartiles and range

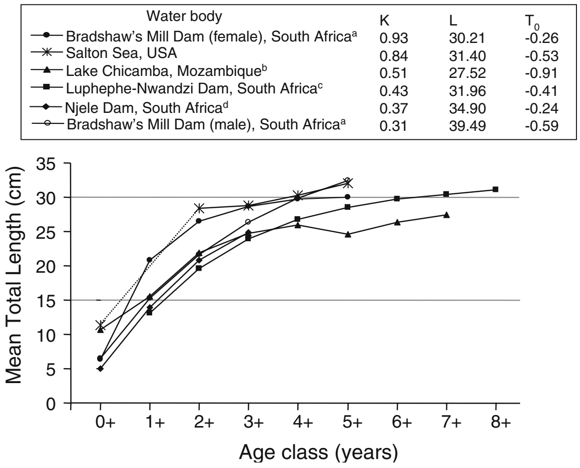

Fig. 9 Mean total length at age and estimated VBGF parameters for *O. mossambicus* from various natural systems. a. James, 1989; b. adapted from Weyl and Hecht, 1998; c. adapted from Hecht, 1980; d. adapted from LeRoux, 1961

Sex ratio

The tilapia sex ratio was consistently skewed toward males in most habitats and seasons (Fig. 10). A decline in the male to female ratio was observed in the nearshore, pelagic and river mouth habitats during the late spring, summer and early fall of 1999. At the river mouth and nearshore stations, males generally comprised 80–100% of the catch except in the late summer and fall. Males returned to dominance in winter or early spring in the river mouth and nearshore habitats except at one station in spring of 2000.

Pelagic stations reflected a dominance of males between February and June of 1999. Catches were generally too small to accurately calculate sex ratio during the summer months except at one station in August 1999. The August 1999 and April 2000 sampling periods yielded a largely female catch while the July and October 2000 sampling periods yielded equal numbers of the sexes.

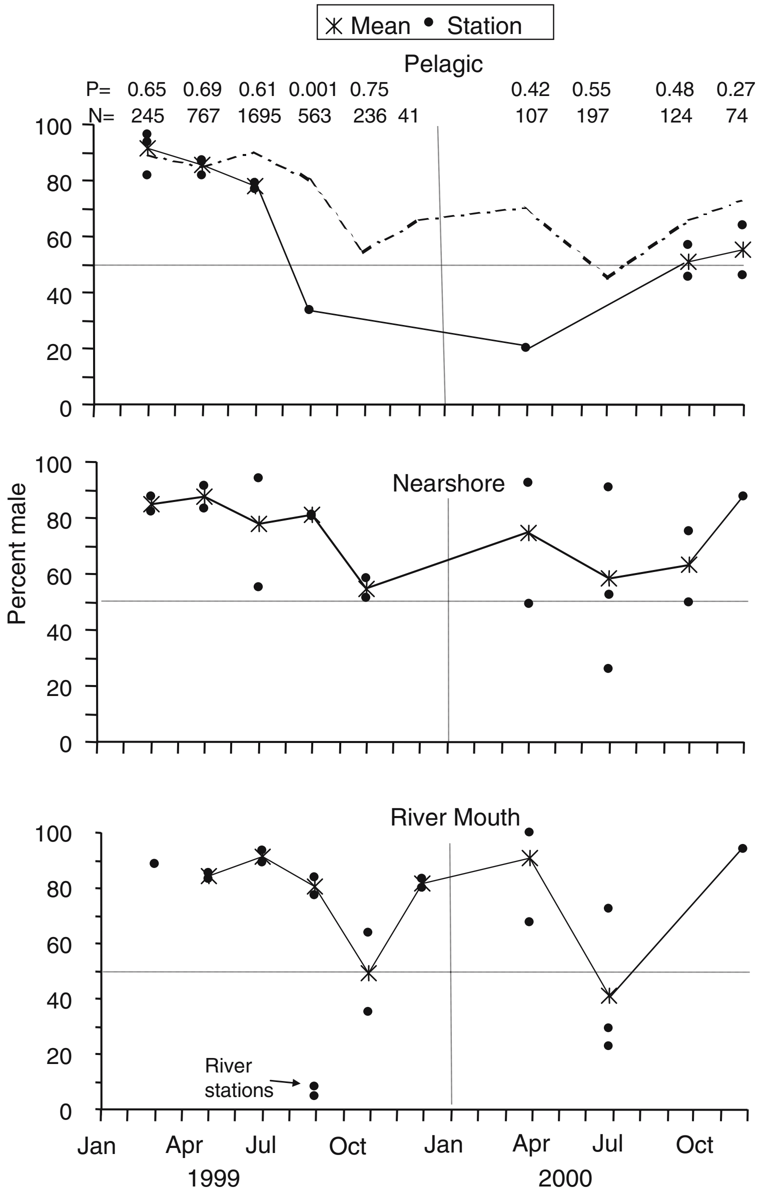

Fig. 10 Sex ratio (percent males) of tilapia caught by habitat type and sampling period. Absence of an X representing a mean indicates that there were data for only a single station on that date. The one set of data for the river stations is shown in the graph for river mouth stations. *P* values are from date-by-date one-way ANOVAs assessing differences among habitat types. Dashed line in the first panel represents sex ratio for total sexed catch (*N*), for all stations except river, on each date

River stations were sampled only in 1999, and these catches were generally too small (<5) to estimate sex ratio with any accuracy. In August 1999, in contrast to all other habitat types, females dominated in the rivers: sex ratios of 4.1 (n = 49) and 8.3 (n = 12) percent males were recorded for the New and Alamo river stations, respectively, yielding a mean of 6.3%. This was contrasted with the sex ratio of 80% males found off the river mouths and in nearshore stations on that date (Fig. 10).

Discussion

Although *O. mossambicus* is known for its ability to adapt to a wide variety of conditions (Noakes & Balon, 1982), the Salton Sea poses a special challenge as it is highly saline, experiences periodic anoxia, and has temperatures that approach the lower and upper lethal limits of this species. It is also a biotically challenging environment as large fluctuations occur in its food supplies (Detwiler et al., 2002; Tiffany et al., 2001, 2007) and as fry are heavily infested by microbial parasites (Kuperman & Matey, 1999; Kuperman et al., 2001, 2002). At least for the last 10 years, the tilapia population has suffered numerous recruitment failures and frequent mass mortalities of adults and has been characterized by narrow and unstable age distributions.

Spring migration to nearshore waters

The springtime abandonment of the open waters of the Sea by tilapia (and other species) and their crowding into nearshore waters may be spurred by a combination of poor water quality conditions, a decrease in food abundance, and breeding behavior. This phenomenon may enhance the tilapia sport fishery and access of fish-eating birds to this resource by creating higher densities of fish in shallow water, nearshore areas. The migration could also facilitate large scale commercial fishing operations if harvesting fish for phosphorus removal from the system (Gonzalez et al., 1998; Moreau et al., 2007) were initiated. Catch per unit effort would increase during the warmer months, and fishing operations would need to cover only a small portion of the Sea's total area. On the other hand, this vacating of the pelagic areas also may indicate that overall fish production is lower than it would be if fish and their prey were able to thrive over the entire Sea throughout the year.

We hypothesize that fish abandon the pelagic areas primarily in response to thermal stratification that is followed by a drop in oxygen levels and build-up of sulfide concentrations in deeper waters, and the first mixing events in spring that lower oxygen and increase sulfide levels throughout the water column. Thermal and chemical stratification develops and then breaks down repeatedly throughout the spring, summer and fall (Watts et al., 2001; Holdren & Montaño, 2002). Since sulfide is highly toxic, it may be the primary stimulus to movement. Bagarinao & Lantin-Olaguer (1998) found that *O. mossambicus* has low sulfide tolerances compared with marine fishes from saltmarsh habitats. They reported that *O. mossambicus* died in 3.2 mg l^{-1} total sulfide (i.e., H_2S and HS^-) in less than 24 h in seawater that was between 26°C and 30°C and contained more than 2 mg l^{-1} of oxygen. After one mixing event, Watts et al. (2001) reported that surface waters contained 0.5–1 mg l^{-1} of sulfide and that waters between 6 and 14 m depth contained 3–5 mg l^{-1}. Bagarinao & Lantin-Olaguer (1998) also found that high sulfide levels exacerbated the effects of hypoxia.

The first phase of this migration may occur when loss of oxygen and accumulation of sulfide in deeper waters drive tilapia toward the surface. Between February and April 1999, tilapia catches increased in surface nets in the pelagic region at the same time they decreased in bottom nets in that region (Figs. 5, 6). Then, as the first moderate mixing event brings significant amounts of sulfide into pelagic surface waters, fish are either killed or driven from these areas of the lake toward its periphery. Thus, prior to June 1999, tilapia catches in both surface and bottom nets in the pelagic region were in decline.

Shallow water areas, especially those <2–3 m deep at the northern and southern ends of the lake (Fig. 1 in Watts et al., 2001), that are distant from deeper (e.g. >8 m) parts of the lake, offer partial refuge because there is little opportunity for sulfide to build up or oxygen to become severely depleted in their shallow water columns. When a strong warm season mixing event occurs, water quality in those shallow water areas will remain high, unless there is significant advection into them of water masses from the central part of the lake. Such advection is likely to be involved in the large, warm season fish kills that have occurred well after fish are already concentrated in nearshore areas. This phenomenon may not be unique to the Salton Sea. Morgan (1972) reported large-scale dieoffs of *Tilapia shirana chilwae* in Lake Chilwa due to deoxygenation of the water column after strong wind events.

The food supply of tilapia is affected by water quality factors and may have directly contributed to abandonment by tilapia of the pelagic region. In the Salton Sea, adult tilapia feed on adult polychaete worms (*Neanthes succinea* Frey & Leuckart), copepods, rotifers and larvae of *N. succinea* and the barnacle *Balanus amphitrite* Darwin (R. Riedel, unpubl. data), as well as detritus and larger phytoplankters. Abundance of adult polychaetes in sediments peaks in March, and shortly thereafter they are almost absent from most of the lake bottom at depths >2 m until the following winter (Detwiler et al., 2002). Additionally, there are massive, periodic declines (>90%, on biomass basis) in the pelagic region of both phytoplankton and zooplankton as a consequence of mixing events in the summer and fall, but such declines seem less frequent or severe at shallow water (4–5 m) stations (Tiffany et al., 2007). In 1999, there was some indication of fish returning to bottom waters, but not surface waters, of the pelagic zone by October (Figs. 5, 6). This might suggest their use of organic detritus accumulated over the summer, for it is unlikely that the polychaete achieves any significant recolonization of deep-water sediments by that time.

The breeding behavior of tilapia may have also stimulated their springtime migration from the pelagic region to shallow nearshore waters. *O. mossambicus* have been observed to migrate to nearshore areas prior to breeding in several African systems (Bruton & Boltt, 1975; James & Bruton, 1992; Cochrane, 1986a). Male *O. mossambicus* are reported to move into shallow water 30–100 cm deep to build nests into which females will deposit their eggs (Bruton & Boltt, 1975). During 1999 and 2000, nesting tilapia were abundant in harbors and inlets around the edge of the Sea, and successful reproduction was confirmed by the later observation of large numbers of tilapia fry and juveniles schooling in shallow waters.

Much remains to be learned, however, about tilapia reproduction in the Salton Sea, including the depth at which they nest. The dark, turbid (Secchi disc depth usually 0.5–1.5 m), zero visibility waters of the Salton Sea render visual inspection and photography of the lake bottom impossible. In early January 1999, however, side scanning sonar inspection of the bottom of the Salton Sea was carried out by the U.S. Navy, as part of a search operation for a small private aircraft that crashed into the Sea on December 25, 1998. But at a depth of 12 m about 4 km southwest of Varner Harbor (Salton Sea State Recreation Area headquarters), it was another plane that was found (Fig. 11). During World War II, the Salton Sea was a training area for pilots of Grumman Avenger torpedo bombers, 10 of which crashed in or near the Salton Sea (Perry, 1999). The Avenger shown here is relatively intact and is surrounded by shallow pits we estimate to be of ca. 80–100 cm in diameter, given that the width of the horizontal stabilizer (lateral tail fin) of an Avenger at its junction with the fuselage is about 1.3 m (Larry Gregory, Lone Star Flight

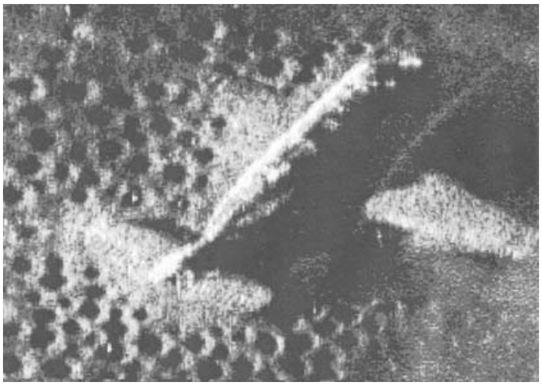

Fig. 11 Side scanning sonar image of a Grumman Avenger torpedo bomber on bottom of Salton Sea, at 12 m depth, surrounded by pits presumed to have been constructed by tilapia. Courtesy U.S. Navy and Riverside County Sheriffs Department

Museum, Galveston, Texas, pers. comm.). We cannot conceive that these pits are constructed by any organism other than tilapia, but clearly anoxia and hydrogen sulfide levels at these depths would prevent fish from utilizing them for reproduction during spring, summer and fall under present lake conditions, and there are no records of *O. mossambicus* nesting at such depths in other lakes. Could tilapia construct such pits to overwinter in them, in a torpid non-feeding state, when these deep waters are unstratified and relatively oxygen-rich? At 12 m, the bottom experiences little disturbance by water movement, and almost no sediment is delivered to this basin by stream flows. Thus, it is possible that these pits are many years old.

Unusual dominance of males

Although the sex ratio for tilapia populations can vary widely, the Salton Sea appears to be an example of a male dominated system. In a review of numerous studies, Bluhdorn & Arthrington (1990) generally found males to constitute between 30 and 69% of *O. mossambicus* populations. In contrast, total catches per sampling date at the Salton Sea (excluding river stations) ranged from 45 to 90% male (Fig. 10), with the total catches for 1999 and 2000 having sex rations of 83% and 60% males respectively. The most likely cause of this male dominance is the genetic background of Salton Sea tilapia. Hickling (1960) reported that crossing male *O. urolepis hornorum* with female *O. mossambicus* produced 89–99% male broods, whereas reverse crosses produced 70–80% male broods. Costa-Pierce & Doyle (1997) reported that Salton Sea tilapia were likely a hybrid of one of these types or a mixture of the two.

Other factors might include temperature and differences in survivorship or behavior of the sexes. High temperature has been documented to favor production of males in various species of tilapia, including *O. mossambicus*, and the Salton Sea is unusually warm in the summer. Temperatures of 28–32°C during the larval phase of *O. mossambicus* encouraged the development of male reproductive organs while temperatures as low as 20°C increased the likelihood of female reproductive organs (Wang & Tsai, 2000). Baras et al. (2000) reported ratios of 87–93% males for larval *O. aureus* subjected to constant temperatures of 35°C. Temperatures that fluctuated between 35 and 27°C on a diurnal cycle produced populations that were 50–87% male. Mean mid-lake water column temperatures at the Salton Sea during the early life history of tilapia ranged from 22 to 34°C (Watts et al., 2001); however, temperatures as high as 40°C occur during the day in shallow waters of the Salton Sea, where tilapia nests and fry often abound (Kuperman & Matey, 1999).

Sex differences in survival rates or behavior are another possibility. As a result of their greater allocation of energy to gametes, mature females may have lower age-specific survival rates than do males. Such a sex differential could be amplified by the harsh conditions in the Salton Sea. Most of the fish caught in this study were 4 or 5 years old. Even a slightly different annual survival rate, compounded over 3–4 years, could cause a large shift in sex ratio from whatever it was at the fry stage. Finally, differences in catchability due to a sex differential in swimming activity or response to contact with nets could also have influenced sex ratios of catches.

Erratic annual production

During the late 1990s, it was the universal impression of fishermen, scientists and other visitors to the Salton Sea that the fish populations, and especially the tilapia population, were in excellent condition. Claims that this was one of the world's most productive fisheries were quoted often in the popular press. A hasty appraisal of our 1999 data even led us to suggest that tilapia productivity or annual yield in the ''nearshore region'' would be about 3,600 kg ha^{-1} year^{-1} (Costa-Pierce & Riedel, 2000). That estimate was based on an unrealistic assumption. The assumption was that there would be no decline in catch per unit effort over time if fishing operations expanded from eight nets set six times a year for 4 h each (roughly our sampling regime for the nearshore region) to 9,800 nets (assuming nearshore region represents about 10% of the Sea's area) set 150 times a year for 4 h each. Such a 30,625-fold increase in fishing intensity would likely cause almost immediate declines in catch per unit effort.

We also assumed that tilapia were successfully reproducing and recruiting to the fishery. Tilapia were abundant in the late 1990s. But that abundance was solely a result of the high success of the 1995-year class. High individual growth rates led to large fish. Production of large numbers of young in 1995 and/or exceptionally high survival of those young during their first year made the Salton Sea tilapia fishery seem healthy. The health of the tilapia fishery was better indicated by the small or non-existent year classes of 1996, 1997, 1998, 1999, and, probably, 1994. There was some recruitment from the 2000-year class, but it was small relative to the earlier recruitment of the 1995-year class. In most recent years, tilapia seems to have experienced massive recruitment failure. In 1998 and 1999, high densities of tilapia fry were observed frequently during the warm months in shallow waters around the edge of the Sea. Essentially no trace of those year classes appeared in our nets in 1999, 2000 or 2002. Hence, we conclude that it is failure to survive their first six months or year, and not reproductive failure per se, that is primarily responsible for the decline of the tilapia population. Between 1999 and 2002, our best estimate is that the population declined by 99.9% (Fig. 7). At the time of this writing (August 2004) there is some indication that a large 2004-year class has been produced (T. Anderson, Salton Sea Authority, and J. Crayon, Calif. Dept. of Fish and Game, pers. comm.).

The apparent massive mortality of tilapia fry and juveniles could be caused by many factors. The success of a year class like that of 1995 requires that all potential lethal factors not be present in serious degree. When salinity of the Salton Sea was less than 90% of what it is now, Black (1988) attributed declines in CPUE of Salton Sea tilapia to periods of cold weather. The salinity of the Sea is now even further above the optimum for tilapia, which renders at least tilapia juveniles more susceptible to the effects of low temperature. In tolerance experiments, 86% of hybrid *O. mossambicus* × *O. urolepis hornorum* juveniles died within 24 h at a salinity of 43 g l^{-1} at 15°C, which is the average water temperature during the coldest part of winter at the Salton Sea; however, no juveniles kept at 43 g l^{-1} and 25°C died (Sardella et al., 2004). Recruitment could fail if temperatures remain near the lethal minimum of *O. mossambicus* for long (Cochrane, 1986b; Le Roux, 1961). Cochrane (1986b) found that cold-induced mortality could eliminate entire year classes of young-of-the-year *O. mossambicus* in Hartesbeesport Dam, South Africa.

Mixing events during the warm half of the year can kill both juvenile and adult fish in massive numbers over large areas. The probable cause of adult fish kills reported in Table 2 was in most cases a combination of low oxygen and high sulfide concentrations throughout the water column produced by wind-induced mixing events (Watts et al., 2001). Although *O. mossambicus* are known to survive in waters with high salinity and low dissolved oxygen (e.g., Popper & Lichatowich, 1975; Hecht & Zway, 1984; Wokoma & Marioghae, 1996), the combination of these with the additional stressors of sulfide and high water temperature may cause the probability of survival to first winter to be exceptionally low.

Parasites, predators and competitors could have also reduced recruitment. Infestations of tilapia fry with the ectoparasitic dinoflagellate *Amyloodinium ocellatum*, ciliate *Ambiphrya ameiuri*, and flagellate *Cryptobia branchialis* have been documented at the Salton Sea and suggested to play a possibly major role in tilapia population dynamics (Kuperman & Matey, 1999; Kuperman et al., 2001, 2002). *A. ocellatum*, in particular, is known for causing high mortalities in aquaria and aquaculture facilities and prefers warm, high salinity water. *A. ocellatum* heavily infested the gills and fins of small tilapia between June and September in 1997 and 1998. By damaging or covering respiratory surfaces, such ectoparasites exacerbate the effects of other factors that reduce oxygen availability to the fish.

Bairdiella and large tilapia were observed to have tilapia fry in their stomachs on occasion. During periods of scarce plankton and benthos and high nearshore concentrations of fishes, large tilapia and other fishes may prey heavily on smaller tilapia. Competition resulting from dietary overlap between tilapia juveniles and other fish, including tilapia adults, also may have contributed to low recruitment through both starvation and increases in vulnerability to predation.

Conclusion

Earlier, we had suggested that ‘‘the gradual rise in salinity over the years in the Salton Sea might have led to the rapid adaptation of tilapia’’ to it (Riedel et al., 2002). If natural selection has achieved some increased tolerance to high salinities—and there is no evidence of this—it has done little to guarantee the viability of this population in the face of a continued rise in salinity and numerous other stress factors. Recruitment has been zero or nearly so during the most recent years, and the only recent moderately successful year class, that of 1995, has now died out. Other fish populations present have also crashed, as have the numbers of fishermen and fish-eating birds at the Sea. This has happened before, but it should be regarded as an episodic rather than a cyclic phenomenon. Permanent recoveries seem unlikely until there is a stabilization of salinity at a lower level, one perhaps close to that of ocean water.

During the past century, the Salton Sea has provided an important source of food for fish-eating birds residing in or migrating through southern California. Many of the wetlands along the California coast or in its Central Valley that had supported fish-eating birds prior to the formation of the Salton Sea have been ‘developed’ or degraded by man. The permanent loss of the Salton Sea fishery would have large impacts on resident and non-resident birds. Some have suggested that despite the bounty that tilapia has provided to birds and fishermen, the Salton Sea is better off without tilapia. After all, dieoffs foul beaches with thousands or millions of dead fish, and sick fish can transmit botulism to fish-eating birds, including the federally endangered brown pelican. But we should not blame the canary for the mine. An exotic species in an accidental lake, the Salton Sea tilapia have, on balance, benefited both people and wildlife.

Acknowledgements The authors thank J. Wagner for his knowledge and skills in vessel operation and ageing otoliths; the staff of the Southwest Fisheries Science Center in La Jolla, California, particularly J. Hunter, L. Robertson, J. Wexler, D. Fuller and B. Macewicz for the use of their facilities and expertise; and J. Watts, B. Swan, K. Reifel, M.F. Moreau, J.S. Dainer, M.A. Tiffany, and S. Horowitz for their expertise and assistance. Our research has been funded in part by the United States Environmental Protection Agency through grant no. R826552-01-0 to the Salton Sea Authority. The research results have not been subjected to the EPA’s peer review and therefore do not necessarily reflect the view of the Agency. Therefore, no official endorsement should be inferred.

References

Bagarinao, T. & I. Lantin-Olaguer, 1998. The sulfide tolerance of milkfish and tilapia in relation to fish kills in farms and natural waters in the Philippines. Hydrobiologia 382: 137–150.

Baras, E., C. Prignon, G. Gohounga & C. Melard, 2000. Phenotypic sex differentiation of blue tilapia under constant and fluctuating thermal regimes and its adaptive and evolutionary implications. Journal of Fish Biology 57: 210–223.

Barnes, J. T. & T. J. Foreman, 1994. Recent evidence for the formation of annual growth increments in the otoliths of young Pacific sardines (*Sardinops gigax*). California Fish and Game 80: 29–35

Black, G., 1988. Description of the Salton Sea Sport Fishery, 1982–1983. Inland fisheries Administrative Report, Number 88-9. Editor, Arthur C. Knutson, Jr., Inland Fisheries Division, Sacramento, California.

Bluhdorn, D. R. & A. H. Arthington, 1990. Somatic characteristics of an Australian population of *Oreochromis mossambicus* (Pisces: Cichlidae). Environmental Biology of Fishes 29: 277–291.

Bowen, S., 1980. Detrital nonprotein amino acids are the key to rapid growth of *Tilapia* in Lake Valencia, Venezuela. Science 207: 1216–1218.

Bruton, M. N. & R. E. Boltt, 1975. Aspects of the biology of *Tilapia mossambica* Peters (Pisces: Cichlidae) in a natural freshwater lake (Lake Sibaya, South Africa). Journal of Fish Biology 7: 423–445.

Caskey, L. L., 2002. Ecology of tilapia (*Oreochromis mossambicus*) in the Salton Sea, California. Master’s thesis, San Diego State University, 259 pp.

Cochrane, K. L., 1986a. Distribution of the three major species of fish in the Hartbeespoort Dam in relation to some environmental factors. South African Journal of Zoology 21: 177–182.

Cochrane, K. L., 1986b. Mortality of young-of-the-year *Oreochromis mossambicus* in Hartebeespoort Dam, South Africa. Journal of Fish Biology 29: 623–630.

Cohen, M., J. I. Morrison & E. P. Glenn, 1999. Haven or Hazard: The ecology and future of the Salton Sea. Pacific Institute for Studies in Development, Environment, and Security, California, USA, 63 pp.

Costa Pierce, B. & R. W. Doyle, 1997. Genetic identification and status of tilapia regional strains in southern California. In Costa-Pierce B. A. & J. E. Rakocy (eds), Tilapia Aquaculture in the Americas, Volume 1. World Aquaculture Society, Baton Rouge, Louisiana, 1–17.

Costa Pierce, B. & R. Riedel, 2000. Fisheries ecology of the tilapias in subtropical lakes of the United States. In Costa-Pierce B. A. & J. E. Rakocy (eds), Tilapia Aquaculture in the Americas, Volume 2. The World Aquaculture Society, Baton Rouge, Louisiana, 1–20.

Detwiler, P. M., M. F. Coe & D. M. Dexter, 2002. The benthic invertebrates of the Salton Sea: distribution and seasonal dynamics. Hydrobiologia 473: 139–160.

Friend, M., 2002. Avian disease at the Salton Sea. Hydrobiologia 473: 293–306.

González, M. R., C. M. Hart, J. Verfaillie & S. H. Hurlbert, 1998. Salinity and fish effects on Salton Sea microecosystems: water chemistry and nutrient cycling. Hydrobiologia 381: 105–128.

Hart, C. M., M. R. Gonzalez, E. P. Simpson & S. H. Hurlbert, 1998. Salinity and fish effects on Salton Sea microecosystems: zooplankton and nekton. Hydrobiologia 381: 129–152.

Hecht, T., 1980. A comparison of the otolith and scale methods of ageing and the growth of *S. mossambicus* (Pisces: Cichlidae) in a Venda impoundment (Southern Africa). South African Journal of Zoology 15: 222–228.

Hecht, T. & P. Zway, 1984. On the stunted Mozambique tilapia, *Oreochromis mossambicus* (Peters, 1852) (Pisces: Cichlidae) of the Matiovila Hot Spring, Kruger National Park. Koedoe 27: 25–38.

Hickling, C. F., 1960. The Malacca tilapia hybrids. Journal of Genetics 57: 1–10.

Holdren, G. C. & A. Montaño, 2002. Chemical and physical characteristics of the Salton Sea, California. Hydrobiologia 473: 1–21.

Hurlbert, A. H., K. Sturm, T. Anderson & S. H. Hurlbert, 2007. Fish and fish-eating birds at the Salton Sea: a century of boom and bust. Hydrobiologia (under review).

James, N. P. E. & M. N. Bruton, 1992. Alternative life-history traits associated with reproduction in *Oreochromis mossambicus* (Pisces: Cichlidae) in small water bodies of the eastern Cape, South Africa. Environmental Biology of Fishes 34: 379–392.

Kuperman, B. I. & V. E. Matey, 1999. Massive infestation by *Amyloodinium ocellatum* (Dinoflagellida) of fish in a highly saline lake, Salton Sea, California, USA. Diseases of Aquatic Organisms 39: 65–73.

Kuperman, B. I., V. E. Matey & S. B. Barlow, 2002. Flagellate *Cryptobia branchialis* (Bodonida: Kinetoplastida) ectoparasite of tilapia from the Salton Sea. Hydrobiologia 473: 93–102.

Kuperman, B. I., V. E. Matey & S. H. Hurlbert, 2001. Parasites of fish from the Salton Sea, California, USA. Hydrobiologia 466: 195–208.

Le Roux, P. J., 1961. Growth of *Tilapia mossambicus* (Peters) in some Transvaal Impoundments. Hydrobiologia 18: 165–175.

Maitipe, P. & S. S. DeSilva, 1985. Switches between zoophagy, phytophagy and detritivory of *Sarotherodon mossambicus* (Peters) populations in 12 man-made Sri Lankan lakes. Journal of Fish Biology 26: 49–61.

Moreau, M. F., J. Surico-Bennett, M. Vicario-Fisher, D. Crane, R. Gerards, R. M. Gersberg, S. H. Hurlbert, 2007. Contaminants in tilapia *(Oreochromis mossambicus)* from the Salton Sea, California, in relation to human health, piscivorous birds and fish meal production. Hydrobiologia 576:127–165.

Morgan, P., 1972. Causes of mortality in the endemic tilapia of Lake Chilwa (Malawi). Hydrobiologia 40: 101–119.

Noakes, D. L. G., E. K. Balon, 1982. Life histories of tilapias: an evolutionary perspective, pp. 61–82. In Pullin R. S. V. & R. H. Lowe-McConnell (eds), The Biology and Culture of Tilapias. ICLARM Conference Proceedings 7. International Center for Living Aquatic Resources Management, Manila, Philippines, 432 pp.

Perry, T., 1999. Divers examine wreck of plane in Salton Sea. The Los Angeles Times, Los Angeles, California, June 15, 1999.

Popper, D. & T. Lichatowich, 1975. Preliminary success in predator control of *Tilapia mossambica*. Aquaculture 5: 213–214.

Riedel, R. & B. Costa-Pierce, 2001. Review of the fisheries of the Salton Sea, California, USA: past, present and future. Hydrobiologia 9: 239–270.

Riedel, R., L. Caskey & B. A. Costa-Pierce, 2002. Fish biology and fisheries ecology of the Salton Sea, California. Hydrobiologia 473: 229–244.

Riedel, R., L. Helvenston & B. Costa-Pierce, 2001. Fish biology and fisheries ecology of the Salton Sea. Final Report May 1, 2001. Salton Sea Authority, Department of Interior.

Sardella, B. A., J. Cooper, R. Gonzalez & C. J. Brauner, 2004. The effect of temperature on the salinity tolerance of juvenile Mozambique tilapia hybrids (*Oreochromis mossambicus* × O. *urolepis hornorum*). Comparative Biochemistry and Physiology A137: 621–629.

Simpson, E. P., M. R. González, C. M. Hart & S. H. Hurlbert, 1998. Salinity effects on Salton Sea microecosystems: benthos. Hydrobiologia 381: 153–177.

St. Amant, J., 1966. Addition of *Tilapia mossambica* Peters to the California fauna. California Fish and Game Bulletin 52: 54–55.

Tiffany, M. A., B. K. Swan, J. M. Watts & S. H. Hurlbert, 2001. Metazooplankton dynamics in the Salton Sea, 1997–1999. Hydrobiologia 473: 103–120.

Tiffany, M. A., M. R. González, B. K. Swan, S. H. Hurlbert, 2007. Phytoplankton dynamics in the Salton Sea, California, 1997–1999. Hydrobiologia (under review).

Walker, B. W., 1961. The ecology of the Salton Sea, California, in relation to the sportfishery. California Department of Fish and Game, Fish Bulletin 113: 1–203.

Wang , Li-Hsueh & C. Tsai, 2000. Effects of temperature on the deformity and sex differentiation of tilapia, *Oreochromis mossambicus*. Journal of Experimental Zoology 286: 534–537.

Watts, J. M., B. K. Swan, M. A. Tiffany & S. H. Hurlbert, 2001. Thermal mixing, and oxygen regimes of the Salton Sea, California. Hydrobiologia 466: 159–176.

Weyl, O. L. F. & T. Hecht, 1998. The biology of *Tilapia rendalii* and *Oreochromis mossambicus* (Pisces: Cichlidae) in a subtropical lake in Mozambique. South African Journal of Zoology 33: 178–188.

Wokoma, K., I. E. Marioghae, 1996. Survival of *Tilapia guineensis* under conditions of low dissolved oxygen and low pH, pp. 442–448. In R. S. V. Pullin, J. Lazard, M. Legendre, J. B. Amon Kothias & D. Pauly (eds), The Third International Symposium on Tilapia in Aquaculture, ICLARM Conference Proceedings 41, 575 pp.