

Length-weight relations and growth rates of dominant fishes of the Salton Sea: implications for predation by fish-eating birds

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Abstract

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The Salton Sea is the largest lake in California. Inflows are primarily from agricultural runoff, which render it eutrophic and able to support extensive fisheries. The lake and its surrounding wetlands are critical links for the Pacific Flyway, providing refuge and food for an extensive and diverse avifauna. We document fish size distributions, body shapes and growth rates and consider how they determine availability of fish to birds. Tilapia (*Oreochromis mossambicus* x *O. urolepis hornorum*) is the most important resource for fish-eating birds. Tilapia grow fast to a size that is readily handled by large birds and are the most abundant fish in the lake. Bairdiella (*Bairdiella icistia*) grow to a smaller size over a longer period. Corvina (*Cynoscion xanthurus*), sargo (*Anisotremus davidsoni*), and shad (*Dorosoma cepedianum*) are less important for fish-eating birds because they quickly grow to sizes outside bird handling capabilities (corvina) or are not readily catchable and currently of low abundance (shad and sargo). Shape, in particular girth, determines the weight of the largest individual fish that a bird can handle; a slender 1,000 g corvina, for example, being more easily ingested than a deeper-bodied 1,000 g tilapia. Shape, however, is of secondary importance to growth rate in determining importance of a fish species in a bird's diet. Predation by corvina on tilapia and other smaller species may have historically played a large role in determining availability of fish to fish-eating birds.

Key words: length-weight relations, tilapia, bairdiella, corvina, sargo, shad, *Oreochromis mossambicus*, *Bairdiella icistia*, *Cynoscion xanthurus*, *Anisotremus davidsoni*, *Dorosoma petenense*, Sciaenidae, pelicans, cormorants

Introduction

The Salton Sea is a 980 km² artificial salt lake in the Colorado Desert of southern California. It was created by heavy Colorado River flows in 1905, which broke through irrigation headworks that diverted water from the Colorado River into the Imperial Valley of California. The River flowed unimpeded for almost 2 years filling the Salton Sink, an ancient, below sea level basin, and created, in a hot, alkaline desert, California's largest lake.

Over 30 species of marine fish were introduced from 1950–56 into the Salton Sea from Mexico's Gulf of California (Walker *et al.* 1961). Of these, only the orangemouth corvina (*Cynoscion xanthurus* Jordan and Gilbert), bairdiella (*Bairdiella icistia* Jordan and Gilbert) and sargo (*Anisotremus davidsoni*

Steindachner) established and flourished. Threadfin shad (*Dorosoma petenense* (Gunther)) persisted in smaller numbers. In 1964–65, tilapia (*Oreochromis mossambicus* Peters x *O. urolepis hornorum* (Trewavas)) escaped to the Sea and by the early 1970s dominated the fish community as salinity rose above seawater levels (Dill and Cordone 1997). Various invertebrates and algae were also introduced to the Salton Sea with these fishes. Barnacles (*Balanus amphitrite*, Linnaeus) occur on solid substrates along the shores of the Sea, and pile worms (*Neanthes succinea* Frey and Leukart) dominate the invertebrate community in sediments (Setmire *et al.* 1993; Simpson and Hurlbert 1998; Simpson *et al.* 1998; Detwiler *et al.* 2002; Dexter *et al.* 2007). Dense phyto- and zooplankton plankton assemblages occur throughout the year (Tiffany *et al.* 2002, 2007; Reifel *et al.* 2007).

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The Salton Sea is designated by the State of California as a repository for nutrient-rich drainage waters from hundreds of commercial farms in the Imperial and Coachella valleys. As a result, it has high primary productivity, which in turn accounts for the high productivity of its fishery (Black 1974, 1988). In 1971, the California Department of Fish and Game recorded recreational fish catches at the Salton Sea at 1.88 fish/angler/h, one of the highest catch rates recorded in the State (CDFG 1971).

Due to an abundant food supply and the destruction of over 90% of California's original wetlands, millions of birds depend on the Salton Sea. It is a critical wetland habitat of the Pacific flyway for migratory species (Jehl 1994; Shuford *et al.* 2002; Hurlbert *et al.* 2007) and is becoming increasingly important in face of the continuing degradation of wetlands in the western United States (Dahl 2000).

Nineteen bird species depend on the Salton Sea's fish as food, from small terns to large herons and pelicans, including the endangered brown pelican (*Pelecanus occidentalis carolinensis*, Linnaeus) (Shuford *et al.* 2002). There has been a strong link between the dynamics of fish biomass and the numbers of breeding and wintering fish-eating birds over the last half century (Hurlbert *et al.* 2007). Fish populations at the Salton Sea have declined dramatically since 2000, the marine species apparently having disappeared and the tilapia population resurging somewhat in 2005-2006 (Caskey *et al.* 2007; J. Crayon, pers. comm.). These crashes could be exacerbating the detrimental effects many bird species are experiencing due to loss of suitable habitat in other parts of their range.

Fish declines at the Salton Sea have been attributed to reproductive failures, high larval mortalities, and the extensive adult fish kills. Proximal factors for the declines include rising salinity of the Sea, currently at 45 g L⁻¹ (Sardella *et al.* 2004, 2007), diseases (Friend 2002; Nol *et al.* 2004; Roche *et al.* 2004), parasites and ectosymbionts (Kuperman and Matey 1999; Kuperman *et al.* 2001, 2002), episodes of cold weather, and deoxygenation and sulfide events during the warm season (Watts *et al.* 2001; Riedel *et al.* 2002; Caskey *et al.* 2007). Those factors have also been associated with extensive deaths of tilapia between 1999 and 2000, and deaths of over 200,000 migratory water birds (Jehl 1996; Kaiser 1999; Caskey *et al.* 2007; Anderson *et al.* 2007).

As fish abundance declines, fish species that remain available longer within a size range suitable to bird handling become more important to the health of bird populations. In such a volatile fishery the size-frequency distributions of fish change markedly over time. Species- and age-specific behavior, such as swimming speed, schooling, and depth preferences also influence availability to fish-eating birds. With 5 species of fish and 19 species of fish-eating birds, full analysis of interactions between fish and fish-eating birds at the Salton

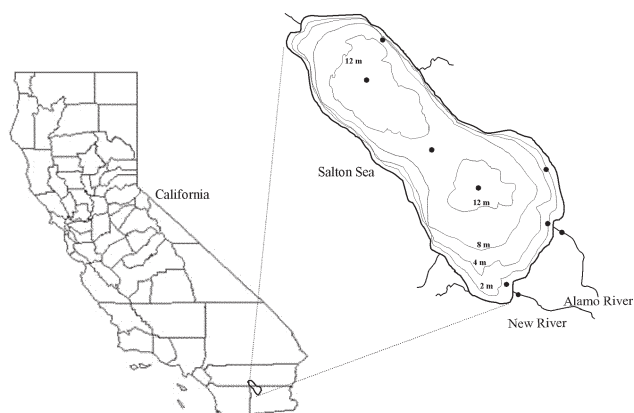


Figure 1.—Station locations for fisheries samplings at the Salton Sea.

Sea would be a large project. The objectives of the present study are to document body shape and growth rate differences among the 5 fish species and to assess the implications of those characteristics for fish-eating birds.

Methods

Salton Sea fish were sampled in 1999 and 2000 using multi-panel gill nets at twelve stations (Fig. 1; Riedel *et al.* 2002; Caskey *et al.* 2007) covering rivers (1999 only), nearshore, pelagic, and estuarine areas. Multipanel gill nets were chosen to enable sampling of all fish sizes present (Lagler 1978; Lott and Willis 1991; Hubert 1996). Gill nets consisted of five 10 m long × 2 m deep twisted nylon panels of 1, 2, 7, 10, and 12.5 cm stretched mesh sizes. Fish were weighed to the nearest gram and total length measured to the nearest millimeter.

Samples from 1999 and 2000 for the five most common species were used to investigate their length-weight (L-W) relations as an indicator of body allometry and their age-length relationships as an indicator of growth. We investigated these relations for bairdiella, corvina, sargo, and tilapia. As we did not age shad, we only investigated L-W relations for that species. Additionally, L-W relations were investigated by sex. Because we were unable to distinguish sex of individual tilapia smaller than 10 millimeters, we included the same data for juvenile tilapia in analyses of L-W relations for both sexes.

We also used data from bairdiella and corvina collected in 2002 (Caskey *et al.* 2007) to compare the body condition of the recent population with that from 1999 and 2000. For bairdiella, we compared length and weight estimates from the L-W models between the population in 1999 and 2000, and that from 2002. We did not separate body condition analysis into gender because fish sampled from the popula-

Table 1.-Abundance, growth and shape characteristics of dominant fish species of the Salton Sea. Weights given in last columns are those predicted by the respective L-W power functions.

Species and Sex	Sample Size	Model Parameters		Weight Range (g)	Length Range (cm)	Weight (g) at		
		α	β			10 cm	20 cm	30 cm
Bairdiella (1999-2000)								
male	2,624	0.014	2.927	6.4-459	8.5-32.2	11.4	87.1	285
female	2,164	0.012	2.942	5.9-370	8.0-33.0	10.9	83.5	275
Bairdiella (2002)	52	0.012	2.979	8.4-240	8.8-27.9	11.6	91.1	305
Corvina								
male	153	0.011	2.966	94.7-5,920	23.3-83.0	9.8	76.7	255
female	150	0.004	3.183	56.7-6800	18.1-88.5	6.7	60.9	221
Sargo								
male	54	0.015	3.040	38.1-443	13.2-30.5	16.0	132	451
female	34	0.014	3.075	35.4-579	13.6-32.3	16.2	136	474
Shad								
male	52	0.015	2.829	4.9-78.1	7.6-19.1	10.3	73.3	231
female	68	0.025	2.684	37.7-94.8	14.9-22.4	12.3	79.0	235
Tilapia								
male	3,911	0.019	2.942	0.4-1045	3.2-40.4	16.5	127.0	419
female	969	0.018	2.993	0.4-800	3.2-34.0	18.0	143.2	482
juvenile	11	-	-	-	-	-	-	-

tion of 2002 were not sexed. Because only four corvina, all of similar size, were sampled during 2002, we were unable to produce a L-W relationship model for that population. Therefore we only provided a graphic showing condition of individuals in the 2002 corvina population relative to that of individuals in the 1999-2000 population.

To assess allometry, we examined the fit of the linear form of the L-W relation power function (Peters 1983; Calder 1984; Reiss 1989). The power function is of the form

$$W = \alpha L^\beta \tag{1}$$

where α is the intercept parameter or shape coefficient and β is the allometric parameter.

The linearized equation of (1) is of the form

$$\ln(W) = \ln(\alpha) + \beta \ln(L) \tag{2}$$

Parameter estimates and fit of (2) was done with ordinary least squares regression. To assess growth, we used the von

Bertalanffy growth function (VBGF), which describes the growth of fish over their lifespan. The VBGF has the form

$$L_t = L_\infty [1 - e^{-k(t-t_0)}] \tag{3}$$

where L_t is the predicted length at time t , L_∞ is mean asymptotic length predicted from (3), k describes the rate at which L_∞ is approached, t is age at time t , t_0 is age at which fish length is zero.

Results

Isometric growth implies that there is no change of body shape as an organism grows and that weight increases as the third power of length, *i.e.*, the allometric parameter (β) is 3.0. Negative allometric growth implies the fish becomes more slender as it becomes longer and is indicated by a $\beta < 3.0$. Positive allometric growth implies the fish becomes relatively stouter or deeper-bodied as it increases in length and is indicated by a $\beta > 3.0$. The coefficient α , it should

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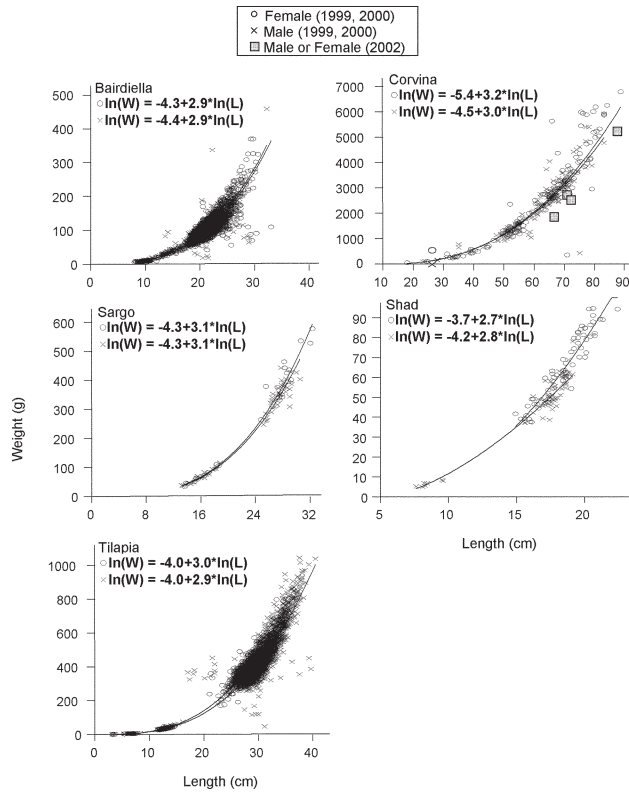


Figure 2.-Length-weight relations of five Salton Sea fish. Squares indicate weights for corvina caught the year before their disappearance from samples.

be noted, is only an imperfect index of shape when growth is not isometric, or of difference in shape when two species or sexes have different allometric parameters. In the latter case, the degree to which one species or sex was deemed slenderer or stouter than another would vary with length. As calculated here, α is directly interpretable as the weight of a fish in grams when it is one centimeter in length.

Model parameters for the L-W relations of bairdiella, corvina, sargo, shad, and tilapia are given in Table 1 and Figure 2. The best fit was for female sargo ($r^2 = 0.991$) and the poorest for female shad ($r^2 = 0.894$). Shad presented a negative allometry and were farthest removed from isometric growth. Mostly slight differences between sexes in estimated weight at length varied among species. For corvina and bairdiella, males at a length were heavier than females. Male corvina between 10 and 30 cm weighed between 15 and 46 percent more than females. In contrast, male bairdiella weighed only 4 to 5 percent more than females in the 10-30 cm

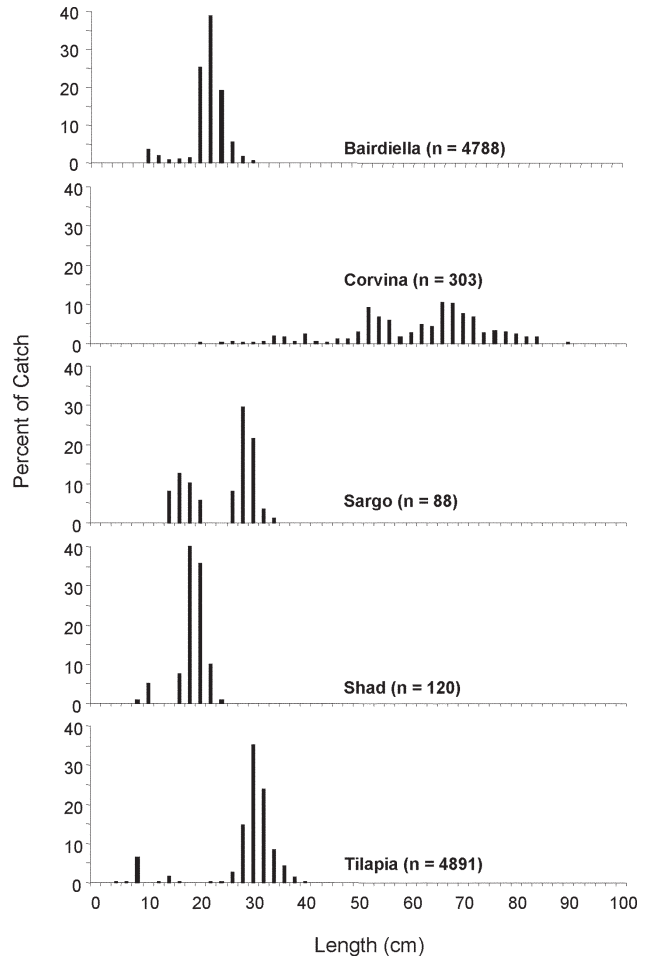


Figure 3.-Length frequency distributions for gillnet catches of the five most abundant species of fish at the Salton Sea during 1999 and 2000.

length range. In the other species, females were heavier at a length. For individuals 10-30 cm long, females weighed 1 to 5 percent more in sargo, 2 to 19 percent more in shad, and 9 to 15 percent more in tilapia. Corvina reached the greatest length and weight, followed by tilapia, bairdiella (third in maximum length and fourth in maximum weight), sargo (fourth in maximum length and third in maximum weight), and shad (Fig. 3, Table 1). Bairdiella and tilapia were the most numerous fish in the total catch, followed by corvina, sargo, and shad.

Lengths of corvina caught during 2002 were consistently below the fitted length-weight line of conspecifics during 1999 and 2000 (Fig. 2). No such difference was found between 2002 and 1999/2000 for bairdiella. Model estimated weights at 10, 20, and 30 cm for the 2002 bairdiella population were consistently above those estimated for the population of 1999-2000 (Table 1), indicating no decline of body condition.

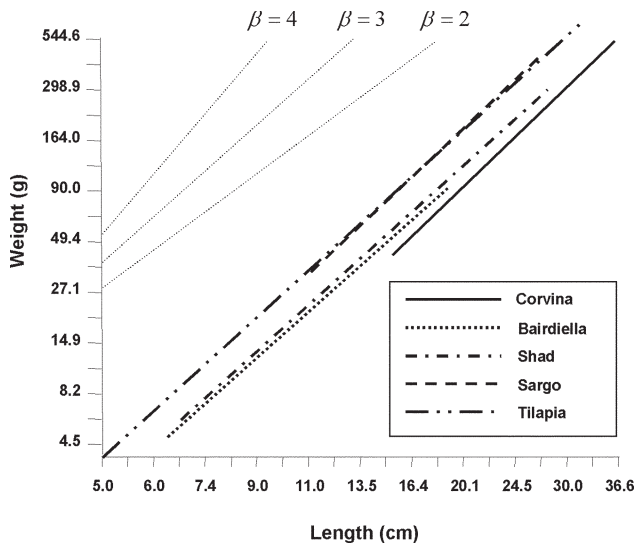


Figure 4.—Length-weight relations of five Salton Sea fish compared with hypothetical fish with isometric ($\beta = 3$), positive allometric ($\beta = 4$), and negative allometric ($\beta = 2$), growth. Fish lengths are restricted to those potentially handled by larger piscivorous birds. Vertical positioning of lines representing hypothetical fish is arbitrary; it is variation in their slopes that is relevant.

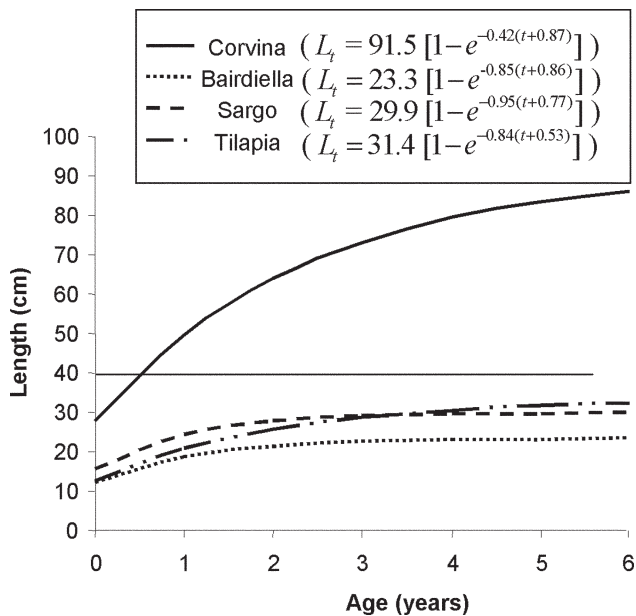


Figure 5.—Predicted growth patterns for four species of Salton Sea fish using the von Bertalanffy equation. Horizontal solid line indicates the upper limit of fish length that can potentially be handled by large Salton Sea piscivorous birds.

For easy comparison of the L-W relations of the five species, all have been plotted on the same log-log plot (Fig. 4). Likewise, the VBG growth functions for four of these species are given and plotted together, showing in particular how corvina quickly exceeds the prey handling abilities of even the largest piscivorous birds (Fig. 5).

Discussion

Condition and girth

Decline in body condition of corvina can be attributed to the collapse of the tilapia population, its main food source, which was already pronounced in 2002 (Caskey *et al.* 2007). Decline of the omnivorous tilapia population may, on the other hand, have resulted in increased abundance of prey of bairdiella, allowing maintenance or even increase in food availability for that species and forestalling decrease in its own body condition. There is evidence that the decline of tilapia population did result in large increases in phytoplankton, and probably zooplankters such as copepods and rotifers, but this increased planktonic production is also thought to have worsened water quality conditions and caused large decreases in the pileworm population (Anderson *et al.* 2007). At least in the mid 1950s, the pileworm was the dominant food item for bairdiella larger than 30 mm in length (Quast 1961).

The value of a given fish species to a fish-eating bird is determined in part by how large a fish the bird can ingest. This limit will be set less by fish length or weight (or volume) than by its girth, a dimension not normally recorded in fisheries work. Girth is the circumference of a cross-section through through the fish where its body is deepest. Thus if a bird ingests a fish with a girth of, for example, 20 cm, it will get a bigger (more kg) meal if the fish is a fusiform one like corvina than if it is stouter bodied, like tilapia or sargo. In other terms, a bird will get a bigger meal per unit girth if it selects fish with a low shape coefficient (Table 1).

Growth rates, the ‘size window’ and availability

The pattern of age-specific growth rates of a fish species is more important than its shape in determining the importance of that species as an energy source for any given fish-eating bird. Two critical variables are 1) the speed at which a fish attains a size large enough to be seen and efficiently captured by a fish-eating bird, and 2) the length of time it remains within a particular ‘size window,’ *i.e.*, smaller than the maximum size easily captured and ingested by the given fish-eating bird.

Growth that is well-described by an asymptotic functional relationship, such as the VBGF (Eq. 3) implies that fish grow faster early in life, as measured by percent increase in body mass per unit time. A faster growth before maturity

may be an adaptation to escape predation (Nikolskii 1965). After maturity, gains in length level off, but weight may still increase in a positively allometric growth pattern. An increase in weight may be an adaptation for increase in fecundity because of the close relation of fecundity to body weight in fish (Spanovskaya *et al.* 1963).

The implication of the above for Salton Sea fish-eating birds is that fish with rapid early growth enter the handleable size range quickly but if a high growth rate is maintained the fish also will move out of that size range quickly. In terms of the VBGF parameters and in relation to any given fish-eating bird, the ideal fish species is one with a high initial growth rate, k , and an asymptotic size, L_{∞} , that is at or near the upper end of the size range the bird can handle (Fig. 5). It would mean that the absolute initial growth rate, *i.e.*, the initial slopes of the curves in Fig. 5, rather than k , that would be most relevant in this context; but for any given L_{∞} within the handleable size range, the higher k is, the faster fry or juvenile fish become useful to birds.

The relative importance of these two parameters will be quite different for different species of fish eating birds. For the larger fish-eating birds such as pelicans, tilapia, bairdiella and sargo may be the best resource in this regard. They have high k values, but low L_{∞} values and remain for several years at a size small enough for pelicans to handle (Fig. 5). During the last couple of decades, tilapia likely has been the principal resource for large fish-eating birds because they are highly prolific, grow to a maximum length of 40 cm and a maximum weight of about 1000 g (Riedel *et al.* 2002; Caskey *et al.* 2007; Hurlbert *et al.* 2007). A 40 cm tilapia would be at least 5 years old, whereas a one year old tilapia, on average, would only be ~50 percent shorter (Riedel *et al.* 2002; Figs. 5), implying a wider time range for tilapia availability as a prey for large fish-eaters.

Corvina, on the other hand, quickly grow past a size for easy handling by pelicans – and all other fish-eating birds – during its first year. A corvina 40 cm long is in its second year (age = 1; Riedel *et al.* 2002) and has a body depth of ~12-15 cm, which is probably at or just above the upper limit of ingestible fish size for pelicans. Corvina grow isometrically to a maximum size above 80 cm, which makes them the most esteemed sport fish at the same time they are the least important for fish-eating birds.

The larger fish-eating birds do seem able to consume fish up to ~40 cm in length (Fig. 5). About 10 percent (by weight) of the diet of double-crested cormorants on Texas reservoirs consisted of catfish (*Ictalurus* spp.), with one ingested catfish measuring 41.5 cm (Campo *et al.* 1993), though here as elsewhere much smaller prey normally dominate the diet (Hatch and Weseloh 1999). White pelicans feeding nocturnally on a river in Manitoba made heavy use of large fish such as walleye (*Sander vitreus* (Mitchill)), white sucker (*Catosto-*

mus commersoni (Lacepède)), and cisco (*Coregonus artedii* LeSueur) (McMahon and Rogers 1992). These fish moved into shallow water shore areas at night, making them easily caught. Of total prey captures, 9 percent were fish longer than the pelicans' beaks, which average 34 cm in males and 29 cm in females (Evans and Knopf 2004). Less information is available for the brown pelican, but D. Anderson (Univ. California, Davis, pers. comm.) reports once seeing a young bird regurgitate a ~45 cm long pacific mackerel (*Scomber japonicus* Houttuyn) and that scavenging adults will ingest, albeit not always easily, fish remains > 2 kg in weight. In general their diet is dominated by much smaller fish, of course (Shields 2002).

Smaller fish-eating birds, such as cormorants, grebes, egrets, herons, terns are limited to correspondingly smaller fish. These would often include only the juveniles less than a year old of all five Salton Sea species, and their different asymptotic sizes (L_{∞}) are irrelevant. The absolute growth rates of these species during their first year would, on the other hand, be a determinant of their availability to these small fish-eaters. Other small fish species with low L_{∞} values are sporadically abundant in the Salton Sea, *e.g.*, longjaw mudsuckers (*Gillichthys mirabilis* Cooper), mosquito fish (*Gambusia affinis* Baird and Girard), and desert pupfish (*Cyprinodon macularius* Baird and Girard). Mostly restricted to shallow water areas, these are likely of great importance to the smaller fish-eating birds.

Other determinants of availability

As of this writing (May 2007), tilapia is the only one of the 5 species treated here that has not gone extinct in the Salton Sea (J. Crayon, pers. comm.) – and that makes contrasts in availability pretty stark! Comparisons thus must refer to past conditions and to possible future ones. Tilapia is much less abundant than in 1999-2000 but present in sufficient numbers to attract hundreds of pelicans and cormorants over the last few years.

Bairdiella is mostly a demersal species, not readily catchable by birds, which makes it of less importance as bird prey, even prior to 2000 when it was close to tilapia in abundance. Threadfin shad has always been extremely scarce in the Salton Sea, and sargo became so after the 1980s, so neither of these species have been important prey for fish-eating birds in recent times (Riedel *et al.* 2002; Caskey *et al.* 2007; Hurlbert *et al.* 2007). Finally, corvina also has been of little value to fish-eating birds because it is a fast-moving, deep water species that quickly grows beyond a size handleable by any fish-eating birds. Corvina has used tilapia as a main food item since the 1970s. Up until 2002 sport fishermen were catching corvina weighing up to 6 kg, and prior to the recent increases in salinity that seem to have eliminated corvina from the lake, corvina could have had a negative impact on

fish-eating birds by keeping tilapia populations – as well as those of several species of small fish - lower than they would have been in the absence of corvina predation.

Conclusions

Populations of fish-eating birds at the Salton Sea seemed to have closely tracked fluctuations in estimated total biomass of fish in the lake over the past half century (Hurlbert *et al.* 2007). However, a great complexity of foodweb interactions must exist among populations of the many fish species and fish-eating bird species that use the Salton Sea and the ongoing changes in those interactions that are being driven by increasing salinity. During the late 1990s, fish in the Salton Sea were mostly of the 1995 tilapia cohort (Riedel *et al.* 2002; Caskey *et al.* 2007). Birds capable of feeding on adult tilapia were abundant, despite poor recruitment to the tilapia population during the 1990s, whereas birds dependent on small, juvenile fish declined in the late 1990s (Hurlbert *et al.* 2007). Though the tilapia population has recovered slightly, it seems likely to soon succumb completely to the lake's gradually increasing salinity, along with most of the small fish species still present. At that point, the phenomena of interest will become interactions between invertebrate populations and invertebrate-eating water birds. Nevertheless, the fish-bird relations discussed here will become relevant once again if, as most people in the region desire, a large salinity-reduction restoration project restores a diverse fish assemblage to at least a large portion of the current lake.

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