

THE IMPORTANCE OF INCORPORATING PROTOGYNOUS SEX CHANGE INTO STOCK ASSESSMENTS

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ABSTRACT

Although it is generally recognized that management strategies should consider life-history variation, little is known about how various reproductive strategies affect stock dynamics. Protogynous (female-to-male) sex change is a relatively common life history pattern in fishes for which standard assessment methods do not exist. We developed a stock-assessment model for a commercially and recreationally exploited sex-changing species [California sheephead, *Semicossyphus pulcher* (Ayres, 1854)] to determine how ignoring or including sex change affects the assessment of the stock. First, we demonstrated that ignoring sex change leads to an overestimate of spawning biomass and very different conclusions regarding the effect of exploitation on the spawning potential ratio (SPR). Furthermore, we found that the stock assessment is highly uncertain (current SPR estimates range from 0.08 to 0.6) because we do not know how male depletion affects reproduction or what determines individual and population variation in the size of sex change. Our results demonstrate that, although incorporating sex change into stock-assessment models is important, assessment of protogynous stocks also requires knowledge of the effect of male depletion on spawning potential and the factors that determine sex change.

Although marine fishes show a wide variety of reproductive patterns both within and among species (Breder and Rosen, 1966; Thresher, 1984; Helfman et al., 1997), most assessment methods are based on the assumptions that fish are broadcast spawners with separate sexes and that male density has little effect on total reproductive output. Reproductive patterns are also usually assumed to be relatively static, depending at most on population density or individual size and age. Yet, reproductive plasticity is common in fishes (Pitcher, 1993) and may lead to rapid changes in reproductive patterns that can have sudden and nonlinear effects on stock dynamics (Coleman et al., 1999; Lorenzen and Enberg, 2002; Garant et al., 2003; Alonzo and Mangel, 2004, 2005). Increasing evidence also indicates that rapid evolution of life-history parameters can arise as a result of fishing mortality (see, e.g., Conover and Munch, 2002; Olsen et al., 2004; de Roos et al., 2006). At present, we have little understanding of how this inter- and intraspecific variation in reproductive patterns affects our ability to assess the current status and future trajectories of exploited species.

One striking example of such variation is the existence of many commercially and recreationally important fish that exhibit protogynous (female-to-male) sex change, such as California sheephead [*Semicossyphus pulcher* (Ayres, 1854)], black sea bass [*Centropristis striata* (Linnaeus, 1758)], gag grouper [*Mycteroperca microlepis* (Goode and Bean, 1879)], and red grouper [*Epinephelus morio* (Valenciennes, 1828)]. Yet almost all stock assessments of sex-changing fishes have failed to incorporate sex change (but see Alonzo et al., 2004; Heppell et al., 2006). Using California sheephead as an illustrative example, we have demonstrated a method for including protogy-

nous sex change into stock-assessment models and compared the predictions of the model when sex change is ignored and when it is included, to determine how different our conclusions would be in these two scenarios. We also examined some potential sources of uncertainty that are specific to sex-changing species, and we discuss the further knowledge needed to reduce this uncertainty.

An important difference between stocks with separate sexes and sequential hermaphrodites is that female biomass is lost not only to fishing and natural mortality but also as individuals change sex from female to male. The relationship between total biomass and female biomass is therefore potentially very different from that in separate-sexed species, yet estimating the spawning potential or spawning biomass of a population is an essential component of fisheries management (Quinn and Deriso, 1999). Sex-specific data are available for some species, but in most, female biomass must be extrapolated from estimates of total biomass and information on patterns of reproductive maturity. In protogynous species, however, if the fishery is size selective, changes in total biomass may not necessarily reflect changes in female biomass (Alonzo and Mangel, 2005).

In addition, the ratio of males to females in a protogynous stock may change as a result of size-selective fishing with relatively unpredictable effects. For example, so long as the pattern of sex change remains the same, a fishery that removes only large individuals may have little effect on female biomass while removing a large amount of male biomass. The spawning potential of the stock could therefore be relatively unaffected by fishing mortality of males, but we know almost nothing about how male depletion (other than in the obvious extreme) affects reproductive output. Whereas the relationship between female biomass and egg production is intuitive and has been estimated empirically, neither the functional form nor parameter values that relate male biomass to population spawning potential are known. Changes in male biomass may have little effect at some levels of exploitation while having sudden and nonlinear effects when male biomass is sufficiently reduced that male or sperm limitation arises (Alonzo and Mangel, 2004, 2005). While male limitation could occur in any species, male depletion is more likely in protogynous species with size-selective fisheries (Alonzo and Mangel, 2004, 2005).

Predicting patterns of male depletion, however, also depends on knowledge of the cues that determine sex change. In many species, patterns of sex change are known to be plastic, so the measured relationship between size and sex change may not be static but instead depend on the local density, size distribution, or sex ratio of the population (see, e.g., Warner and Swearer, 1991; Lutnesky, 1994). The relationship between total biomass and female (or male) biomass may therefore not be fixed but instead change indirectly in response to fishing. In addition, whether male depletion occurs and has an effect on the spawning potential of the population will depend on the cues that determine sex change. As a result, if the plasticity of and cues that determine sex change are not known, we must consider patterns that range from fixed sex change to complete plasticity when estimating the current spawning potential of an exploited sex-changing species.

Even when sex change is taken into account in our modeling methods, the above-described issues necessitate consideration of whether typical target reference points reliably assess the status of sex-changing species. For example, the spawning potential ratio (SPR) is often used as a target measure. SPR is defined as the spawning potential per recruit in the presence of fishing divided by the spawning potential per

recruit in an unfished population. In most cases, estimated female biomass (typically extrapolated from total biomass) is used to represent the spawning potential of the population. For protogynous species, measures of SPR that use estimated female biomass may be incorrect because they do not correctly assess changes in female biomass or because changes in male biomass also affect the spawning potential of the population. Regulations often define target measures such as $SPR_{50\%}$ but are not explicit about how these targets should be calculated. For sequential hermaphrodites, calculations may include using female biomass only, total mature biomass, or some weighted measure of male and female biomass. As a result, how to apply these regulations to sex-changing stocks without further knowledge of how best to estimate female biomass and how male depletion affects the spawning potential of the stock is not necessarily clear.

Here, we describe an age and size-structured stock-assessment model we have developed for California sheephead, then demonstrate how an adaptation to the maturity function can incorporate sex change and allow us to estimate male and female biomass in protogynous stocks. We then compare the conclusions of the model with and without this adaptation to determine how considering sex change affects the outcome of the model. Finally, we calculate the SPR for California sheephead and show how our assumptions about the effect of male biomass on spawning potential and intraspecific variation in pattern of sex change affect our assessment of the current status of the stock. Many factors can lead to uncertainty and error in stock assessments. Here, we focus on the ways the above-described issues that are specific to sex-changing species affect stock assessment.

THE BIOLOGY AND LIFE HISTORY OF CALIFORNIA SHEEPHEAD

California sheephead are large labrids that can grow to sizes exceeding 80 cm total length and are found in shallow temperate waters along the Pacific coast from Monterey Bay, California, to Cabo San Lucas, Mexico, and into the Gulf of California (Fig. 1). The California sheephead is a protogynous sequential hermaphrodite (Warner, 1975). Individuals mature at about 4 yrs of age (range 3–6) at a mean standard length of 20 cm (range 12–27 cm, Warner, 1975; Cowen, 1990). Sex change occurs at approximately 30 cm standard length at an age of 7–8 yrs, although it can occur at standard lengths as low as 17 cm and ages as young as 4 yrs (Warner, 1975; Cowen, 1990). The oldest fish ever reported was thought to be 53 yrs old (Fitch, 1974), but more reliable age estimates indicate a maximum observed age of 21 yrs (range among populations 9–21, Cowen, 1990) in populations with some fishing mortality.

Adults show little evidence of dispersal (Davis and Anderson, 1989; DeMartini et al., 1994). Although some genetic differences have been found between southern California and Baja California, Mexico (Waples and Rosenblatt, 1987), the observed pattern of genetic variation within and between sites is consistent with frequent dispersal among populations. Dispersal probably occurs at the early life stages (Cowen, 1985). Bernardi et al. (2003) found no genetic structure among populations of California sheephead when comparing the Pacific and Gulf of California populations or when comparing the Californian with Mexican populations along the Pacific coast ($F_{ST} = 0$). Levels of gene flow among populations of California seem, therefore, to be high, at least on evolutionary time scales (Bernardi et al., 2003). The degree to which patterns of recruitment are due to local retention of larvae or long-term dispersal is

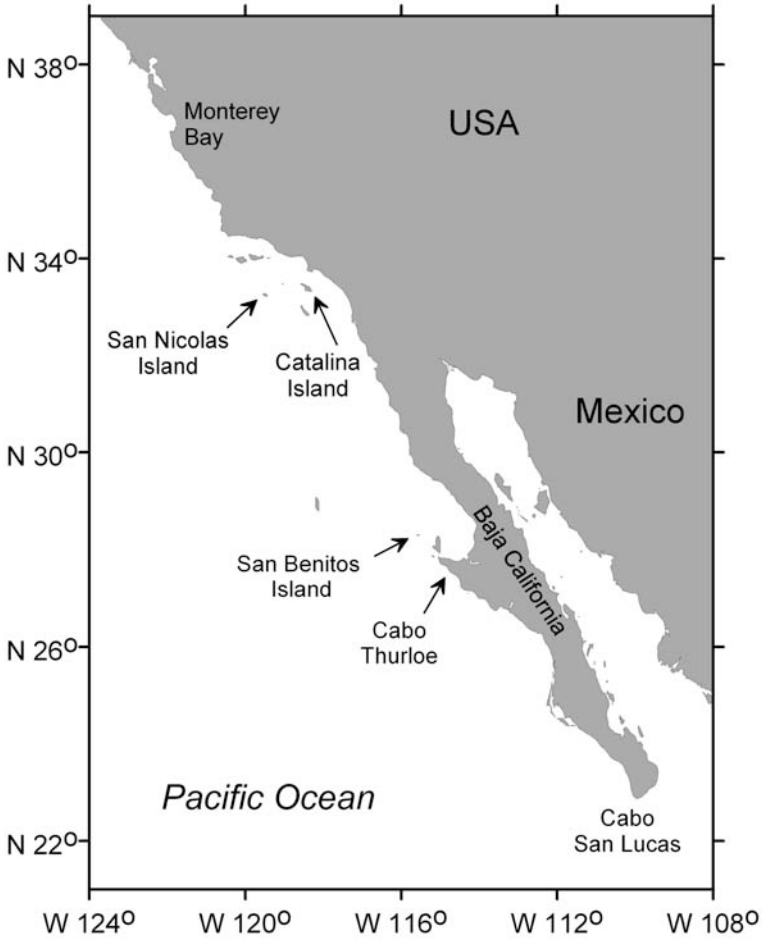


Figure 1. Nearshore populations of California sheephead (*Semicossyphus pulcher*) for which life history data were available (from Warner, 1975 and Cowen, 1990).

not known, so the connectivity among populations on ecological time scales remains unknown.

Despite high levels of gene flow and little genetic population structure, regions differed greatly in life-history characteristics such as size at maturity, size at sex change, and maximum size (Cowen, 1990). The degree to which sex change is determined by endogenous or by exogenous cues is not known, but sex change appears to depend on size rather than age, and intraspecific variation in the size at sex change is consistent with predictions of the size-advantage model (Cowen, 1990). Populations with higher growth rates and higher survival also have larger sizes at sex change, and local sex ratio may affect population patterns of sex change as well (Cowen, 1990). Sites differ in the precise growth patterns as well as size and age distributions of California sheephead, which also vary over time (Warner, 1975; Cowen, 1990; DeMartini et al., 1994). Recent evidence also exists that population sex ratio, age at maturity and age at sex change may have decreased in recent years (Caselle and Hamilton, 2006; Young and Lowe, 2006).

As with most marine fishes, nothing is known about fertilization rates or sperm production in California sheephead. At high fishing mortality, the potential for sperm limitation exists if fishing removes large males preferentially (Alonzo and Mangel, 2004), but in California sheephead, large males may experience sperm competition from smaller males (Adreani et al., 2004). Sperm production may therefore be high in this species (Birkhead and Møller, 1998), making it less prone to sperm limitation. Large males also defend spawning sites and thus may play a disproportionate role in reproduction in this species (Adreani et al., 2004). No data are available from which to estimate a function relating male density or biomass to population reproductive output.

California sheephead have supported commercial and recreational fisheries since the 1800s (Stephens, 2001) and currently account for more than 88% of the fish landed in the live-fish fishery (Palmer-Zwahlen et al., 1993). A rapid increase in this fishery in recent years has contributed to a large increase in total commercial landings of the species (Palmer-Zwahlen et al., 1993). California sheephead also represent a large proportion of the artisanal fishery in Baja California, Mexico, comprising over 25% of the catch (Rosales-Casian and Gonzalez-Camacho, 2003). At present, California sheephead fall under Nearshore Fishery Regulations of the California Department of Fish and Game. Little regulation of California sheephead existed before 1996, when catch limits were set in place for recreational and commercial fisheries. In recent years, minimum size limits (12–13 in total length) have been enacted for both commercial and recreational fisheries.

MODELING METHODS AND PARAMETER ESTIMATION

We used the size- and age-structured version of the Stock Synthesis program (hereafter referred to as Synthesis, Methot, 1990, 1998, 2000) to model the population dynamics of the California sheephead stock. Synthesis is an age- and size-structured model that projects the survival, growth, and reproduction of individual age classes. It consists of three main components: (1) A population model that projects the size and age structure. (2) An observation model that uses data inputs (in this case landings, abundance indices, and length composition data) and selectivity functions (logistic functions with potentially both ascending and descending components) to relate the simulated population to the data. (3) A statistical model that uses a likelihood approach to estimate the best-fit parameters for the model. Synthesis allows a variety of data types to be combined and used to estimate parameters in one formulation. Multiple data inputs are used in the model, including fisheries catch data (1947–2003), length composition data from each fishery, fisheries catch-per-unit-effort data, and fisheries-independent larval abundance indices (CalCOFI). The first stock assessment of California sheephead was completed by Alonzo et al. (2004), who provide more detailed information on the biological and fisheries data available for this species. A single log-likelihood function is used to calculate the total log-likelihood value associated with the model and allows emphasis factors to control the weight of each type of data and parameter in influencing the total likelihood. The likelihood calculation of the model assumed a multinomial error structure for the length compositions and log-normal error for the abundance indices. For more details on Synthesis see Methot (2000).

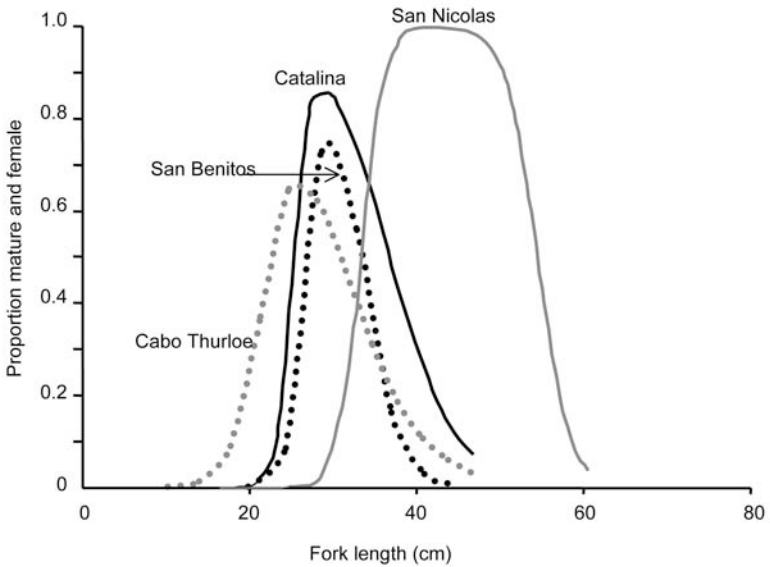


Figure 2. The combined maturity and sex-change double logistic function for the length and maturity data for the four nearshore populations. Parameters are given in Table 1.

As is typical for stage-structured stock-assessment models, Synthesis uses a two parameter logistic function to calculate spawning biomass (mature female biomass) as a function of the frequency of individuals in each age and size class. The parameters for this logistic function are typically estimated from age- or size-at-maturity data. In order to incorporate sex change into the stock assessment model, we estimated a double logistic maturity and sex-change function that gives the probability an individual is mature and female as a function of individual length (Fig. 2). This function can be used to estimate female biomass (and male biomass) from total biomass so long as a static sex-change pattern is assumed. For the results reported here, we used a version of Synthesis modified by Rick Methot to allow the maturity function to have both ascending and descending portions (*synl32r.exe*, compiled 5 April 2004). We compare the predictions of otherwise identical versions of the model that either include a typical reproductive maturity function or include both reproductive maturity and sex change.

This simple extension of the existing modeling framework incorporates removal of individuals that change sex from the spawning (or at least egg-producing) biomass of the population, but it does not consider the potential effect of male biomass on reproductive output and therefore assumes that reproduction in the population is not currently male limited. Despite this important simplifying assumption, the model is an improvement over all previous stock assessments of sex-changing fishes, none of which has incorporated sex change in any way. Furthermore, although one could theoretically include an assumed effect of male limitation, no data are available that would allow one to estimate the functional form, let alone the parameters, for a relationship relating male numbers or biomass to population reproductive output. For further discussion of these issues see Alonzo and Mangel (2004, 2005). To examine the potential for male limitation in the model, we calculated changes in both fe-

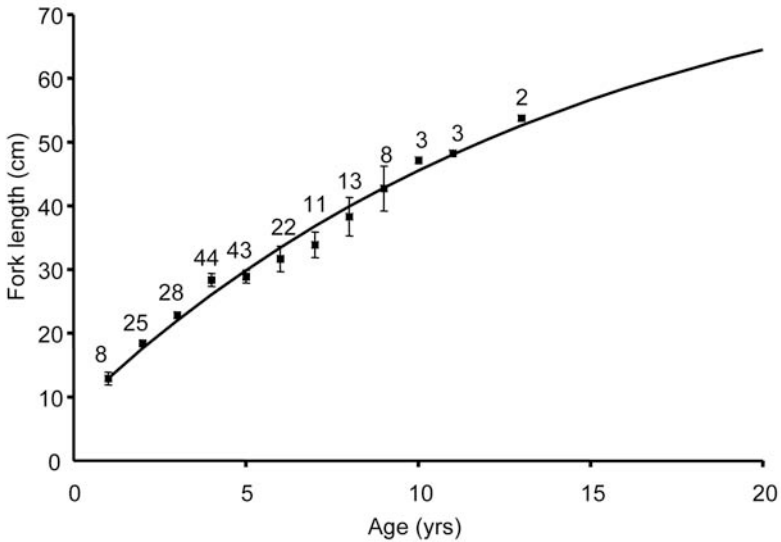


Figure 3. Size at age predicted from the best-fit growth parameters (squares) compared with the observed mean size-at-age data from Warner (1975) (curve). Error bars show the 95% confidence interval around the mean sizes at age; numbers above the points are sample sizes.

male and male biomass using the maturity and sex-change function described above. We could thus compare changes in total mature biomass, female-only biomass, and male-only biomass as functions of exploitation and determine how our conclusions were affected.

We found the best-fit estimates of growth parameters (slope k and asymptotic size L_{inf} , Fig. 3) using a Ford plot (Ford, 1933; Quinn and Deriso, 1999) with unconstrained asymptotic size and then minimizing the sum of squared deviations between the predicted and observed size at age (Hilborn and Mangel, 1997). By minimizing the sum of squared deviations between the observed and predicted patterns for the best available data, we also estimated the slope (k) and size at maturity or sex change (L_{50}) of one ascending and one descending logistic function (Hilborn and Mangel, 1997). The maturity function is the product of these two functions (Fig. 2). For the baseline model, we used the best available growth and age data, which came from Catalina Island (Warner, 1975). In order to examine the effect of variation in patterns of growth, maturity, and sex change on the predictions of the model, we used the same method to find these parameters for the three other nearshore populations for which data were available (Cabo Thurloe and San Benitos Island, in Mexico, and San Nicolas Island, off southern California; Warner, 1975; Cowen, 1990) and used each set of growth and reproductive parameters (given in Table 1, Fig. 2) in a separate run of the model. Although data were also available for Guadelupe Island (Fig. 1), we did not include them in our analyses, as this population is very isolated from the nearshore populations and probably represents a separate stock. Because maturity and sex-change schedules are likely to interact strongly with growth curves, we treated these existing sets of life-history parameters as “packages” rather than examining all possible combinations of parameter estimates. To estimate individual variation in growth, we used the variation in mean size-at-age data for Catalina Island reported in by Warner (1975: fig. 3.2) to estimate the coefficient of variation in size at age

Table 1. Total mortality (natural and fishing), growth, maturity, and sex-change parameter estimates for four nearshore populations from Warner (1975) (Catalina Island) and Cowen (1990) (other locations). All lengths have been converted to fork lengths (in cm) for consistency with the available fisheries data. The data from Catalina Island were the best available for estimation of these parameters and were therefore used in the baseline stock-assessment model.

Parameter	Catalina Island	San Benitos Island	Cabo Thurloe	San Nicolas Island
Total mortality	0.35	0.43	0.41	0.29
Maximum age in sample	20	10	12	21
Estimated L_{mf}	83.86	130.00	145.86	85.19
k growth	0.068	0.026	0.028	0.064
L1 (age 1)	12.92	7.35	10.16	16.40
L2 (age 13)	52.49	40.22	49.38	53.30
L_{50} maturity	25.24	26.90	21.80	33.30
L_{50} sex change	36.77	33.40	30.90	54.50
k maturity (slope)	1.060	0.880	0.520	0.780
k sex change (slope)	0.32	0.46	0.21	0.54

by taking the average across all age groups ($CV = 0.11$). We estimated the variation in growth externally because the available fishery length-composition data did not show any clear modal progression of cohorts that would allow the model to estimate the variation in individual growth reliably. We used the best available data on female fecundity (Warner, 1975; DeMartini et al., 1994) to estimate female size-dependent egg production [individual annual egg production = (somatic weight in kg) (15,000 eggs per batch per kg) (86 egg batches per year)]. No information on spatial or temporal variation in fecundity was available for California sheephead.

We also examined the effect of uncertainty in natural mortality (M) on the predictions of the model. Existing estimates of total mortality (Z) for California sheephead did not separate natural mortality (M) from fishing mortality (F) and ranged from 0.29 to 0.55 (Table 1, Cowen, 1990). Similarly, estimates of maximum observed age range from 9 to 21 and are probably distorted by fishing mortality (Limbaugh, 1955; Warner, 1975; Cowen, 1990). We used the best estimates of maximum age and the Hoenig (1983) relationship to estimate a range of reasonable M values for California sheephead. A single fish reported to be 53 yrs old on the basis of its opercles (Fitch, 1974) was not used, because all other reported samples gave much lower estimates of maximum ages, between 15 and 30 yrs (Limbaugh, 1955; Warner, 1975; Cowen, 1990). Because the best-documented maximum observed age of a fish was 21 yrs (Cowen, 1990), we used the Hoenig relationship (Hoenig, 1983) to estimate a baseline $M = 0.20$, but we also considered the possibility that the M was lower ($M = 0.15$, consistent with maximum age of 30 yrs) as maximum observed age would be reduced by exploitation. We also examined the effect of a higher value ($M = 0.3$, consistent with maximum age of 15 yrs) on the results of the model.

Given the best-fit model, Synthesis estimates the total biomass, spawning (i.e., mature female) biomass, and recruitment at equilibrium as functions of different levels of exploitation. The estimated total biomass and the size at maturity and sex-change function (Fig. 2) were used to estimate the total mature biomass (mature male and female) and male biomass. On the basis of the model's estimates, SPR was calculated from the estimated female biomass, total mature biomass, and male biomass. The SPR based on male biomass is included as a measure of the potential for male limitation.

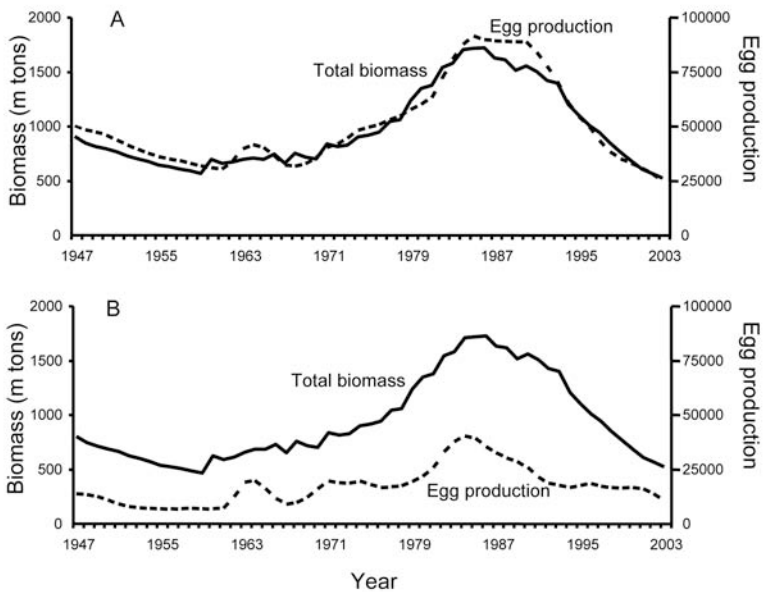


Figure 4. Historical total biomass and egg production estimated from the baseline California sheephead stock assessment model with (A) and without (B) inclusion of sex change (for $M = 0.2$ and the Catalina Island parameters from Table 1).

Synthesis can also be used to estimate the selectivity functions associated with the fisheries for California sheephead on the basis of fishery length-composition data. The statistical model found the parameters for the ascending and if applicable the descending portions of the selectivity functions that best fit the data and population projections. Because no age data associated with the fisheries or surveys exist, the selectivities were fit as only size dependent. See Alonzo et al. (2004) for further information on data inputs, parameter estimation, and initial model selection.

RESULTS

THE EFFECT OF INCLUDING SEX CHANGE ON STOCK DYNAMICS.—Unless otherwise noted, results are given for the life history parameters from Catalina Island with $M = 0.2$ (Table 1; Warner, 1975). Independent of whether sex change was considered, both total and spawning-stock biomass were estimated to be lower in the 1950s than at any time since, and current biomass is higher than this “initial” biomass but lower than that estimated for 1960–1990 (Fig. 4). The estimated spawning-stock biomass and total biomass show similar trends. Incorporation of sex change did not affect the reconstructed pattern of total biomass (Fig. 4), but spawning biomass (egg production) was overestimated when sex-change was omitted (Fig. 4A,B). The fishery selectivities estimated from fishery length-composition data indicated that all of the fisheries were positively size selective, although fisheries differed in the precise form of selection (Fig. 5). Although the live-trap and recreational fisheries remove smaller fish than the hook-and-line and setnet commercial fisheries, all four fisheries select mainly large individuals (as evidenced by the absence of a descending portion of the

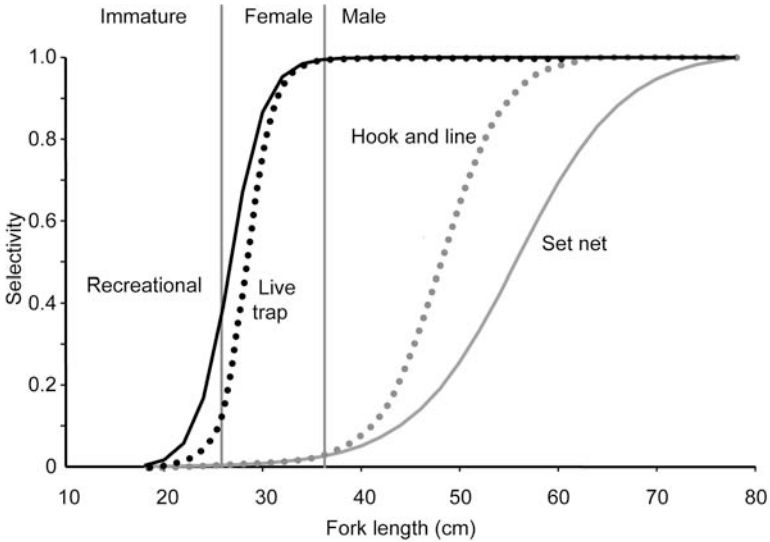


Figure 5. Size selectivities for the recreational and commercial (live trap, setnet, and hook-and-line) fisheries estimated with the baseline Synthesis model. The vertical solid lines represent the L_{50} size at maturity and size at sex change for the baseline model. Results are shown for the case where $M = 0.2$ and for the Catalina Island life-history parameters but are essentially the same for other values from Table 1.

selectivity functions). Therefore, although mature females are taken by some fisheries, the largest proportion of fish removed by the fishery are males (Fig. 5).

THE EFFECT OF FEMALE AND MALE BIOMASS ON TARGET MEASURES.—On the basis of the policy set forth in the Nearshore Fishery Management Plan from the California Department of Fish and Game (CDFG, 2002), we focused on determining how the estimated SPR (at the estimated level of current exploitation) compares to a target $SPR_{50\%}$. Although the validity of $SPR_{50\%}$ as a target measure could be debated, we use this measure for illustrative purposes to determine how our assessment of the current status of the stock, including estimated SPR and our conclusions about it, depends on sex change, the reduction of male biomass, and variation in patterns of sex change.

SPR was estimated to be higher at a given level of exploitation (i.e., to be reduced less) when sex change was not taken into account than when it was; because the fisheries remove mainly large individuals (which are male), omitting sex change leads to overestimation of the reduction in female biomass as a result of fishing. As would be expected, however, the estimated change in total mature (male and female) biomass was the same whether or not sex change was included (Fig. 6). When the estimated exploitation rate for California sheephead in 2003 from the baseline Synthesis model (0.23) was used, the female SPR was estimated to be reduced to 55% of the unfished level (Fig. 7A), but male and total mature SPR were estimated to be reduced by a much greater amount (total mature SPR = 0.17, male SPR = 0.07, Fig. 7A). If sex change is not compensatory in this species (e.g., if sex change does not depend on current sex ratio), male depletion and possibly limitation are predicted at the current level of exploitation.

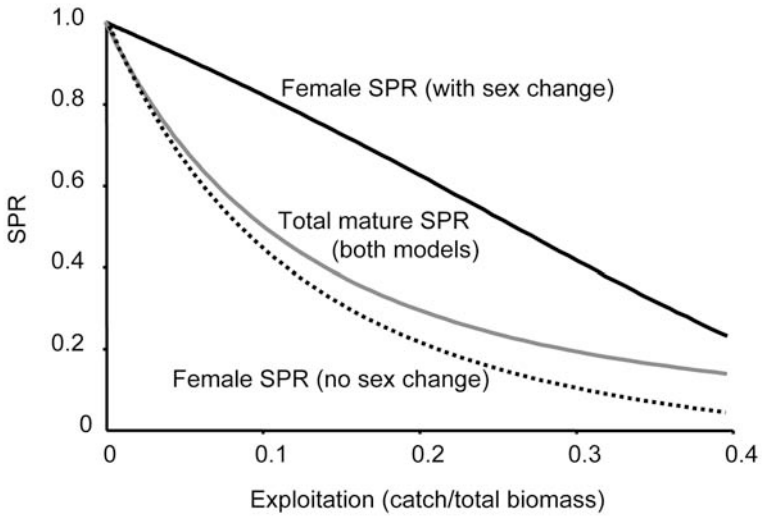


Figure 6. Spawning potential ratio (SPR) as a function of exploitation, estimated from female or total mature biomass, for versions of the stock assessment model that include or ignore sex change (with Catalina Island life-history parameters from Table 1 and $M = 0.2$).

For the most likely level of natural mortality ($M = 0.2$), the SPR based on total mature biomass was estimated to be (at the current exploitation rate of 0.23) approximately 15% of the unfished SPR. Lower M resulted in prediction of even greater estimated reduction in SPR (total mature SPR = 0.09, Fig. 7B), but with higher M , the prediction fell at the target level (total mature SPR = 0.5, Fig. 7C). Clearly, both M and the biomass measure used to estimate SPR affect assessment. (Fig. 7). As expected, uncertainty in M leads to uncertainty in the assessment of the current status of the stock (e.g., female SPR for $M = 0.15$ to 0.30 leads to SPR = 0.45 to 0.78, Fig. 7A–C), but uncertainty in whether female biomass or total mature biomass better captures spawning potential yields similar uncertainty (e.g., SPR = 0.16 vs 0.55, Fig. 7A) all else being equal.

THE EFFECT OF SITE-SPECIFIC LIFE HISTORY PARAMETERS.—Although California sheephead is thought to be a single genetic stock, regional differences in age and size at maturity and sex change have been observed. Our comparison of various patterns of fixed maturity and sex change does not capture the effect of individual plasticity on the stock dynamics, but it does allow us to consider how realistic differences in growth, maturity, and sex-change parameters are predicted to affect our estimates of the current status of the stock. It therefore gives a sense of how our estimates of SPR might differ if we are wrong about the best estimates of these life-history parameters either because they vary spatially or because they are plastic and change in response to local circumstances.

Our comparison of the four nearshore California study areas revealed that results predicted for Cabo Thurlow are quite similar qualitatively to those for Catalina Island (Fig. 8A,D). In contrast, for the life-history parameters for San Nicolas Island and San Benitos Island, a severe depression of the female SPR is predicted at the current exploitation rate (Fig. 8B,C). Maturity and sex change at San Nicolas Island occurred at much larger sizes (see Table 1), and few fish would reach maturity or sex change

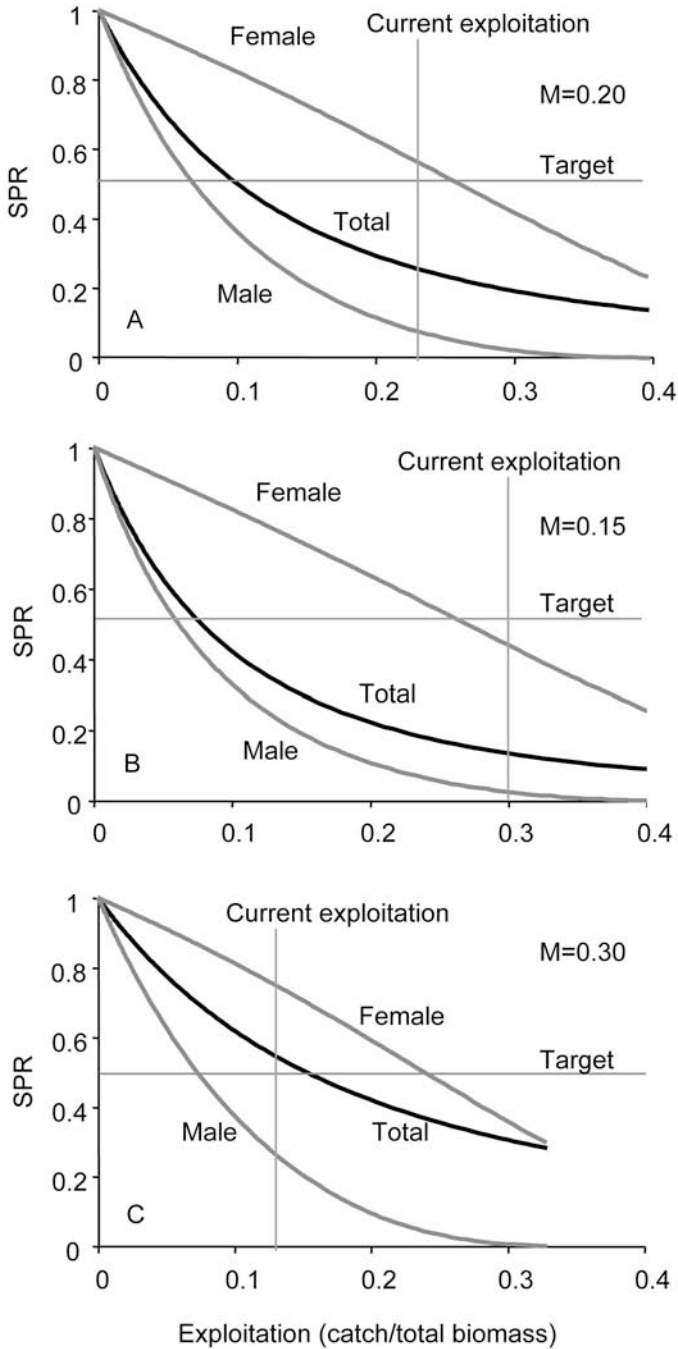


Figure 7. Spawning potential ratio (SPR) as a function of exploitation (estimated from female, male, or total mature biomass) for three different natural mortality values. Estimated current exploitation rates and target $SPR_{50\%}$ are also shown (baseline model with Catalina Island life-history parameters from Table 1 otherwise).

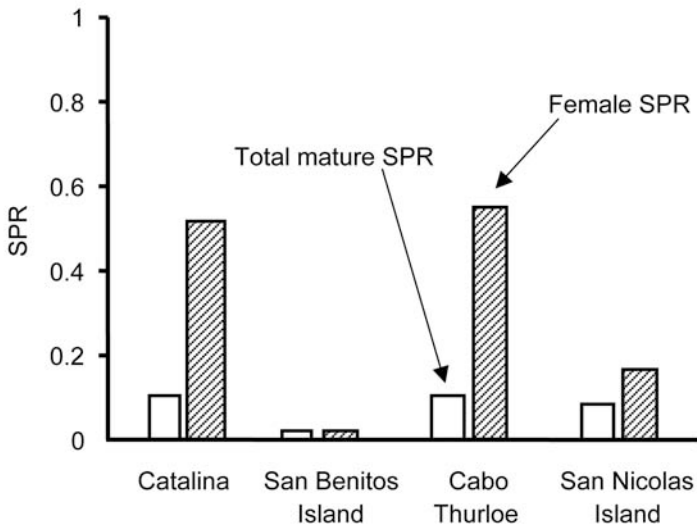


Figure 8. SPR based on total mature and female biomass estimated from life-history parameters (from Table 1) from the four populations at the estimated current level of exploitation (0.23 for $M = 0.2$).

given the estimated fishery selectivities (Fig. 5). For the parameters obtained from San Benitos Island, sex change happens so soon after maturity that overall production of females is low and would be less able to withstand exploitation. The growth, maturity, and sex-change parameters used obviously have a large effect on the estimated SPR independent of whether female or total mature biomass is used, but these parameters also affect the relative difference between the estimates of SPR based on female and on total mature biomass (e.g., the populations differ in the height of the bars).

DISCUSSION

Although increasing evidence indicates that protogynous sex change affects stock dynamics, we clearly still do not have standard methods to address the many issues that arise when this relatively common reproductive pattern is considered. Our results show that ignoring protogynous sex change not only fails to take into account the tendency of size-selective fisheries to remove proportionally more large males than mature females but can also lead to failure to detect changes in recruitment to the fishery until a large degree of male depletion has occurred. We demonstrate that assessments ignoring sex change can underestimate spawning biomass while overestimating the effect of a size-selective fishery on female biomass (Figs. 4, 5). However, if sex change is plastic, such that the size at sex change decreases when large individuals are removed from the population (see, e.g., Warner and Swearer, 1991), then our estimates of changes in female biomass, made on the assumption of fixed sex change, would underestimate the effect of fishing on the female spawning biomass of the stock. Our results demonstrate that, given the importance for stock assessment of correctly calculating changes in total mature and female biomass, the effect of protogynous sex change on stock dynamics should be considered, but they also

indicate that incorporating sex change alone will not be sufficient. Some knowledge of male depletion, plasticity in sex change, and how these factors affect the spawning potential of the stock will also be necessary.

Our results clearly show that male depletion can be substantial in the presence of a strongly size-selective fishery and a fixed pattern of sex change (Fig. 7), yet no convention exists regarding how changes in male spawning potential should be considered when stocks are managed. Although arguments can be made that female biomass is the most essential to reproductive output in a population, assuming that male biomass plays no role may not be wise. The relationship between male biomass and reproductive output is also unlikely to exhibit the same functional form as that for female biomass. Instead, changes in male biomass may lead to abrupt nonlinear changes in stock dynamics, having little effect at low levels of exploitation but large effects when males are sufficiently reduced in biomass to affect fertilization rates (Alonzo and Mangel, 2004, 2005). Where the appropriate target levels for female SPR and male SPR fall will depend on the biology and mating system of the particular species. Further empirical data are needed before we can determine how and when male density affects population reproductive output in protogynous species. The need to understand the effect of males on reproductive output is not limited to protogynous species but will affect any species in which fishing imposes greater mortality on males than on females.

Our comparison of life-history parameters from various locations leads to very different conclusions regarding the status of the stock, but we do not know the extent to which these parameters represent population-specific fixed differences or plastic responses to local circumstances. Furthermore, these parameters affected the degree to which use of female biomass and total mature biomass led to different conclusions. Spatial and temporal variation in life-history characteristics obviously represents a key source of uncertainty for management, but in protogynous species, knowledge is also needed of what biological factors determine patterns of sex change. As described above, if local sex ratio affects size at sex change (i.e., if the largest individuals always change sex, independent of absolute body size) then male depletion would not occur, but female spawning biomass would be reduced more than it would in species that change sex at fixed size. Because we know little about the cues that trigger sex change in California sheephead, we cannot know how environmental conditions, density, size distribution, age structure and sex ratio affect the process. Clearly, drawing reliable conclusions about the relative importance of male depletion and reduction of female spawning biomass in this species depends on better information about intraspecific variation, the relative importance of endogenous and exogenous cues to sex change, and the effect of removing large males on sex ratio and reproductive patterns.

The results presented here demonstrate that incorporating sex change into stock-assessment models is possible and important, but inclusion of sex change alone is clearly not sufficient. First, we must consider the effect of male density or biomass on reproductive output. Although modeling methods that address this issue are certainly needed, more empirical work is also needed to determine the circumstances under which males limit reproduction and the functional form of the relationship between male density and reproductive output. These results will probably show that the relationship depends strongly on the biology and mating system of individual species, so more information on reproductive behavior and allocation will be needed before

this issue can be fully addressed. In addition, our modeling methods need a greater ability to incorporate plasticity in reproductive patterns (including but not limited to sex change). Again, theoretical methods will not be sufficient; more information on species-specific patterns of plasticity in sex change and other reproductive patterns will be needed. Developing standard stock-assessment methods that can incorporate the effects of protogynous sex change, male density, and plasticity in reproductive pattern on spawning potential certainly represents a challenge, but inclusion of these biological issues should reduce uncertainty and error in our ability to manage and assess the status of commercially and recreationally exploited species.

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LITERATURE CITED

- Adreani, M. S., B. E. Erisman, and R. R. Warner. 2004. Courtship and spawning behavior in the California sheephead, *Semicossyphus pulcher* (Pisces: Labridae). *Environ. Biol. Fish.* 71: 13–19.
- Alonzo, S. H. and M. Mangel. 2004. The effects of size-selective fisheries on the stock dynamics of and sperm limitation in sex changing fish: California sheephead (*Semicossyphus pulcher*) as an illustrative example. *Fish. Bull., U.S.*, 102: 1–13.
- _____, and _____. 2005. Sex change rules, stock dynamics, and the performance of spawning per recruit measures in protogynous stocks. *Fish. Bull., U.S.*, 103: 229–245.
- _____, M. Key, T. Ish, and A. MacCall. 2004. Status of the California Sheephead (*Semicossyphus pulcher*) stock. California Department of Fish and Game Report, <www.dfg.ca.gov/mrd/sheephead2004>.
- Ayres, W. O. 1854. Description of new fishes from California. *Proc. Calif. Acad. Natl. Sci.* 1: 3–22.
- Bernardi, G., L. Findley, and A. Rocha-Olivares. 2003. Vicariance and dispersal across Baja California in disjunct marine fish populations. *Evolution* 57: 1599–1609.
- Birkhead, T. R. and A. P. Møller. 1998. Sperm competition and sexual selection. Academic Press, San Diego. 826 p.
- Breder, C. M. and D. E. Rosen. 1966. Modes of reproduction in fishes. T.F.H. Publications, Neptune City. 941 p.
- Caselle, J. E. and S. Hamilton. 2006. California sheephead stock assessment. California Department of Fish and Game Report P0470012.
- CDFG (California Department of Fish and Game). 2002. Nearshore fishery management plan. California Department of Fish and Game, Marine Region, Monterey, California. 222 p.
- Coleman, F. C., A. Eklund, and C. B. Grimes. 1999. Management and conservation of temperate reef fishes in the grouper-snapper complex of the southeastern United States. *Am. Fish. Soc. Symp.* 23: 233–242.

- Conover, D. O. and S. B. Munch. 2002. Sustaining fisheries yields over evolutionary time scales. *Science* 297: 94–96.
- Cowen, R. K. 1985. Large-scale pattern of recruitment by the labrid, *Semicossyphus pulcher*: causes and implications. *J. Mar. Res.* 43: 719–742.
- _____. 1990. Sex change and life history patterns of the labrid, *Semicossyphus pulcher*, across an environmental gradient. *Copeia* 1990: 787–795.
- Davis, G. E. and T. W. Anderson. 1989. Population estimates of four kelp forest fishes and an evaluation of three in situ assessment techniques. *Bull. Mar. Sci.* 44: 1138–1151.
- de Roos, A. M., D. S. Boukal, and L. Persson. 2006. Evolutionary regime shifts in age and size at maturation of exploited fish stocks. *Proc. R. Soc. Lond. B Biol. Sci.* 273: 1873–1880.
- DeMartini, E. E., A. M. Barnett, T. D. Johnson, and R. F. Ambrose. 1994. Growth and production estimates for biomass-dominant fishes on a southern California artificial reef. *Bull. Mar. Sci.* 55: 484–500.
- Fitch, J. E. 1974. Offshore fishes of California. Department of Fish and Game, State of California, Sacramento, California. 79 p.
- Ford, E. 1933. An account of the herring investigations conducted at Plymouth during the years from 1924–1933. *J. Mar. Biol. Assoc. U.K.* 19: 305–384.
- Garant, D., I. A. Fleming, S. Einum, and L. Bernatchez. 2003. Alternative male life-history tactics as potential vehicles for speeding introgression of farm salmon traits into wild populations. *Ecol. Lett.* 6: 541–549.
- Helfman, G. S., B. B. Collette, and D. E. Facey. 1997. The diversity of fishes. Blackwell Science, Malden. 528 p.
- Heppell, S. S., S. A. Heppell, F. C. Coleman, and C. C. Koenig. 2006. Models to compare management options for a protogynous fish. *Ecol. Appl.* 16: 238–249.
- Hilborn, R. and M. Mangel. 1997. The ecological detective: confronting models with data. Princeton Univ. Press, Princeton. 315 p.
- Hoenig, J. M. 1983. Empirical use of longevity data to estimate mortality rates. *Fish. Bull., U.S.*, 81: 898–903.
- Limbaugh, C. 1955. Fish life in the kelp beds and the effects of kelp harvesting. University of California, Institute of Marine Resources, La Jolla.
- Lorenzen, K. and K. Enberg. 2002. Density-dependent growth as a key mechanism in the regulation of fish populations: evidence from among-population comparisons. *Proc. R. Soc. Lond. B Biol. Sci.* 269: 49–54.
- Lutnesky, M. M. F. 1994. Density-dependent protogynous sex change in territorial harem fishes: models and evidence. *Behav. Ecol.* 5: 375–383.
- Method, R. D. 1990. Synthesis model: an adaptable framework for analysis of diverse stock assessment data. Pages 259–277 *in* L. L. Low, ed. Proc. Symp. Application of Stock Assessment Techniques to Gadids. International Northern Pacific Fisheries Committee Bulletin. Seattle, Washington.
- _____. 1998. Program documentation for the Stock Synthesis model. Northwest Fisheries Science Center, National Marine Fisheries Service. 40 p.
- _____. 2000. Technical description of the Stock Synthesis assessment program. U.S. Department of Commerce. NOAA Tech. Memo. NMFS-NWFSC-43. 46 p.
- Olsen, E. M., M. Heino, G. R. Lilly, M. J. Morgan, J. Brattey, B. Ernande, and U. Dieckmann. 2004. Maturation trends indicative of rapid evolution preceded the collapse of northern cod. *Nature* 428: 932–935.
- Palmer-Zwahlen, M., J. O'Brien, and L. Laughlin. 1993. Live-fish trap fishery in southern California 1989–1992 and recommendations for management. Marine Resources Division, Department of Fish and Game, State of California, Sacramento, California.
- Pitcher, T. J. 1993. Behaviour of teleost fishes. Chapman and Hall, London. 715 p.
- Quinn, T. J. and R. B. Deriso. 1999. Quantitative fish dynamics. Oxford University Press, Oxford. 542 p.

- Rosales-Casian, J. A. and J. R. Gonzalez-Camacho. 2003. Abundance and importance of fish species from the artisanal fishery on the Pacific Coast of Northern Baja California. *Bull. South. Calif. Acad. Sci.* 102: 51–65.
- Stephens, J. 2001. California sheephead. Pages 155–156 in W. S. Leet, C. M. Dewees, R. Klingbeil, and E. J. Larson, eds. California's living marine resources: a status report. The Resources Agency, California Department of Fish and Game, Sacramento, California.
- Thresher, R. E. 1984. Reproduction in reef fishes T.F.H. Publications, Neptune City. 399 p.
- Waples, R. S. and R. H. Rosenblatt. 1987. Patterns of larval drift in southern California USA marine shore fishes inferred from allozyme data. *Fish. Bull., U.S.*, 85: 1–12.
- Warner, R. R. 1975. The reproductive biology of the protogynous hermaphrodite *Pimelometopon pulchrum* (Pisces: Labridae). *Fish. Bull., U.S.* 73: 262–283.
- _____ and S. E. Swearer. 1991. Social control of sex change in the bluehead wrasse, *Thalassoma bifasciatum* (Pisces, Labridae). *Biol. Bull. (Woods Hole)* 181: 199–204.
- Young, K. and C. Lowe. 2006. Breeding season assessment of gonadal form and function in California sheephead. California Department of Fish and Game Report, Sacramento, California.

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