

Variability in Length–Weight Relationships Used to Estimate Biomass of Estuarine Fish from Survey Data

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Abstract.—The biomass of fish populations is often calculated from abundance-by-length data using length–weight (LW) relationships from separate studies (e.g., from the literature). Estimates of biomass determined this way have two principal sources of error: (1) error in total numbers and size distribution of fish due to sampling variability; and (2) prediction error, including that arising from the use of a LW relationship from another time, place, population, or species. We developed LW relationships from 6,390 measurements of fish of 24 species in the San Francisco Estuary. Our principal objective was to evaluate the errors that arise when calculating biomass from length data. Data were obtained from four sampling studies (none designed for this purpose) and analyzed with analysis of covariance on log-transformed data. Differences in LW relationships among studies were apparent. Five tests were applied to assess the influence of these differences on predictions of biomass from length data. Three of these tests indicated some bias arising from several sources, including differences in the range of lengths used to develop the relationships. The remaining two tests compared the sampling variability of two common fish species with variability and bias introduced by means of different alternative LW relationships from our data and from the literature. Length–weight relationships from the literature introduced some bias and somewhat more variability into the biomass estimates compared with estimates based on LW relationships obtained from the San Francisco Estuary. However, sampling error was the largest source of error in all cases. Although it is preferable to calculate biomass from LW relationships of fish from the same area and time period, the error induced by using relationships from other time periods, other areas, or the literature is typically small compared with sampling error, particularly when only relative measures of biomass are needed.

The biomass of a fish population, or of individual fish, is an essential component of many investigations, including bioenergetic modeling studies, ecosystem or population models, and food web studies (Anderson and Neumann 1996). Although programs for monitoring the abundance and distribution of fish typically include length

measurements, weight measurements are less commonly incorporated into sampling protocols. It is easy to measure lengths of live fish immediately after capture and then release them unharmed. Weighing fish under field conditions can be difficult and time-consuming; furthermore, the results can be inaccurate because of factors such as wind and boat movement. The alternative is to kill the fish and return them to the laboratory to weigh them there, which is not only more time-consuming but also wasteful. The usual approach to this problem is to measure all fish or a subsample from

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TABLE 1.—Information on sample collection in the four studies from which fish were taken. See text for additional details.

Factor	BREACH II	Suisun Marsh	Delta Wetlands	Delta Predators
Period of collection	Apr 2001–Feb 2002	1979–1983, 1998–1999	Apr 2000–Apr 2001	Jun 2000–Oct 2001
Frequency	Approximately quarterly	Monthly	Irregular	Monthly
Collection year	Fyke net; 3-mm mesh	Otter trawl; 2.5 m ² , 35–6-mm mesh	Beach and purse seines	Seines and gill nets
Preservation	Live	Preserved in 10% formaldehyde	Frozen, then thawed for weighing	Preserved in 10% formaldehyde
Length	Fork	Standard	Fork	Fork
Weight and accuracy	Field scale; 0.1 g	Laboratory balance; 0.1 g	Laboratory balance; 0.01 g	Laboratory balance; 0.01 g
Number of fish	2,691	2,748	536	415
Number of species	17	13	9	8

each sample and then calculate weights from length–weight (LW) relationships developed for each species (e.g., Schaus et al. 2002).

The weight or condition (Le Cren 1951) of an individual fish of a given species at a given length can vary with feeding success, health, season, and location. Ideally, LW relationships used to reconstruct biomass in a sampling program should be determined from a stratified subsample of fish from the same sampling program. This seems to be rare in practice. For example, in the San Francisco Estuary, eight different sampling programs routinely collect fish (Kimmerer 2004), and most of these programs routinely measure lengths of all fish of each species or a subsample of abundant species. None routinely weighs the fish collected. The only way to determine biomass retrospectively from these data is to use LW relationships for the same species from other times and places.

In this paper we investigate the variability of LW relationships determined on juvenile and adult fish from four sampling studies in the San Francisco Estuary, California. Our principal objective was to answer the question, What are the consequences of using LW relationships determined in separate studies to estimate biomass? To answer this question, we compared the LW relationships from these studies with each other and with literature values for the same species. We then applied the LW relationships to abundance and length data from selected field samples to determine how biomass estimates differed (1) among LW relationships and (2) between measured values and those predicted from LW relationships.

In general, the biomass estimate for a sample of fish collected in the field is

$$\hat{B} = \sum_k \sum_i a_k L_{ik}^{b_k}, \quad (1)$$

where L_{ik} is the length of fish i , and the subscript

k refers to species, life stage, or other attributes over which the LW relationships are stratified. This equation may incorporate bias due to differences in condition between fish in the sample and the reference fish used to construct the LW relationship, as well as error due to variability in measurements in length in the sample and reference fish and weight in the reference fish, and due to variability in weight at length among individual fish. If the biomass estimate is to represent the biomass of fish in the environment, additional variance arises as a result of sampling error. These various sources of error are probably additive; that is, there is no reason to expect covariance among them. Therefore, total variance of an estimate of total biomass from an environmental sample is

$$V_B = V_S + V_I + V_L + V_{LW}, \quad (2)$$

where the subscripts refer to total biomass (B), sampling (S), individual variability in weight of fish in the sample (I), length measurement in the sample (L), and the LW relationship, which includes both bias (as a squared term) and error. We assume the error in length measurement is negligible. Our objective, then, was to determine whether V_{LW} was substantial in relation to the other sources of error, particularly sampling error, and whether the bias inherent in equations (1) and (2) would be acceptable. These principles also apply to biomass estimates of gut contents that have added variance in length measurements caused by shrinkage or partial digestion of prey.

Methods

Length and weight data were obtained from four sampling studies, each undertaken for different purposes, at different times and places, and using different gear (Table 1; Figure 1). In BREACH II (Simenstad et al. 2000), fish were collected at nine sites in marshes and breached levees adjacent to

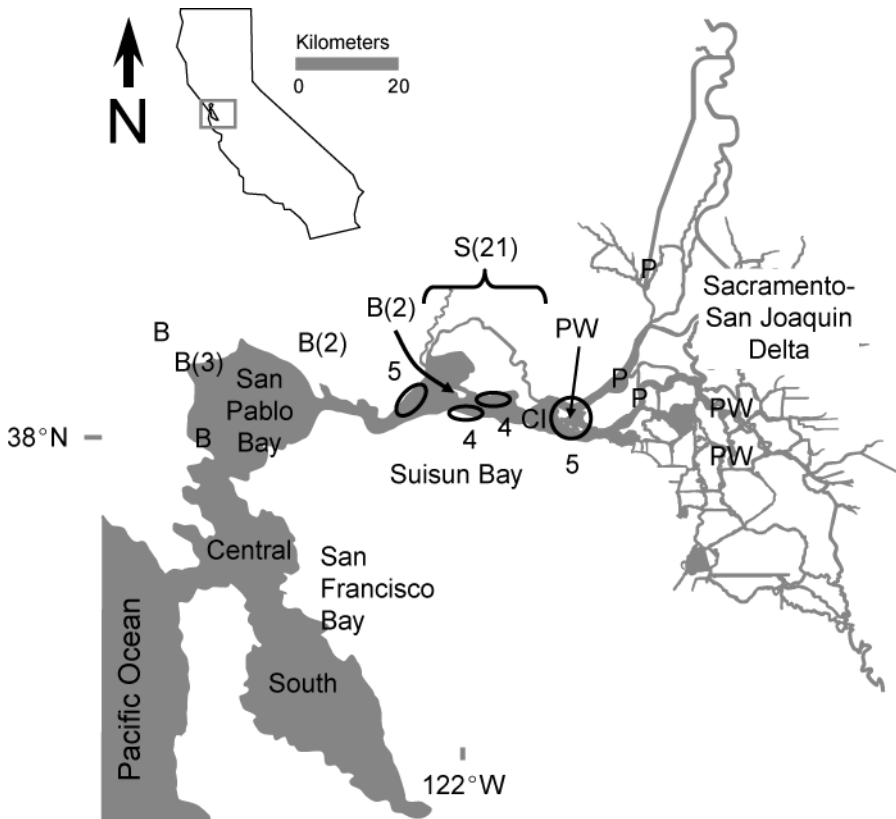


FIGURE 1.—Map of the San Francisco Estuary showing sampling stations for each of the four separate studies from which data were obtained to develop and compare length-weight relationships for 24 species of fish. Letters refer to the stations for each of the sampling studies (B = BREACH II, S = Suisun Marsh, W = Delta Wetlands, and P = Delta Predators); the numbers in parentheses indicate the number of stations if there was more than one. Stations for the Suisun Marsh study were distributed throughout the sloughs in Suisun Marsh north of Suisun Bay. Ovals indicate groups of stations in the fall midwater trawl survey used for analysis of the biomass of striped bass; CI refers to the Chipps Island salmon trawling station.

San Pablo and Suisun bays. The Suisun Marsh study began collecting fish in marsh channels in 1979 (Moyle et al. 1986; Meng et al. 1994; Matern et al. 2002), and fish were retained for weighing during two time periods. The Delta Wetlands study collected fish at three wetlands created by breaching levees in the Sacramento-San Joaquin Delta (Toft et al. 2003; L. F. Grimaldo, unpublished). The Delta Predators study (Nobriga et al. 2001) collected fish from six nearshore sites in the Sacramento-San Joaquin Delta, some of which were the same as in the Delta Wetlands study.

Length and weight values were comparable among the studies, except that the Suisun Marsh study measured standard length instead of fork length. For that study, fork lengths were calculated using ratios determined using data from the Delta Predators study for several species, from Feyrer

and Baxter (1998) for splittail *Pogonichthys macrolepidotus*, from Karpov and Kwiecien (1988) for several other species from the San Francisco Estuary, or from FishBase (Froese and Pauly 2003) for several marine species.

The general approach to modeling the LW relationships from these data was to log-transform both values and apply linear regression (Anderson and Neumann 1996). We excluded data for a species from a study that collected fewer than 10 individuals. We also applied nonlinear regression to the raw data (Hayes et al. 1995), but the error structure of the data indicated the presence of outliers, making this approach inappropriate.

Instead, robust regressions were used because of the numerous apparent outliers. Robust techniques are useful when the data meet the assumptions of linear regression but have some data points

that are probably not from the same distribution (e.g., from procedural or transcriptional errors). We used function `rlm` in S-Plus, which down-weights outliers with iteratively reweighted least squares and is 95% efficient for normally distributed data (Venables and Ripley 1997). Normal probability plots of residuals from pooled regressions showed a core of normally distributed points and some apparent outliers. The fraction of outliers was estimated by calculating the fraction with robust regression weights less than 0.25, and normality of the core data was assessed by means of the Kolmogorov–Smirnov goodness of fit of residuals to a normal distribution and, if significant at $P < 0.01$, removing points progressively until the deviation from normality was no longer significant. Slopes and intercepts of robust regressions were within at most 1.45 standard errors of values calculated with ordinary least-squares regression with outliers removed, as described above.

When more than one study had collected at least 10 individuals of a particular species, we tested for differences in exponent and intercept among studies with analysis of covariance (ANCOVA). In most cases, differences in exponent were significant, indicating that predictions would be different among the regressions from individual sampling studies. However, the ranges of lengths also differed. The studies that collected more fish over a longer time period generally had the greatest range. Assuming similar sources of error, the data set with the greater range of values should give more accurate estimates of the parameters of the LW relationship.

We conducted five tests to examine how alternative LW relationships would predict fish weight. These tests generally involved evaluating the bias in equation (1) and the variance component V_{LW} in equation (2) in the context of the other variance components. Prediction tests 1–3 focused on the magnitude of V_{LW} , and prediction tests 4 and 5 examined the influence of V_S . Since the objective of all prediction tests was to draw comparisons among similar data, no correction was made for the bias in back-transformation of the log–log relationships (Hayes et al. 1995), which in any case would have raised biomass estimates only 0.3% to 2.3% (Bird and Prairie 1985). In prediction test 1 we compared prediction errors among alternative LW relationships for each species (Table A.1 in the appendix) with our pooled regression. For each species we took the extreme values of length from each study and calculated predicted weight from

each LW relationship with 95% confidence limits (CL) based on residual standard errors and degrees of freedom from that relationship. The test consisted of a comparison of overlap in confidence limits, with emphasis on the range of lengths used to develop the relationships. Prediction test 2 was a graphical analysis of predicted mean weight based on our pooled regression with that from selected literature relationships (Table A.1).

In prediction test 3 we calculated the mean weight for each BREACH II sample for every species numbering at least 10. For each species–sample combination meeting this criterion, we calculated weights of all fish from each of the regressions available from the other three sampling studies and the literature. The various calculated mean weights for each species and sample were then compared with the measured mean weights as the percentage difference between them and through correlation coefficients.

Prediction tests 4 and 5 explicitly considered sampling error as well as prediction error from the pooled LW relationships. In prediction test 4 we examined consequences of differences among LW relationships by applying the relationships to field data on striped bass *Morone saxatilis* and comparing variability in biomass arising from these different relationships with that arising from sampling variability. We used data on striped bass from the fall midwater trawl monitoring program (Von Geldern 1972) because of its high sampling density. Striped bass were selected because they were measured and weighed in all four of the sampling studies and because they were abundant in many of the midwater trawl samples in Suisun Bay (Figure 1). Stations no more than 6 km from each other were aggregated into groups; this distance is below the tidal excursion of 10–20 km in this part of the estuary (Kimmerer et al. 2002). Stations within each group were treated as replicate samples of the same population of young striped bass, but groups were used only from those dates when all stations in the group had at least one fish (median, 5; maximum, 300). ANCOVA and correlation analysis were then used to ensure that the stations within each group did not have different means ($P > 0.1$) and that their abundances were positively correlated in time, which justified treating these groups of stations as replicate samples of striped bass. The resulting four station groups (Figure 1) had 4–5 stations with 14–43 sample dates/group.

We applied a graphical approach and a power analysis to compare predictions of the LW relationships. These analyses focused on comparing

V_S , the sampling error, with the effect of V_{LW} in equation (2). First, we calculated means and confidence limits (representing V_S) for biomass of striped bass from each date and station group with the pooled LW relationship based on all four sampling studies. We then recalculated the means for each station group with each alternative LW relationship. This gave 103 different estimates of biomass from the pooled regression (with sampling error), individual regressions, and literature values. An additional estimate was made with the pooled regression, but the weight estimate of each fish was altered by a random sample from a normal distribution with zero mean and variance equal to the prediction mean square error from the pooled regression (to represent V_I in equation 2). Plotting each estimate against the pooled value with error bars gave us a sense of the degree of error and bias in each LW relationship relative to the pooled relationship. The power analysis consisted of an estimate of the number of samples required in an unpaired t -test to detect differences between mean log biomass estimates made with the Delta Predators data (which had a large N and provided results that differed the most from the other results) with estimates made with other relationships. If we had known the actual biomass in the samples, this would be equivalent to an analysis of the variance with components indicated by equation (2). Since we had to use one of the LW relationships to calculate biomass and compare this estimate with that predicted by other relationships, we were unable to assess the effects of V_I or V_L . Instead, we determined the number of samples needed to detect V_{LW} given the observed V_S and assuming the Delta Predators regression was "correct." For each comparison, the calculated t -value was

$$t(N) = \frac{LB_{DP} - LB_i}{SE_{pooled}(N)} \quad (3)$$

where LB_{DP} is the grand mean log biomass estimated with the Delta Predators regression, LB_i is the grand mean log biomass estimated with any other regression, SE_{pooled} is the pooled standard error determined from log-transformed biomass estimates from all 476 samples with sample group means subtracted out, and (N) indicates that both the SE and the t -value depend on the number of samples N . This equation was then solved iteratively to calculate the smallest N for which the tabulated t -value was no larger than that calculated in equation (3).

Prediction test 5 applied a similar approach to

Chinook salmon *Oncorhynchus tshawytscha* from a long-term sampling program at Chipps Island in which nominally 5–20 replicate trawls were taken each day (Brandes and McLain 2001). We reduced these data to a series of 323 sets of 10 trawls each in which at least 1–328 (median, 21) Chinook salmon were collected. The range of sizes in this study was rather narrow (10th percentile, 74 mm; 90th percentile, 100 mm). Because we had data to develop a LW relationship only from the Delta Wetlands study, we developed LW relationships for Chinook salmon with additional data from two sampling programs. The first was a set of 65 hatchery-reared fish recovered in the Chipps Island trawl that were weighed and measured (P. Brandes, U.S. Fish and Wildlife Service, personal communication). The second was a set of 2,484 Chinook salmon collected from Deer Creek (a tributary of the Sacramento River) that were weighed and measured (C. Harvey Arrison, California Department of Fish and Game, personal communication). We used a pooled regression from these two sampling programs and the Delta Predators study to obtain best estimates of the weight of the fish in each sample and then compared the errors associated with differences among the LW relationships (including two from the literature) with sampling error as described above for striped bass. The power test was similar to that in prediction test 4, but we used the Delta Wetlands study as a basis for comparison because its LW relationship appeared to differ the most from the other relationships.

Results

Length-weight data were available for 24 species of fish sampled in at least one study (Tables 2, A.1). For all 11 species sampled in more than one study, LW relationships differed either in exponent or in intercept based on ANCOVA ($P < 0.05$). This result is not presented in detail because such differences could be expected as a result of differences in methods, locations, and times of sampling. Judging from normal probability plots (not shown), many of the LW relationships had outliers. A small fraction of points were down-weighted by the robust regression with weights less than 0.25 (maximum weight is 1.00) and a somewhat higher fraction of points fell outside a normal distribution, but otherwise the Kolmogorov-Smirnov goodness-of-fit test corroborated the normal probability plots ($P < 0.01$; Table 2).

Regression slopes (i.e., the exponents in the LW relationships) generally fell in the range of 2.8–

TABLE 2.—Pooled length–weight (LW) relationships of the fishes examined in this study. Source studies are as follows: B, BREACH II; S, Suisun Marsh; W, Delta Wetlands; and D, Delta Predators (see text for further details). Length is fork length (mm; standard length in the case of common carp in the Suisun Marsh study); weight is expressed in milligrams to reduce the number of leading zeros in the constants. Slopes (exponents) are given with 95% confidence limits of the mean. The number of data points included in each regression is given in parentheses. The number of fish of each species from each source study is given in the appropriate column under the heading “Source study.” Percent outliers are the percentages of residuals with robust regression weights <0.25 (“weight”) and those that did not fit a normal distribution (Kolmogorov–Smirnov [K–S] test). Data from individual regressions and the literature are in the appendix.

Species	LW relationship ^a	Percent outliers		Source study			
		Weight	K–S test	B	S	W	P
American shad <i>Alosa sapidissima</i>	0.0074 $L^{3.09 \pm 0.06}$ (113)	0	0		37	50	26
Arrow goby <i>Clevelandia ios</i>	0.0035 $L^{3.19 \pm 0.30}$ (38)	0	0	38			
Bay goby <i>Lepidogobius lepidus</i>	0.0015 $L^{3.38 \pm 0.78}$ (17)	0	0	17			
Common carp <i>Cyprinus carpio</i>	0.0670 $L^{2.85 \pm 0.07}$ (59)	2	2		59		
Chinook salmon <i>Oncorhynchus tshawytscha</i>	0.0018 $L^{3.44 \pm 0.12}$ (68)	0	0			68	
Delta smelt <i>Hypomesus transpacificus</i>	0.0018 $L^{3.38 \pm 0.09}$ (113)	0	0		60		53
Inland silverside <i>Menidia beryllina</i>	0.0097 $L^{2.87 \pm 0.03}$ (1,181)	2	7	880		267	34
Longfin smelt <i>Spirinchus thaleichthys</i>	0.0005 $L^{3.69 \pm 0.08}$ (117)	0	0		117		
Northern anchovy <i>Engraulis mordax</i>	0.0015 $L^{3.37 \pm 0.06}$ (123)	1	9	123			
Pacific herring <i>Clupea pallasii</i>	0.0015 $L^{3.44 \pm 0.21}$ (89)	1	0	89			
Pacific staghorn sculpin <i>Leptocottus armatus</i>	0.0090 $L^{3.06 \pm 0.03}$ (689)	2	2	305	384		
Prickly sculpin <i>Cottus asper</i>	0.0037 $L^{3.30 \pm 0.03}$ (564)	1	5	15	533	16	
Rainwater killifish <i>Lucania parva</i>	0.0061 $L^{3.18 \pm 0.13}$ (186)	1	7	186			
Sacramento sucker <i>Catostomus occidentalis</i>	0.0146 $L^{3.01 \pm 0.05}$ (82)	0	0		82		
Splittail <i>Pogonichthys macrolepidotus</i>	0.0030 $L^{3.27 \pm 0.02}$ (694)	1	5	32	634	11	17
Shimofuri goby <i>Tridentiger bifasciatus</i>	0.0017 $L^{3.47 \pm 0.25}$ (45)	0	0	32		13	
Starry flounder <i>Platichthys stellatus</i>	0.0082 $L^{3.13 \pm 0.04}$ (72)	0	0		72		
Striped bass <i>Morone saxatilis</i>	0.0066 $L^{3.12 \pm 0.02}$ (537)	1	1	98	276	10	153
Threadfin shad <i>Dorosoma petenense</i>	0.0072 $L^{3.16 \pm 0.07}$ (201)	0	0	21	45	74	61
Threespine stickleback <i>Gasterosteus aculeatus</i>	0.0086 $L^{3.04 \pm 0.14}$ (148)	2	2	148			
Topsmelt <i>Atherinops affinis</i>	0.0038 $L^{3.17 \pm 0.03}$ (183)	1	6	183			
Tule perch <i>Hysterocarpus traskii</i>	0.0204 $L^{3.03 \pm 0.04}$ (243)	1	1	12	205		26
Western mosquitofish <i>Gambusia affinis</i>	0.0066 $L^{3.15 \pm 0.12}$ (156)	0	0	156			
Yellowfin goby <i>Acanthogobius flavimanus</i>	0.0087 $L^{2.98 \pm 0.02}$ (647)	1	3	338	244	27	38

^a L = length; the dependent variable is weight.

3.5 and most were over 3.0 (i.e., most species become more heavy-bodied as they grow; Figure 2). Taxonomic differences were not striking, although the two smelt species and salmon (Salmoniformes) had relatively high exponents, and suckers and one of the two minnows (Cypriniformes) had relatively low exponents. The values from the literature were correlated across species with the corresponding values from the pooled regressions; the geometric mean slopes were not different from 1.0, but the CLs were wide ($r = 0.61$; $P = 0.04$; geometric mean slope = 1.1 ± 0.6 [95% CLs]). The CLs from pooled regressions overlapped only 4 of 18 literature values (Figure 2).

Despite the variation in slope, the differences among regression lines generally appeared small in the context of the ranges of length and weight. We use striped bass as an example because of its rather high abundance and the availability of several alternative relationships from the literature (Figure 3). The outliers discussed above are ap-

parent in this figure: six data points had robust regression weights less than 0.25, whereas all but seven fit a normal distribution. The ANCOVA for striped bass showed a significant difference among exponents ($P < 0.05$). However, over the range of data, the differences among the lines were rather small and may have arisen largely from a difference in the range of sizes of fish included in the data (Figure 4D; Table A.1). For example, about half of the data came from the Suisun Marsh study, which also had the widest range of lengths. The Delta Wetlands study included only 10 striped bass and had the narrowest range of lengths as well as the lowest slope of any of the studies.

Prediction test 1 revealed that for several species the CLs of predicted values were broader than those from the pooled regression, and in some cases the predicted weight was outside the error bars for the pooled regression (Figure 4). For example, the predicted weight at minimum length for striped bass from the Suisun Marsh study was about 25%

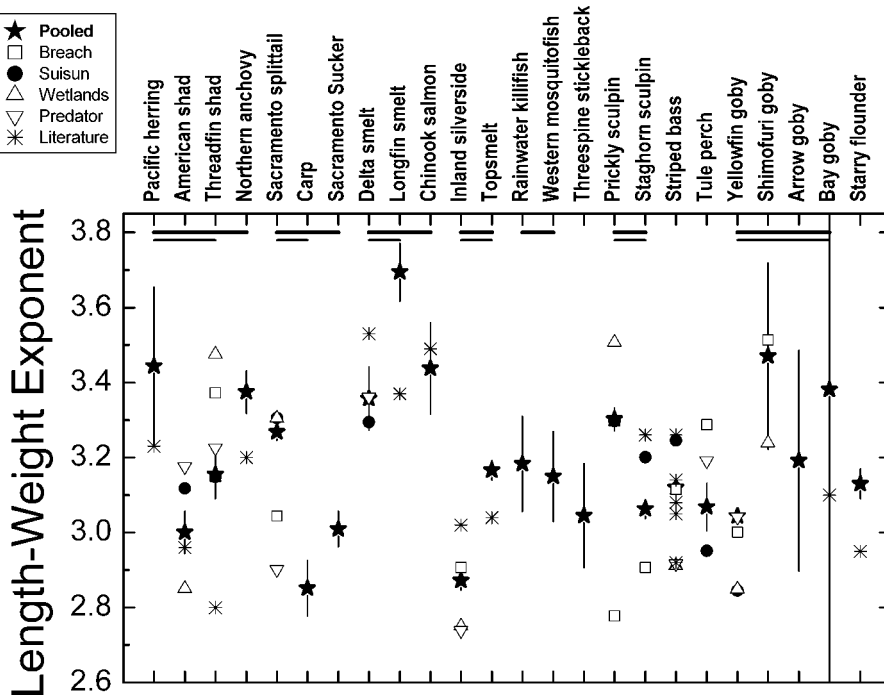


FIGURE 2.—Regression slopes (length-weight [LW] exponents) for all species for which LW relationships were developed and compared across the four San Francisco Estuary studies and those reported in the literature. The error bars associated with the stars are 95% confidence limits for the pooled regressions (or single regressions if only one study collected that species). The thin horizontal lines connect families, the thick ones orders. One literature value for Chinook salmon is out of the range of this graph (see Results).

lower than that from the pooled regression, whereas that from the Delta Predators study was about 50% higher. These differences can also be seen in the left side of Figure 4A, where data points from these two studies diverged substantially. Generally, the differences among studies were greater for small fish than for large fish.

The predicted weights from relationships in the literature differed substantially from those from the pooled regression for some species (prediction test 2; Figure 5). The literature values were generally between 50% and 170% of the predictions from the regression, but this range was considerably smaller for fish larger than 40–50 mm.

In prediction test 3, the means of the predicted weights of fish collected in BREACH II that were based on regressions from the other three studies or the literature differed from the measured mean weights by up to 35% (Table 3). The median absolute error for all such comparisons was 9%. Literature values had generally wider ranges and larger absolute medians than values from our regressions, except for inland silverside. Correlations be-

tween measured and predicted mean weight were high (Table 3).

Biomass estimates for striped bass from the mid-water trawl program had a large sampling error owing to substantial variation in fish abundance and size among samples (prediction test 4; Figure 6A–C; Table 4). Replicate samples had a median coefficient of variation of 90%, which is an underestimate of sampling error because groups of samples with zero catch were excluded. This sampling error was much greater than prediction errors from any of the LW regressions. Residual error from the pooled regression added a negligible amount to the overall variation (Figure 6A). Using any of the four separate regressions introduced a negligible amount of bias (worst case in Figure 6B). Regressions reported by Cooper et al. (1998; Table A.1) resulted in underestimates of weight of 13–22% relative to the pooled regression. None of the predictions from any of the LW relationships were outside the 95% CLs for the means of the grouped data. Furthermore, the power analysis (Table 4) showed that hundreds to more than one

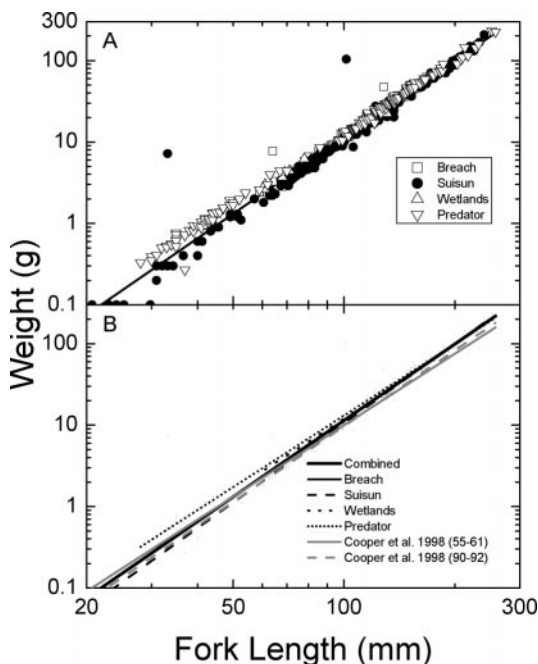


FIGURE 3.—Examples of length-weight relationships for striped bass from data drawn from the four San Francisco Estuary studies and the literature. Panel (A) shows data from the four sampling studies (see Table 2 for sample sizes), along with the regression for all pooled data. Panel (B) shows individual regression lines from the sampling studies and the literature for the same data. Two of the four regression lines provided by Cooper et al. (1998; see Table 1) are included. The scales in both panels are logarithmic.

thousand trawls would be required to detect the mean differences between the biomass estimates using the Delta Predators regression and those using the other regressions.

Prediction Test 5 for Chinook salmon gave similar results as the above analysis for striped bass, although the variation was lower and the original sample size was larger. Repeated trawls had a median coefficient of variation of 51%. Residual error from the pooled regression was negligible (Figure 6D). Using any of the three regressions that we calculated (or the relationships from Petrusso and Hayes [2001] or MacFarlane and Norton [2002]) gave small biases (Figure 6B–D). The predictions that differed most from the pooled regression (MacFarlane and Norton 2002) had 5 of 323 values outside the 95% CLs for the mean of 10 values; the other predictions had 1 or none outside the 95% CLs. The power analysis revealed that 30 trawls would have been required to detect a difference between biomass estimates based on

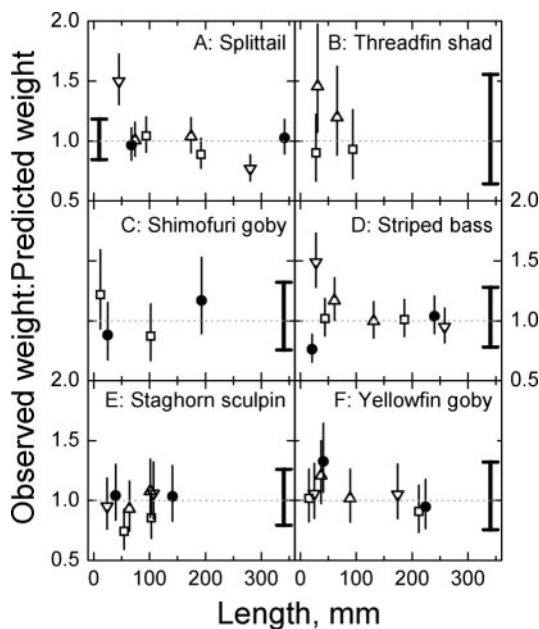


FIGURE 4.—Prediction test 1: prediction errors for six species selected at random from those sampled in more than one study. For each study that measured the length of at least 10 fish of each species, there are two identical symbols. Along the x-axis, these symbols represent the minimum and maximum lengths observed; along the y-axis, they show the ratios of the weights predicted from individual regressions to those predicted from the pooled regression at those lengths, along with the associated 95% confidence limits. Heavy bars indicate the overall prediction errors. Symbols are the same as in Figure 2. Note the correspondence between the overprediction stemming from the data from the Delta Predators study for striped bass with the cluster of points from that study in Figure 3A.

MacFarlane and Norton (2002) and those based on the Delta Wetlands study, and 44 or more trawls would have been required to distinguish biomass estimates between the Delta Wetlands study and the other studies (Table 4).

Discussion

The LW relationships of juvenile and adult fish from different sources may differ in the exponent, indicating a difference in growth trajectory or in the weight for a given length, which points to a difference in condition or, possibly, morphotype (Bernatchez 1995; Sada et al. 1995). An exponent above 3.0 indicates that fish become wider or deeper as they grow, while an exponent below 3.0 indicates they become more slender. Length-weight exponents for most animals fall roughly around 3.0 (e.g., Siegfried 1980; Uye 1982; Hopcroft et

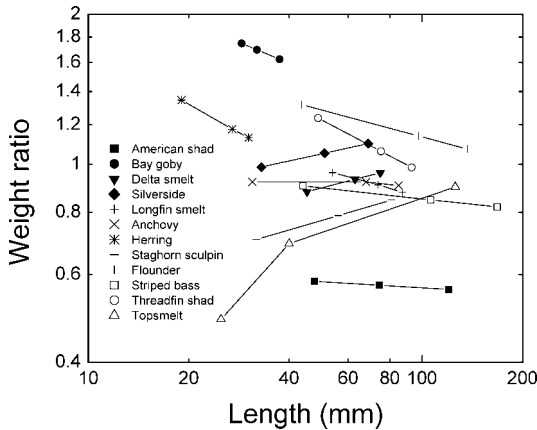


FIGURE 5.—Prediction test 2: comparison of predictions from the pooled regression for species sampled in the four studies with values from the literature identified in Table A.1. Each line represents data from one species; the three points denote the 10th, 50th, and 90th percentiles of our length data. The y-axis is the ratio of the weight predicted by the literature relationship to that predicted by the pooled regression. Predicted weights from the literature for striped bass were averaged among several sources (see Table A.1). Both scales are logarithmic.

al. 1998), with humans, for some reason, at the low end of that range (the body mass index uses an exponent of 2.0; e.g., Calle et al. 1999). Based on data presented here as well as those cited from other studies (e.g., Figure 2), exponents for fish cover a similar range. Exponents from 4,458 LW relationships in FishBase (Froese and Pauly 2003) not selected randomly with respect to the species measured had a 10th percentile of 2.7, a 90th percentile of 3.3, and a median of 3.0.

Length-weight relationships for a single species of fish may differ substantially from one study to the next (Figure 2). Reasons for these differences can generally be categorized as biological, procedural, and statistical. Biological causes of different LW relationships consist of real differences in weight at length among data sets. The weight of fish varies as a result of feeding history and the allocation of energy to growth and reproduction, so weight at a given length may vary spatially (especially between regions) and temporally (particularly by season) (e.g., Winters and Wheeler 1994; Filbert and Hawkins 1995; Meretsky et al. 2000). An additional potential source of difference is variation in growth trajectory among locations caused by environmental or genetic influences. Detecting such fine-scale differences is beyond the scope of this study. Our main point here is that

LW relationships determined for a species of fish may differ simply because the fish were collected at different times and places.

The exponent of the LW relationship may change from one life history stage to another, as would be expected during the metamorphosis from larva to juvenile. A transition in growth trajectory is apparent in the comparison of our exponent for Chinook salmon (3.45), most of which were resident fry, with that of MacFarlane and Norton (2002), whose exponent of 2.22 was for smolts emigrating from the San Francisco Estuary. This is because Chinook salmon become more slender during the transition from fry to smolt (MacFarlane and Norton 2002). Our exponent is similar to those obtained from the Chippis Island trawl data and Deer Creek data, as well as to that for Chinook salmon fry from the Sacramento River (3.49; Petrusso and Hayes 2001).

Procedural differences among LW measurements may include differences in collection methods, handling, preservation, and weighing and measuring techniques. There were statistically significant differences among our four studies, but no consistent direction of these differences among species, either in slopes (Figure 2) or predicted weights (Figure 4). Procedural differences would probably result in consistent biases in weight. Thus, although procedural differences may not have been negligible, they were probably small compared with measurement error and with other differences among the four studies.

Statistical differences may arise from several sources. Regression methods assume that the independent variable is measured without error; in practical terms this means that the measurement error in the x variable should be small in relation to that in the y variable (Prairie et al. 1995), which may not always be the case. Weighing small fish may introduce statistical errors (e.g., Figures 3 and 4); that is, weights may be near the limit of accuracy of the equipment used or may be small relative to fluctuations under rigorous field conditions. In addition, the weight of adhering water may be a large fraction of the weight of small fish (Anderson and Neumann 1996). The choice of regression model may make a difference in the outcome. For example, using a linear fit to log-transformed data and back-transforming give a lower weight prediction than using a nonlinear fit to the raw data (Hayes et al. 1995); however, the distribution of error terms may require alternative fitting methods, such as robust techniques or alternative error distributions. Normal probability

TABLE 3.—Results of prediction test 3. For each species with at least 10 fish in an individual sample in the BREACH II study, the mean weight of the catch in that sample was compared with predictions from alternative length–weight (LW) relationships using the lengths of the fish in that sample. The data presented are the range and median percentage difference between the predicted mean weight and the mean weight determined by weighing the fish; correlation coefficients (r) between alternative estimates of mean weight are also given (except for striped bass, for which there were only two samples). A blank line indicates that there was no LW relationship from that source.

Species (number of samples)	Alternative study			
	Suisun		Delta Wetlands	
	Range (median)	r	Range (median)	r
Inland silverside (15)			–18 to 0 (–7)	0.98
Northern anchovy (3)				
Pacific herring (4)				
Pacific staghorn sculpin (11)	–18 to 10 (1)	0.998		
Striped bass (2)	–11 to –11		–9 to 6 (–2)	
Topsmelt (3)				

plots (not shown) and tests of normality (Table 2) on residuals from the pooled LW regressions indicated a normal distribution of residuals, but with 0–9% extreme values. These were data points presumably not from the same statistical distribution as the bulk of the data, possibly arising from measurement or transcription errors. These results did not suggest a need for an alternative error distribution in fitting the models, but for some species ruled out the use of regression techniques requiring normally distributed residuals.

Several statistical traps await the unwary when comparing LW relationships or when estimating condition of fish based on their weight and length (see Bird and Prairie 1985). First, a plot of constant versus exponent for a set of LW relationships for the same species will have a negative slope, which can arise as an artifact of the intercept in the regression being far from the data's center of mass. That artifact can be removed by plotting the exponent against the y -intercept at the mean length, but a more informative comparison among LW relationships would be predicted weight at a selected length or range of lengths (e.g., Figure 4). Second, slopes can vary ontogenetically (as in Chinook salmon), and the slope of a regression can be affected by the range of the independent variable. Therefore, comparisons should ideally be made on data from the same range of length. Subsampling can be stratified by size-class to ensure good coverage at the ends of the distribution (Hayes et al. 1995) in the absence of ontogenetic changes within the size range. Third, standardized condition factors can be grossly biased and are no longer recommended (Anderson and Neumann 1996).

The alternative LW relationships, particularly those from the literature, had biases resulting in differences in predicted biomass of single samples

up to 35%, although most were lower (Tables 3 and 4). Given this magnitude of bias and measurement error, how can an investigator use literature values for LW relationships to reconstruct biomass from length data? The literature relationship will probably have an unknown (and unknowable) bias with respect to the fish being sampled. Two factors demonstrated in this study mitigate that bias. First, the bias has little influence on relative measures of biomass of a single species (prediction tests 1 and 3–5) because most of the bias is caused by differences in mean weight at length (i.e., the constant a_k in equation 1) rather than the exponent. For example, the deviation of points from the lines in some panels of Figure 6 indicate bias but little difference in slope (i.e., relative differences in biomass are similar regardless which LW relationship is used). Second, the variability added using LW relationships from other studies or locations, including this bias, was small compared with error resulting from sampling variability in abundance and size distribution (prediction tests 4 and 5; Figure 6; Table 4). The power analysis in these tests indicated that a large number of samples (at least 30) would be required for the bias and variability caused by the LW relationships (V_{LW} in equation 2) to significantly alter an estimate of mean weight because of the overwhelming effect of sampling error V_S ; based on our other tests, the other terms in equation (2) appear rather small compared to these two sources of error. Prediction tests 4 and 5 were conservative because only groups of samples with all nonzero catches were included in the analysis and because we based the power analyses on the studies most likely to result in bias. Furthermore, prediction test 5 was based on an unusually consistent sampling program in which the size range of fish was narrow

TABLE 3.—Extended.

Species (number of samples)	Alternative study			
	Delta Predators		Literature	
	Range (median)	<i>r</i>	Range (median)	<i>r</i>
Inland silverside (15)	-5 to 16 (7)	0.98	-5 to 15 (6)	0.98
Northern anchovy (3)			-14 to 10 (-9)	0.999
Pacific herring (4)			-1 to 35 (-9)	0.94
Pacific staghorn sculpin (11)			-35 to -12 (-19)	0.998
Striped bass (2)			-27 to -20 (-24)	0.9999
Topsmelt (3)	-1 to 15 (7)		-15 to -5 (-15)	

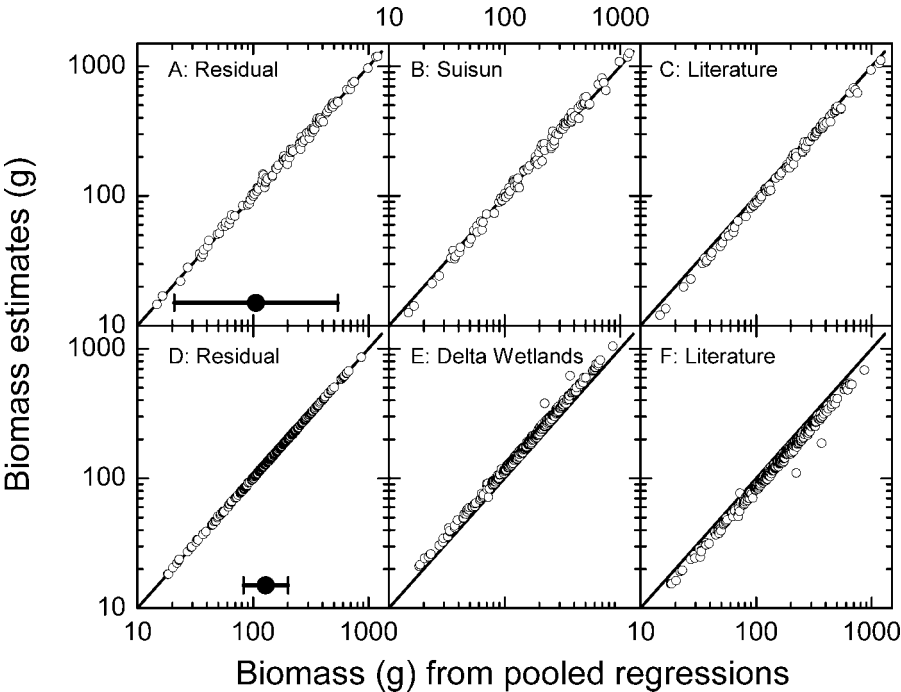


FIGURE 6.—Prediction tests 4 (A–C) for striped bass and 5 (D–F) for Chinook salmon. The *x*-axis shows the biomass determined from the respective pooled regressions from the length–weight (LW) data drawn from the four sampling studies, the *y*-axis shows various alternative biomass estimates. Panel (A) shows the pooled regression with residual standard error used to generate random variability in the individually measured fish; panel (B) shows the regression from the Suisun Marsh study, which had the highest variability; and panel (C) shows the regression reported by Cooper et al. (1998) for 1990, which had the greatest difference in slope from our pooled regression. Similarly, panel (D) shows the pooled regression as in panel A; panel (E) shows the regression from the Delta Wetlands study; and panel (F) shows the LW relationship reported by MacFarlane and Norton (2002), which was the most different from our LW relationships. The line in each panel is 1:1; the bars in panels (A) and (D) show the geometric means and 95% confidence limits for the pooled regressions. All scales are logarithmic.

TABLE 4.—Power analysis from prediction tests 4 (striped bass) and 5 (Chinook salmon). The mean difference is the percentage bias between each LW regression and the reference regression (Delta Predators for striped bass and Delta Wetlands for Chinook salmon [see text]). The number of replicate trawls that would be needed for the mean difference between the reference regression and the alternative regression to be statistically significant at $P < 0.05$ (i.e., for which the t -value in equation 3 exceeded the tabulated value) is shown in the last column.

Species	Source of LW regression	Mean difference (%)	N required
Striped bass	Pooled (all four studies)	7	>1,000
	BREACH II	7	>1,000
	Suisun Marsh	11	>1,000
	Delta Wetlands	9	>1,000
	Cooper et al. (1998) for 1955–1961	24	215
	Cooper et al. (1998) for 1990	19	398
	Cooper et al. (1998) for 1991	27	172
	Cooper et al. (1998) for 1992	23	238
Chinook salmon	Pooled	14	137
	Chippis Island	23	44
	Deer Creek	14	142
	Petrusso and Hayes (2001)	7	642
	MacFarlane and Norton (2002)	28	30

and catches were higher and more consistent than in any other sampling program we are aware of. Nevertheless, it would have taken 30 samples to detect a difference in predicted biomass between the LW regression from the Delta Wetlands study and that of MacFarlane and Norton (2002), which had an exponent more than one unit lower than the Delta Wetlands study.

Similar arguments apply to estimating the biomass of the gut contents of piscivores using LW relationships. Generally, the number of prey items per gut is small, so sampling variability, V_S (i.e., between predators), is very high. Although other difficulties arise in such estimates (e.g., error in length measurements as a result of partial digestion), similar errors would also arise in weighing the prey. Thus, variability in the biomass of gut contents among individual piscivores is probably large, irrespective of the error in converting length to weight.

Length–weight relationships are least subject to bias if the data are collected close to the time and location of the study to which the relationships are applied. Investigators should be aware that, in instances where weight data are needed with minimum bias, literature values should be used with caution. In addition, variation among sites and seasons may be important and should not be ignored when using these relationships. Finally, Table 4 makes it clear that large sampling variability as a result of small catches and variable sizes of fish is typical of even highly consistent and regular sampling programs collecting abundant species. We suggest that additional work to increase sam-

pling effort will generally provide better biomass estimates than the equivalent effort devoted to refining LW relationships.

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Appendix: Other Length–Weight Relationships

TABLE A1.—Length–weight (LW) relationships of fishes from individual studies, the literature, and other sources used to draw comparisons of biomass estimates. Length is in millimeters and is either fork length or standard length (indicated by SL); weight is expressed in milligrams to reduce the number of leading zeros in the constants. Regression slopes (exponents) from the studies listed in Table 1 are given with 95% confidence limits. The number of data points in each relationship is given in parentheses.

Species	LW relationship	Source	Length
American shad	0.0071 $L^{3.11 \pm 0.13}$ (37)	Suisun Marsh	56–199 SL
	0.0192 $L^{2.85 \pm 0.29}$ (50)	Delta Wetlands	52–86
	0.0057 $L^{3.18 \pm 0.09}$ (26)	Delta Predators	25–133
	0.0071 $L^{2.96}$	Carlander (1969)	
Arrow goby	0.0035 $L^{3.19 \pm 0.30}$ (38)	BREACH II	22–54
Bay goby	0.0015 $L^{3.38 \pm 0.78}$ (17)	BREACH II	26–47
Chinook salmon	0.0017 $L^{3.45 \pm 0.13}$ (68)	Delta Wetlands	34–87
	0.0113 $L^{2.99 \pm 0.02}$ (2,484)	Deer Creek (Sacramento River)	32–158
	0.0058 $L^{3.11 \pm 0.06}$ (65)	Chippis Island	42–184
	0.0013 $L^{3.49}$	Petrusso and Hayes (2001)	50–90
	0.3000 $L^{2.22}$	MacFarlane and Norton (2002)	67–113
Common carp	0.0670 $L^{2.85 \pm 0.07}$ (59)	Suisun Marsh	79–375 SL
Delta smelt	0.0050 $L^{3.15 \pm 0.15}$ (60)	Suisun Marsh	30–105 SL
	0.0020 $L^{3.36 \pm 0.15}$ (53)	Delta predators	37–78
		B. Baskerville-Bridges, University of California–Davis, personal communication	
Inland silverside	0.0009 $L^{3.53}$	BREACH II	11–100
	0.0085 $L^{2.91 \pm 0.03}$ (880)	Delta Wetlands	26–77
	0.0152 $L^{2.75 \pm 0.06}$ (267)	Delta Predators	26–92
	0.0183 $L^{2.74 \pm 0.13}$ (34)	Suisun Marsh	25–91 SL
Longfin smelt	0.0005 $L^{3.69 \pm 0.08}$ (117)	Cailliet et al. (2000)	SL
	0.0024 $L^{3.37}$	BREACH II	16–99
Northern anchovy	0.0015 $L^{3.37 \pm 0.06}$ (123)	Messersmith (1969)	SL
	0.0040 $L^{3.20}$	BREACH II	16–47
Pacific herring	0.0015 $L^{3.44 \pm 0.21}$ (89)	Spratt (1981)	SL
	0.0043 $L^{3.23}$	BREACH II	12–102
Pacific staghorn sculpin	0.0162 $L^{2.91 \pm 0.04}$ (305)	Suisun Marsh	20–164 SL
	0.0051 $L^{3.20 \pm 0.04}$ (384)	Cailliet et al. (2000)	
	0.0032 $L^{3.26}$	BREACH II	33–59
Prickly sculpin	0.0243 $L^{2.78 \pm 0.64}$ (15)	Suisun Marsh	16–133 SL
	0.0038 $L^{3.29 \pm 0.03}$ (533)	Delta Wetlands	26–75
	0.0014 $L^{3.51 \pm 0.28}$ (16)	BREACH II	18–41
Rainwater killifish	0.0061 $L^{3.18 \pm 0.13}$ (186)	Suisun Marsh	27–328 SL
Sacramento sucker	0.0146 $L^{3.01 \pm 0.05}$ (82)	BREACH II	94–192
Splittail	0.0090 $L^{3.04 \pm 0.22}$ (32)	Suisun Marsh	37–325 SL
	0.0026 $L^{3.30 \pm 0.02}$ (634)	Delta Wetlands	74–174
	0.0027 $L^{3.30 \pm 0.22}$ (11)	Delta Predators	45–280
	0.0188 $L^{2.90 \pm 0.09}$ (17)	BREACH II	29–94
Shimofuri goby	0.0012 $L^{3.51 \pm 0.18}$ (32)	Delta Wetlands	30–66
	0.0051 $L^{3.24 \pm 0.41}$ (13)	Suisun Marsh	22–153 SL
Starry flounder	0.0082 $L^{3.13 \pm 0.04}$ (72)	Cailliet et al. (2000)	
	0.0213 $L^{2.95}$		

TABLE A1.—Continued.

Species	LW relationship	Source	Length
Striped bass	0.0068 $L^{3.11 \pm 0.06}$ (98)	BREACH II	44–186
	0.0034 $L^{3.25 \pm 0.02}$ (276)	Suisun Marsh	13–206 SL
	0.0181 $L^{2.91 \pm 0.21}$ (10)	Delta Wetlands	61–131
	0.0192 $L^{2.92 \pm 0.01}$ (153)	Delta Predators	28–258
	0.0144 $L^{2.92}$	Cooper et al. (1998) for 1955–1961	
	0.0053 $L^{3.14}$	Cooper et al. (1998) for 1990	
	0.0074 $L^{3.05}$	Cooper et al. (1998) for 1991	
	0.0066 $L^{3.08}$	Cooper et al. (1998) for 1992	
Threadfin shad	0.0023 $L^{3.37 \pm 0.27}$ (21)	BREACH II	54–103
	0.0069 $L^{3.15 \pm 0.11}$ (45)	Suisun Marsh	37–133 SL
	0.0018 $L^{3.48 \pm 0.30}$ (74)	Delta Wetlands	64–101
	0.0057 $L^{3.23 \pm 0.10}$ (61)	Delta Predators	24–107
Threespine stickleback	0.0086 $L^{3.04 \pm 0.14}$ (148)	BREACH II	20–87
Topsmelt	0.0038 $L^{3.17 \pm 0.03}$ (183)	BREACH II	10–155
	0.0089 $L^{3.04}$	Cailliet et al. (2000)	SL
Tule perch	0.0057 $L^{3.29 \pm 0.33}$ (12)	BREACH II	68–138
	0.0289 $L^{2.96 \pm 0.05}$ (205)	Suisun Marsh	26–152 SL
	0.0100 $L^{3.19 \pm 0.11}$ (26)	Delta Predators	42–168
Western mosquitofish	0.0066 $L^{3.15 \pm 0.12}$ (156)	BREACH II	19–50
Yellowfin goby	0.0079 $L^{3.00 \pm 0.02}$ (338)	BREACH II	15–212
	0.0150 $L^{2.87 \pm 0.05}$ (244)	Suisun Marsh	35–190 SL
	0.0169 $L^{2.85 \pm 0.21}$ (27)	Delta Wetlands	37–89
	0.0073 $L^{3.04 \pm 0.08}$ (38)	Delta Predators	25–174