SIZE-SELECTIVE HARVESTING ALTERS LIFE HISTORIES OF A TEMPERATE SEX-CHANGING FISH

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Abstract. Selective mortality, whether caused naturally by predation or through the influence of harvest practices, initiates changes within populations when individuals possessing certain heritable traits have increased fitness. Theory predicts that increased mortality rates will select for changes in a number of different life history characteristics. For example, fishing often targets larger individuals and has been shown repeatedly to alter population size structure and growth rates, and the timing of maturation. For sex-changing species, selective fishing practices can affect additional traits such as the mature population sex ratio and the timing of sexual transformation. Using historical comparisons, we examined the effects of exploitation on life history characteristics of California sheephead, *Semicossyphus pulcher*, a temperate protogynous (female–male sex changer) labrid that inhabits nearshore rocky environments from central California, USA, to southern Baja California, Mexico. Recreational fishing intensified and an unregulated commercial live-fish fishery developed rapidly in southern California between the historical and current studies. Collections of *S. pulcher* from three locations (Bahía Tortugas, Catalina Island, and San Nicolas Island) in 1998 were compared with data collected 20–30 years previously to ascertain fishery-induced changes in life history traits. At Bahía Tortugas, where fishing by the artisanal community remained light and annual survivorship stayed high, we observed no changes in size structure or shifts in the timing of maturation or the timing of sex change. In contrast, where recreational (Catalina) and commercial (San Nicolas) fishing intensified and annual survivorship correspondingly declined, males and females shifted significantly to smaller body sizes, females matured earlier and changed sex into males at both smaller sizes and younger ages and appeared to have a reduced maximum lifespan. Mature sex ratios (female : male) increased at San Nicolas, despite a twofold reduction in the mean time spent as a mature female. Proper fisheries management requires measures to prevent sex ratio skew, sperm limitation, and reproductive failure because populations of sequential hermaphrodites are more sensitive to size-selective harvest than separate-sex species. This is especially true for *S. pulcher,* where different segments of the fishery (commercial vs. recreational) selectively target distinct sizes and therefore sexes in different locations.

Key words: historical comparisons; kelp forest fish; maturation; protogyny; selective fishing pressure; Semicossyphus pulcher; *sequential hermaphrodite; sex ratios; size-at-age.*

INTRODUCTION

Mortality is an important agent of selection. By targeting individuals with specific traits, selective mortality exerts evolutionary changes within populations when it influences reproductive success. Both natural and artificial selection will enhance the fitness of certain phenotypes, triggering shifts in morphological and life history characteristics through time. For example,

natural selection caused Darwin's finches (*Geospiza fortis*) to undergo shifts in body size and beak size owing to climatic effects on resource availability (Grant and Grant 1993), while natural guppy (*Poecilia reticulata*) populations exhibit rapid and predictable life history evolution (e.g., changes in the timing of maturation) in response to size-selective predation (Reznick et al. 1990, Reznick and Ghalambor 2005). Human-induced evolutionary change is becoming a pervasive global problem (Palumbi 2001), and there is a growing concern that selective harvesting may have detrimental consequences for life histories of exploited organisms (Stokes et al. 1993, Hutchings 2000, Law

2000). Fishing commonly targets the largest and thus the fastest-growing individuals of an age class, thereby selecting for smaller sizes and reduced yields. After only a few generations, this type of selection has been shown experimentally to favor slow-growing phenotypes (Conover and Munch 2002). Following the cessation of human-induced selection, it is unknown whether natural selection is of sufficient strength in the short-term to counter that evolutionary change (e.g., Law 2000). Modern fishing practices are essentially large-scale, uncontrolled selection experiments with unknown future consequences.

The development of life history theory (e.g., Stearns 1992) allows predictions about how extrinsic mortality can influence the evolution of traits that determine how organisms allocate resources to reproduction (e.g., growth rate, timing of maturation, reproductive investment, fecundity). Selection resulting from extractive fishery practices induces changes in life histories and has been shown to decrease the age and size at sexual maturity (Jørgensen 1990, Rijnsdorp 1993, Grift et al. 2003, Olsen et al. 2004, 2005), affect growth rates (Millner and Whiting 1996, Sinclair et al. 2002), and reduce mean sizes (Ricker 1981). These life history shifts are predicted to affect fecundity, population growth rates, and ultimately fisheries yields (Jennings et al. 1998, Hutchings 2005, Rijnsdorp et al. 2005). Unfortunately, many management strategies do not recognize the potential for selective harvesting to induce changes within populations, and they can cause detrimental impacts to important yield-related life history traits.

Fisheries that exploit hermaphroditic species may alter other life history characteristics, including operational (i.e., mature) sex ratios (Alonzo and Mangel 2004, 2005, Heppell et al. 2006). Operational sex ratios in sequential hermaphrodites (i.e., individuals which mature first as one sex and are capable of changing to the other sex) are often skewed in favor of the sex that matures first (Allsop and West 2004), and thus the sex that is smaller in size and younger in age. Size-selective harvest mortality targeted at the largest fish is therefore indirectly sex-selective, and it often introduces greater bias in already skewed operational sex ratios (Beets and Friedlander 1992, Buxton 1993, Birkeland and Friedlander 2001). Changes in the operational sex ratio are worrisome because they create an increased potential for sperm limitation and reproductive failure in exploited populations (Alonzo and Mangel 2004, Heppell et al. 2006, Sato and Goshmia 2006).

Size and sex-selective harvest mortality also have predictable consequences for the timing of sex change in sequential hermaphrodites. For species in which sex change is under social control and is a phenotypically plastic response to local conditions (Robertson 1972, Shapiro 1980), the size-advantage hypothesis (Ghiselin 1969, Warner 1975a) predicts that sex change will occur when individuals experience higher reproductive success as one sex when small or young and a greater payoff in reproductive success as the opposite sex when large or old. By recasting the size-advantage hypothesis in terms of reproductive value (i.e., expected future reproductive success) and applying it to the scale of a local mating group, an individual is predicted to change sex based on its reproductive value as a male or female, relative to the size and sexual composition of other individuals in the mating group (Warner 1988, Munday et al. 2006). Generally, individuals refrain from changing sex when small or young in populations characterized by many large individuals of the alternate sex or a near-optimal sex ratio. When a population contains few individuals of the secondary sex or has a sex ratio skewed severely from its optimum, sex change can occur at smaller sizes and younger ages. Because fisheries often target the largest individuals in a population (which are predominately one sex for sequential hermaphrodites), it is expected that harvest practices will shift the timing of sexual transformation to smaller sizes and younger ages. What is not clear in most cases is whether these shifts will be immediate (e.g., social control and local conditions) or long-term (e.g., evolutionary). A number of studies have implicated fishing pressure as a cause for declines in the size at sex change (shrimp [e.g., Hannah and Jones 1991]; fish [e.g., Platten et al. 2002, Hawkins and Roberts 2003]). This becomes particularly problematic when the timing of sexual transformation is developmentally fixed (e.g., McGovern et al. 1998, Alonzo and Mangel 2004).

Numerous researchers have examined the effects of fishing mortality on life histories of gonochoristic (single-sexed) species (reviewed in Law 2000); however, fewer have investigated the impacts on hermaphroditic species (e.g., Beets and Friedlander 1992, Buxton 1993, McGovern et al. 1998, Platten et al. 2002, Hawkins and Roberts 2003), probably because the major global fisheries are temperate and few of the target species are hermaphroditic. Yet, the effects of selective fishing practices on sequential hermaphrodites need to be considered because many of the snapper and grouper species composing important tropical fisheries are sex changers (Bannerot et al. 1987). Here we use historical comparisons to examine the effects of fishery-induced selective mortality on life histories of California sheephead (*Semicossyphus pulcher*), a temperate protogynous (i.e., female first) wrasse (family Labridae) which inhabits kelp forests and nearshore rocky reefs along the Pacific coast of North America. In 1998, at the height of the commercial fishery, we collected samples of *S. pulcher* from sites in southern California and Baja California, Mexico. Historical data, collected 20–30 years previously at three locations by Warner (1975b) and Cowen (1990), allowed us to examine whether recent increases in exploitation at two of the three sites has altered population parameters and induced shifts in life history traits. Additionally, recent models parameterized with data from *S. pulcher* provide a unique opportunity to test predictions about the effects of size-

selective fishing and sex change rules on life history characteristics of this protogynous hermaphrodite (Alonzo and Mangel 2004, 2005).

California sheephead fishery

A relatively important commercial fishery for California sheephead existed in southern California during the beginning of the 20th century, but declined due to poor market demand. By 1950 this species was no longer targeted by commercial fisherman (Stephens 2001). However, in the late 1980s, commercial interests were revived by the development of a live-fish fishery supplying the Asian seafood market. Unregulated commercial landings rapidly increased, with peak landings of over 163 000 kg in 1997 (Stephens 2001). This fishery uses both hook-and-line gear and traps to land live, plate-sized fish, a size at which individuals are predominately female (Alonzo et al. 2004). Due to their conspicuous coloration and curious nature, *S. pulcher* have been a popular target of spear fisherman and recreational anglers since the mid-1960s, and recreational landings often exceed commercial landings (Stephens 2001, Alonzo et al. 2004). Recreational anglers catch all size classes of *S. pulcher*, preferring to retain large individuals, while spear fisherman selectively pursue the largest fish that are predominately male and provide easy targets owing to their territory-guarding behavior (Adreani et al. 2004). Since the inception of the commercial fishery and the peak of the recreational fishery in the 1980s, catch per unit effort has declined precipitously in both fisheries (Alonzo et al. 2004). Recent regulatory changes after 1999 (e.g., size and bag limits, limited entry to commercial fishery) have been implemented in order to decrease the take of small fish for the live-fish trade and reduce fishing pressure on this species (Stephens 2001, Alonzo et al. 2004). California sheephead also form a fairly significant portion of the catch (~25%) in the artisanal fisheries of Baja California, Mexico (Rosales-Casian and Gonzalez-Camaho 2003).

Because the intensity of commercial and recreational harvesting often differs from site to site and movements of adult *S. pulcher* are minimal (Topping et al. 2005, 2006), populations are exposed to different forms of size-selective mortality throughout their range. This variation makes it difficult to forecast an overall species-level, range-wide response to exploitation, but localized effects are somewhat more predictable. At sites where the commercial live-fish fishery selectively harvests smaller and younger females, we predict that maturation will occur at earlier ages and smaller sizes. Shifts in the timing of sex change will also be expected at sites where intense commercial fishing reduces the mean lifespan and at sites where males are selectively targeted. Selective extraction may also disrupt sex ratios, depending on the rapidity at which individuals change sex and compensate for removals due to fishing.

Methods

General biology and study locations

California sheephead, *Semicossyphus pulcher*, are large (up to 94.1 cm in total length) temperate wrasses (family Labridae) which inhabit nearshore rocky reefs and kelp beds from Monterey Bay, central California, USA to Cabo San Lucas, Baja California, Mexico, including the Gulf of California and Isla Guadalupe from the intertidal zone to depths of 90 m (Love et al. 2005). Fish are occasionally reported north of Point Conception and become rare south of Punta Abreojos, Baja California. Like many labrids, *S. pulcher* are protogynous hermaphrodites and are capable of changing sex from female to male through a documented series of gonadal changes as well as morphological color changes (Warner 1975b). Males in the terminal phase (TP) are dichromatic with a black head and tail region and a pinkish midsection, while females in the initial phase (IP) are predominately monochromatic with red to pink body coloration. Large males establish and defend territories where they court females with whom they pair spawn during the reproductive season (Adreani et al. 2004), which lasts roughly from May through September (Warner 1975b, Cowen 1990). These fish are important predators on sea urchins, crabs, and other benthic invertebrates, although feeding preferences (Cowen 1986) and growth rates (Cowen 1990) change with prey availability throughout their range. Home ranges are relatively small (averaging 15 000 m^2; Topping et al. [2005]) and individuals appear to show site fidelity (Topping et al. 2006). Recruitment of sheephead is generally consistent from year to year in the southern and central part of its range, but it becomes more episodic to the north, reportedly corresponding with El Niño flow reversals (Cowen 1985).

To examine changes in life history characteristics of *S. pulcher*, from May to October 1998 we collected samples at three focal sites (Fig. 1) targeted 20–30 years previously by Warner (1975b) and Cowen (1990). These sites included Bahía Tortugas (BT; 27°37′ N, 114°51′ W; sampled by Cowen from 1981 to 1982 and labeled as Cabo Thurloe), Catalina Island (CAT; 33°27′ N, 118°29′ W; studied by Warner from 1969 to 1971), and San Nicolas Island (SNI; 33°12′ N, 119°28′ W; investigated from 1980 to 1982 by Cowen). Additional samples were collected historically at Isla Guadalupe and Islas San Benitos by Warner and Cowen and in 1998 at Isla Cedros, Punta Canoas, Isla San Martin, and San Clemente Island as a part of this study (Fig. 1). All study locations were characterized by moderate to high-relief rocky substrate and giant kelp, *Macrocystis pyrifera*. Populations of *S. pulcher* were virtually unfished (sites BT and SNI) or received low levels of recreational fishing pressure (site CAT) when the previous studies were conducted (see Warner 1975b, Cowen 1990). The degree to which fishing intensity has changed at these sites over the last 20–30 years differed among the study locations.
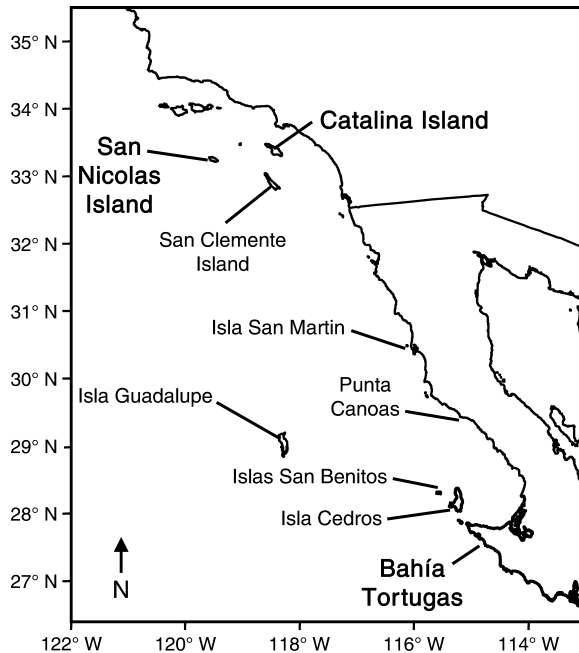
FIG. 1. Map of southern California and Baja California depicting the study area. Focal sampling locations for historical comparisons of changes in life history traits at Bahía Tortugas, Catalina Island, and San Nicolas Island are labeled in large boldface type. Other labeled sites represent historical or current collection locations used to compare the mean time spent as a mature female with population sex ratios (see Fig. 5).

Currently, BT supports a small population of artisanal fishers and receives some fishing pressure from visiting sport fishers; however, the overall effort remains light. With its proximity to population centers in southern California and popularity among sport anglers, CAT populations are subjected to heavy recreational fishing pressure (spear and hook-and-line) and low levels of commercial (live-trap) fishing. SNI is a long distance from any port and is controlled by the U.S. Navy. Recreational fishing is discouraged in much of the area; however, commercial trap fishing is allowed in its surrounding waters and increased dramatically in the late 1980s to supply the demand for live fish. Our assessment of the current fishing pressures in each location arose from discussions with fisherman, our own personal observations, and California Department of Fish and Game landing data (Wright et al. 2000). Historical assessments of the lack of fishing activity were reported by Cowen (1990). To verify whether fishing pressure has changed at these sites, we also compared estimates of annual survivorship (1 − [natural + fishing mortality]) of mature age classes between the historical and recent samples. We used age-structure data of recent samples to estimate survivorship with the Chapman-Robson equation, as reported in Cowen (1990). This comparison assumes that mortality is constant for all age classes used in the estimate and that differences in mortality rates among time periods can be solely attributed to fishing mortality.

Field collections and measurements

Individual *S. pulcher* were collected by spear similarly to methodology reported in Warner (1975b) and Cowen (1990). To ensure an unbiased collection of particular size classes in each population, we pursued and speared each fish encountered, regardless of size or sex, before proceeding to another individual (BT, $n = 91$ fish; CAT, $n = 121$ fish; SNI, $n = 57$ fish). We recorded the standard length (SL), total length (TL), wet mass (WT), and coloration (IP or TP) of each individual. Sex was determined macroscopically by observing the color, texture, and appearance of the gonads or by examining unripe ovaries for the presence of maturing eggs (as in Cowen 1990). Because reproductive activity commences in May (Warner 1975b, Cowen 1990) and our sampling occurred during or after this month, we encountered little difficulty in separating fish into immature, female, and male sexual classes. All transitional individuals (i.e., undergoing sex change and identified by intermediate morphological coloration), of which few were collected, were categorized as male for presentation and analysis.

The first three dorsal spines were removed, cleaned, and frozen for age determination using methods modified from Warner (1975b). For a random sample of 30 fish from each site, we prepared cross sections of the first dorsal spine. We used a Dremel tool to cut thin sections by removing the base and top of each spine. Sections of spine were embedded vertically in Crystal-bond (Electron Microscopy Sciences, Hatfield, Pennsylvania, USA) and polished using a lapping wheel (South Bay Technologies, San Clemente, California, USA) with 3- and 9-µm polishing films to improve ring clarity. Three observers counted annual rings using an image analysis system (Image Pro 4.5, Bethesda, Maryland, USA) connected to a compound microscope at 40× power. To determine the maximum age of *S. pulcher* at each location, we also aged the dorsal spines of the two or three largest individuals. Overall, fairly strong relationships were found between size and age for this species ($n = 211$, $r^2 = 0.62$, $P < 0.001$).

Data analysis

We extracted data reported in previous studies (Warner 1975b, Cowen 1990) in order to examine changes in life history traits and population parameters over the last 20–30 years. Raw size and mass data from the previous studies were not available beyond that in the published manuscripts, which limited certain statistical analyses. We compared growth rates by plotting mean size-at-age with corresponding 95% CI. Because raw data were not available for the historical data, significance was determined by non-overlap of 95% CI. Size-frequency distributions of mature females and males were compared between the historical and recent collections using Komolgorov-Smirnov two-sample tests. Plots of the proportion of individuals in each size or age class were used by Warner (1975b) and Cowen (1990) to visually estimate the size or age at maturity
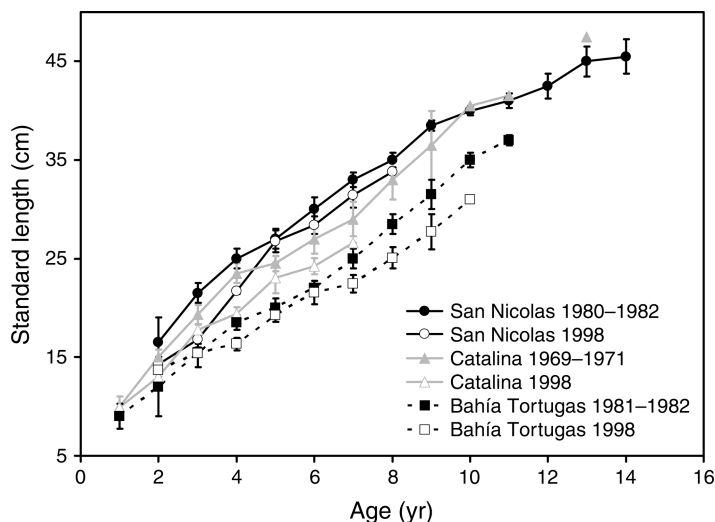
FIG. 2. Size-at-age relationships: age (yr) vs. mean standard length (cm) for each population of *Semicossyphus pulcher* for both historical and recent samples. Error bars represent 95% CI. When no error bars are present, the value represents only one fish.

and the size or age at sexual transformation. In each study, the size or age at maturity was defined as the size or age at which females began to predominate over immatures in the population (i.e., $L_{50♀}$ or $A_{50♀}$; length or age at 50% mature female). Comparably, the size or age at sex change was defined as the size or age at which males began to predominate in the population (i.e., $L_{50♂}$ or $A_{50♂}$; length or age at 50% male). In addition to visual assessments, we used logistic regression to determine the predicted timing (L_{50} and A_{50}) of maturation and sexual transformation, where the data allowed. Cowen (1990) reported a strong positive relationship between sex ratio and the mean time spent as a mature female (i.e., difference between age at maturity [$A_{50♀}$] and age at sexual transformation [$A_{50♂}$] of each population) across six sites. Therefore, we used ANCOVA to compare this relationship between historical samples (Cowen 1990) and the 1998 collections at

the three core sites and the four additional sites (see Fig. 1). Similarly to Cowen (1990), we did not find significant relationships between sex ratios and population density, growth rate (i.e., slope of mean size-at-age), or survivorship among sites using the recent data, and we lacked information on recruitment levels (which were not related to sex ratio in the historical data). Statistical analyses were performed in JMP 6.0 and SPSS 11.0.

RESULTS

Growth rates, size frequencies, and survivorship

Growth rates of *Semicossyphus pulcher* differ more spatially than through time (Fig. 2). Size-at-age plots show that, in general, fish grow fastest on San Nicolas Island (SNI), moderately fast at Catalina Island (CAT), and slowest at Bahía Tortugas (BT). At each site, fish grew faster historically than during 1998 (i.e., non-overlap of 95% CI). Size-frequency distributions from

TABLE 1. Results of Komolgorov-Smirnov two-sample tests comparing size-frequency distributions of the entire sample and each sex individually, between historical and recent collections at each site.

Site and group	N (historic, recent)	Z	P	Direction of change in mean size from historical to recent samples
Bahía Tortugas				
Females	39, 43	0.50	0.97	no change
Males	32, 29	1.02	0.25	no change
Combined	71, 72	0.85	0.46	no change
Catalina				
Females	153, 24	2.03	**0.001**	decrease
Males	77, 21	2.78	**<0.0001**	decrease
Combined	230, 45	2.15	**<0.0001**	decrease
San Nicolas				
Females	166, 36	4.17	**<0.0001**	decrease
Males	47, 9	2.16	**<0.001**	decrease
Combined	213, 45	3.98	**<0.0001**	decrease

Note: P values that were statistically significant after sequential Bonferroni corrections are shown in boldface text.
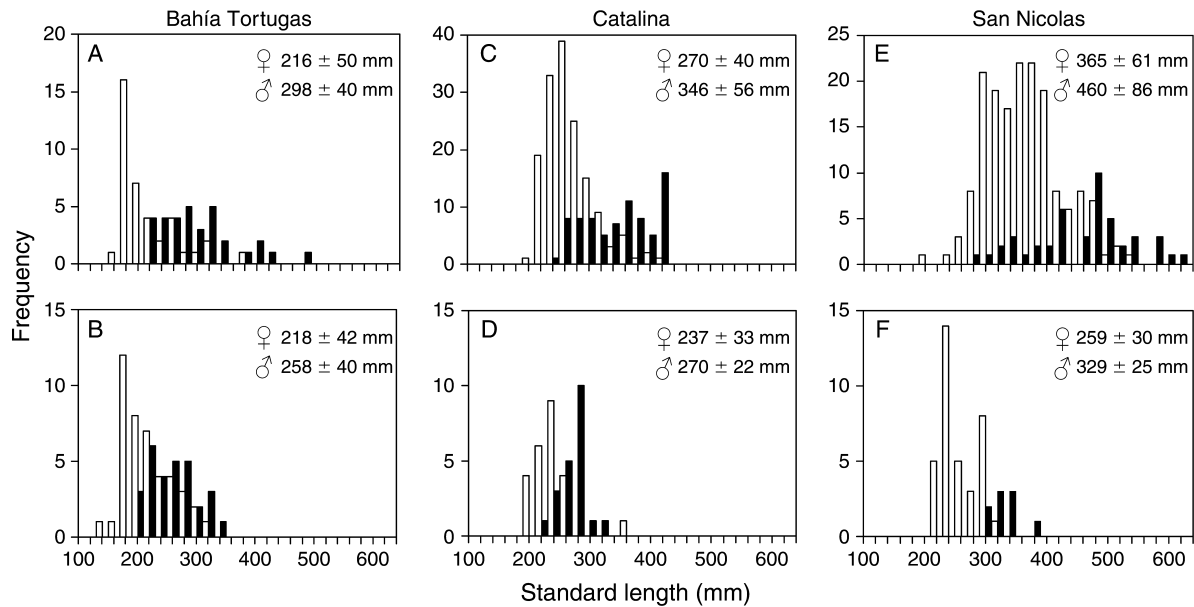
FIG. 3. Size-frequency distributions of mature female (open bars) and mature male (solid bars) *Semicossyphus pulcher* at the three study locations in successive 20-mm size bins. Mean sizes of each sex ± SD are shown in the upper right of each panel. Shown are (A, C, E) historic vs. (B, D, F) recent size frequencies: (A) Bahía Tortugas, 1981–1982, data from Cowen (1990); (B) Bahía Tortugas, 1998; (C) Catalina, 1969–1971, data from Warner (1975b); (D) Catalina, 1998; (E) San Nicolas, 1980–1982, data from Cowen (1990); (F) San Nicolas, 1998.

historical and recent samples suggest that both sexes of *S. pulcher* have not changed size appreciably at BT but have shifted significantly to smaller sizes at CAT and SNI (Table 1, Fig. 3). On CAT, males exhibited more extreme changes in size frequency than females, while at SNI, sizes of both sexes have been reduced substantially (Table 1, Fig. 3). The SNI population experienced an extreme truncation of its size distribution since the early 1980s. Interestingly, despite variation among locations, the first appearance of males in each population (BT = 220–240 mm, CAT = 240–260 mm, SNI = 280–300 mm) has not shifted in size, even though the means shifted significantly to smaller sizes at CAT and SNI (Fig. 3). Overall, the largest sizes (i.e., the top 10% of the size distribution) of *S. pulcher* have been lost from each population, including BT (see Table 2). Annual survivorship of mature fish, which combines natural and fishing mortality, declined at CAT (0.66 to 0.56) and SNI (0.75 to 0.59), but increased at BT (0.66 to 0.74) for recent samples (Table 2). Maximum longevity, as determined by aging the largest fish collected at each

location, suggests that the lifespan has not changed at BT where fishing is light, but has declined at CAT and SNI where exploitation is common (Table 2).

Timing of maturation and sex change

The timing of maturation and the timing of sex change has not changed in certain locations, but has shifted to smaller sizes and to earlier ages at other locations over the last 20–30 years (Table 3, Fig. 4). We were only able to obtain raw data to calculate size at maturation ($L_{50\,\female}$) from Warner (1975b) for CAT. At BT and SNI, we used estimated values of $L_{50\,\female}$ from the 2004 sheephead stock assessment model (Alonzo et al. 2004). These estimates were made by converting age at maturation to size at maturation using known size-at-age relationships because sizes of immature individuals were not reported in Cowen (1990). $L_{50\,\female}$ decreased significantly (non-overlap of 95% CI from logistic regression) at CAT (Table 3). At BT, $L_{50\,\female}$ may have declined slightly, while at SNI, $L_{50\,\female}$ decreased by 90 mm. The size at sexual transformation ($L_{50\,\male}$) remains

TABLE 2. Annual survivorship (mean ± SD), maximum age, and maximum size for mature fish from the historical and recent collections of each population of *Semicossyphus pulcher*.

Population	Year of study	n	Survivorship (SD)	Maximum age (yr)	Maximum size (mm)
Bahía Tortugas	1981–1982	71	0.664 (0.03)	12	480
	1998	91	0.743 (0.04)	12	340
Catalina	1969–1971	230	0.656 (0.02)	20	600
	1998	121	0.560 (0.07)	11	320
San Nicolas	1980–1982	213	0.745 (0.02)	21	640
	1998	57	0.589 (0.06)	8	360

TABLE 3. Size at maturation ($L_{50♀}$) and size at sex change ($L_{50♂}$) for historical and recent populations of *Semicossyphus pulcher*. Values are means with 95% CI in parentheses.

Trait and time period	Bahía Tortugas	Catalina	San Nicolas
Size at maturity (mm)			
Historic (1969–1982)	190†	221 (216–227)	291†
Recent (1998)	160 (138–171)	202 (195–212)	202 (NA)‡
Size at sex change (mm)			
Historic (1969–1982)	258 (235–288)	327 (314–343)	479 (456–515)
Recent (1998)	254 (230–294)	255 (236–278)	311 (299–347)

Notes: Sizes were determined by logistic regression. The 95% CI is the confidence interval around the predicted size at maturity and size at sex change based on the logistic regression model.

† Due to the lack of reporting of immature sizes in Cowen (1990), we used estimates from the 2004 sheephead stock assessment model that incorporated site-specific life history data from Cowen (Alonzo et al. 2004). Fork lengths were converted to standard lengths using the FL to SL conversion ⟨www.fishbase.org⟩. Conversions of model estimates from FL to SL for historical size at sex change (at all sites) and the size at maturity (at Catalina) fell within 8 mm of the predicted values determined by logistic regression when raw data were available.

‡ The 95% CI could not be estimated in the logistic model because lengths of immatures and females did not overlap.

unchanged at BT but has decreased significantly at CAT by 80 mm and at SNI by 170 mm (Table 3).

Because we were not able to obtain raw age data (i.e., number of individuals of each age class) by sex for any site other than CAT in 1970, we visually estimated and compared the age at maturation ($A_{50♀}$) and age at sex change ($A_{50♂}$) similarly to methods in Warner (1975b) and Cowen (1990), using plots depicting the proportion of individuals of each sexual type in each age class (Fig. 4). Logistic regression analyses showed that $A_{50♀}$ has

not changed at BT or CAT, but has decreased by 1–2 years at SNI (Figs. 4, 5A). *Semicossyphus pulcher* were reported historically to mature at BT between three and four years of age, at age four on CAT, and between ages five and six on SNI (Fig. 5A). Our 1998 collections show that *S. pulcher* matures between three and four years at BT (3.7 years, logistic regression), at age four on CAT (4.0 years), and between three and four years at SNI (3.9 years; Fig. 5A). More dramatic changes occurred in $A_{50♂}$ from the historical to recent collections at
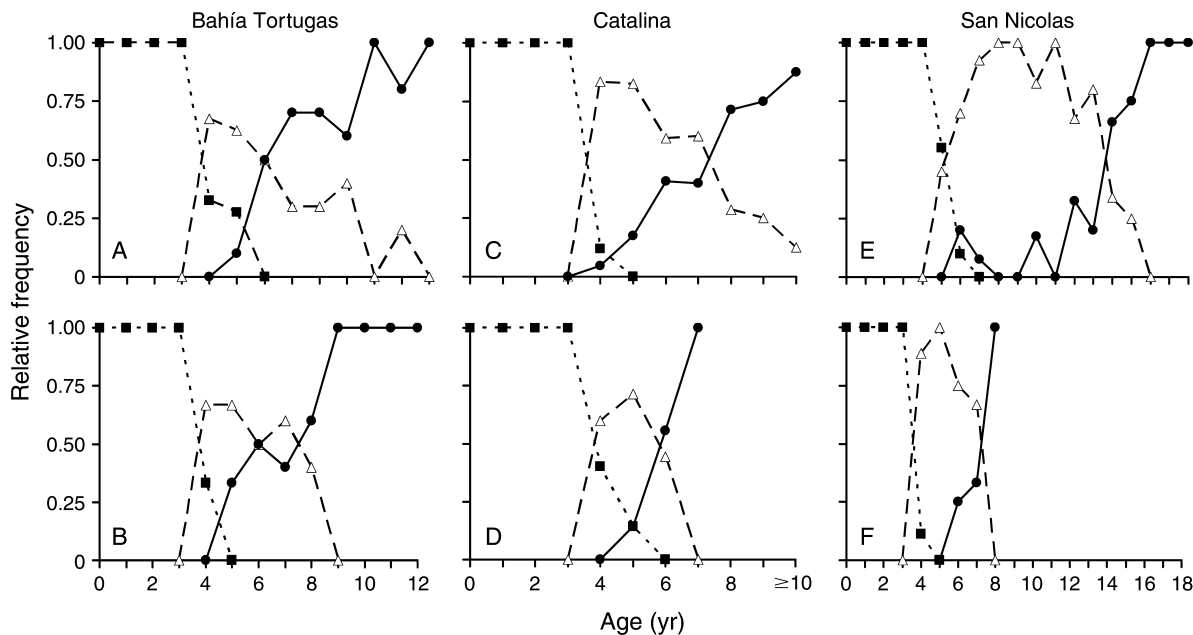

FIG. 4. Plots of the proportion of each sexual stage in each year class of the studied populations of *Semicossyphus pulcher*. Age at maturity is defined as the predicted age at which 50% of the population is female and occurs when the immature and female lines cross. Age at sex change is defined as the predicted age at which 50% of the population is male and occurs when the female and male lines cross. Shown are immatures (dotted line with solid square), females (dotted line with open triangle), and males (solid line with solid circle). (A, C, E) Historic vs. (B, D, F) recent sexual compositions are shown for: (A) Bahía Tortugas, 1981–1982 (data from Cowen [1990]); (B) Bahía Tortugas, 1998; (C) Catalina, 1969–1971 (data from Warner [1975b]); (D) Catalina, 1998; (E) San Nicolas, 1980–1982 (data from Cowen [1990]); (F) San Nicolas, 1998.
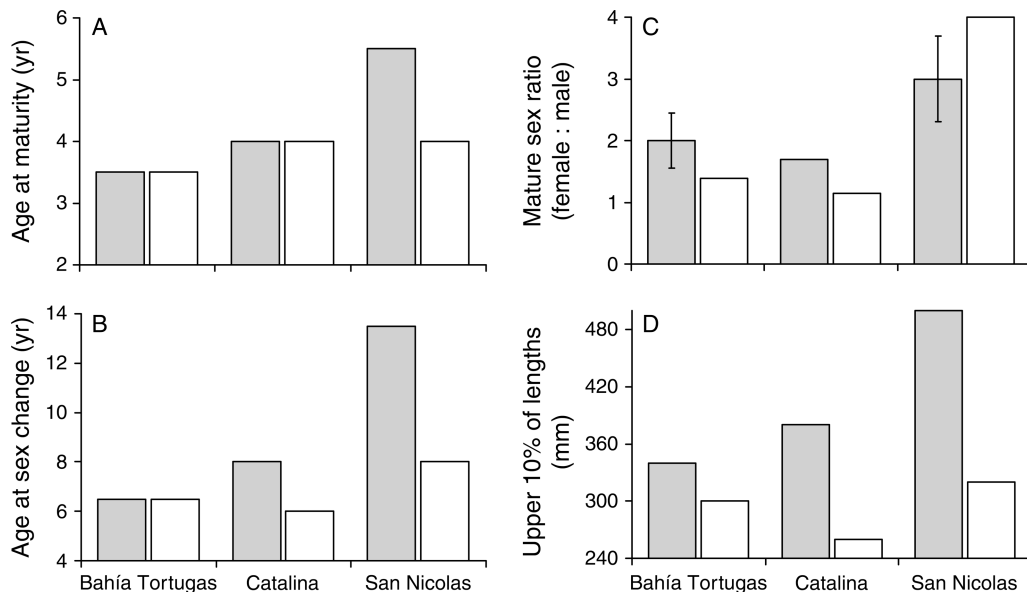
FIG. 5. Summary of changes in population parameters of *Semicossyphus pulcher* from historical (solid bars) to recent (open bars) samples at Bahía Tortugas, Catalina Island, and San Nicolas Island. Bars show (A) age at maturation, (B) age at sex change, and (C) mature population sex ratio (female : male). Error bars are 95% CI provided in Cowen (1990) from replicate surveys. (D) Cutoff of the upper 10% of the combined (male and female) size-frequency distribution.

exploited locations (Figs. 4, 5B). *Semicossyphus pulcher* were reported historically to undergo sexual transformation between six and seven years at BT, at age eight on CAT, and between 13 and 14 years of age at SNI. In comparison, we determined $A_{50\delta}$ for recent collections to be 6–7 years at BT (no change), six years at CAT (decrease by two years), and 7–8 years at SNI (decrease of 6–7 years).

Sex ratios

The mean time spent as a mature female ($A_{50\delta} - A_{50\female}$) in each population currently corresponds to about three years at BT, two years at CAT, and four years at SNI. Historically, Warner (1975b) and Cowen (1990) reported the mean time spent as a female to be approximately three years at BT (no change), four years at CAT (decrease of two years), and eight years at SNI (decrease of four years). Therefore, *S. pulcher* are on average spending fewer annual breeding seasons contributing to egg production while mature at CAT and SNI. Using data from all our 1998 collections (three core sites plus four additional sites) we found that, similar to the historical data (Cowen 1990), sex ratios for all sites increased with an increase in the mean amount of time spent as a mature female (Fig. 6). Although the best-fit regression line appears to deviate from that reported by Cowen (1990) when we include data from all sites, the slopes are not significantly different (nonsignificant interaction term in the ANCOVA including all points; Table 4a). Removal of one extreme outlier (SNI 1998) not only improves the statistical fit but shows that the relationship between time spent as a female and the

operational sex ratio is virtually identical from historical to recent collections, even though several of the sites contributing to the relationship differed between the time periods (Table 4b). As mentioned previously, SNI collections from 1998 suggest that individuals are spending half as long on average as females. However, the operational sex ratio has increased from collections in 1980–1982 to 1998 instead of decreasing, as would be predicted (Figs. 5C, 6). In contrast, operational sex ratios have decreased slightly at BT and CAT (Fig. 5C).

DISCUSSION

The extent to which life histories and population parameters of California sheephead, *Semicossyphus pulcher*, have changed over the last 20–30 years appears to depend on site-specific histories of fishing pressure. Comparisons of annual survivorship of mature age classes provide an independent measure of changes in mortality rates due to fishing, assuming that natural mortality rates remain similar over time. Confirming our predictions, survivorship decreased significantly at Catalina (CAT) and San Nicolas (SNI), the two sites reported to have experienced increasing fishing pressure. In contrast, survivorship increased at Bahía Tortugas (BT), where we inferred that fishing pressure remains light. At sites heavily exploited by the recreational and commercial fisheries (CAT and SNI, respectively [Wright et al. 2000, Alonzo et al. 2004]), size distributions appear truncated and the timing of maturation and sexual transformation have generally shifted to smaller sizes and younger ages. In the early 1980s the population at SNI was dominated by large and old individuals and
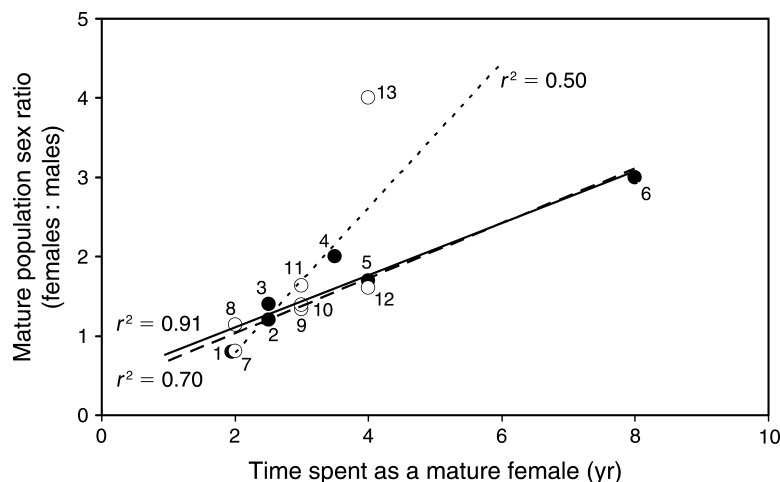
FIG. 6. Relationship between the mean time (yr) spent as a mature female in each population (i.e., the difference between the age at maturity and the age at sex change) and that population's mature sex ratio (i.e., number of females to number of males). Historic data are solid circles replotted from Cowen (1990), and recent data are open circles. Historic 1970–1982 collections are as follows: (1) Islas San Benitos, (2) Isla Guadalupe (Warner 1975b), (3) Isla Guadalupe (Cowen 1990), (4) Bahía Tortugas, (5) Catalina Island, (6) San Nicolas Island. Recent 1998 collections are as follows: (7) Isla Cedros, (8) Catalina Island, (9) Punta Canoas, (10) Bahía Tortugas, (11) San Clemente Island, (12) Isla San Martin, (13) San Nicolas Island. Regression lines from historic samples (solid line), recent samples (dotted line), and recent samples removing the outlier from San Nicolas 1998 (dashed line) are depicted.

is now composed mainly of small, young females. Although our sample size at SNI was lower for recent collections ($n = 57$ vs. 213), a random sample of 50 individuals given the historical size structure would likely have resulted in a maximum age and size well above those we detected in 1998. Overall, our results are consistent with predictions regarding the effects of exploitation on life history traits as well as the results of studies modeling the impacts of size-selective fishing on protogynous fish populations (e.g., Alonzo and Mangel 2005).

While we cannot discount the possibility of environmental change affecting life histories of these populations, no changes occurred to an unexploited population at Isla Guadalupe from 1970 to 1982 (Cowen 1990), despite the Pacific Decadal Oscillation shifting from a cool to a warm phase in the middle of that period (Mantua and Hare 2002). While not measured in this study, Cowen (1985) showed that recruitment of S. pulcher is variable throughout the species range. Episodic large pulses at SNI were hypothesized to result from El Niño flow reversals (Cowen 1985); however, recent evidence has called this upstream–downstream paradigm into question (Selkoe et al., in press). We made recent collections at northern sites following a large El Niño event, but that year class was not represented in our collections. In addition, we did not see signatures of other year classes dominating the age structure at these sites, which suggests that the populations were not out of demographic equilibrium. Regardless of the cause of recruitment variation, the magnitude and frequency of replenishment may have demographic consequences for exploited populations. The effects of selective fishing are

potentially ameliorated by high and consistent recruitment in Baja California, while increased mortality rates may reduce the resiliency of populations in southern California by diminishing the benefits afforded by the storage effect (i.e., ability to buffer populations during a string of low recruitment years; Warner and Chesson 1985).

The observed differences in growth rates among sites were consistent with Cowen (1986) and are likely attributable to continued site-specific differences in diet composition, prey availability, and population density. Slower growth rates of fish from recent collections may be a result of shifts in the availability of preferred prey items as a consequence of variable prey recruitment or environmental change (e.g., PDO, ENSO). Despite

TABLE 4. ANCOVA results testing the relationship between the mean time spent as a female (i.e., age at 50% sex change) and the mature population sex ratio (female : male) for historical and recent collections of Semicossyphus pulcher.

Factor	df	SS	F	P
a) Including all points				
Historic vs. recent	1, 9	0.59	1.48	0.26
Time as female	1, 9	5.40	13.58	**0.005**
Historic vs. recent × time as female	1, 9	1.22	3.07	0.11
b) San Nicolas 1998 removed				
Historic vs. recent	1, 8	0.013	0.26	0.62
Time as female	1, 8	1.18	23.40	**0.0013**
Historic vs. recent × time as female	1, 8	0.001	0.03	0.87

Note: Boldface text denotes P values that are significantly significant after Bonferroni corrections for multiple tests of the same hypothesis.

finding both spatial and temporal differences in growth rates, the dramatic changes in the size-frequency distributions of males and females over time appears to reflect the intensity of exploitation. As a consequence of the light exploitation rate at BT, size distributions of both sexes have not changed from the early 1980s to 1998. At CAT, males show the most striking change in their size distribution, as would be expected through the selective removal of this class by the recreational fishery (especially spear fisherman). Similar shifts in the female size distribution to smaller sizes at this site likely occurred for three reasons: (1) large females are targeted by both recreational anglers and spear fisherman, (2) a moderate commercial trap fishery selectively removes females, and (3) females would be expected to undergo sexual transformation at a smaller size upon the disappearance of large males (Warner 1975a, Munday et al. 2006). SNI, the site with the highest commercial fishing pressure and largest decline in survivorship, displayed the most dramatic truncation of the size-frequency distribution for both males and females. The intensity of the commercial harvest at SNI may have extracted most fish before they could achieve a size refuge, and before females had a chance to undergo sexual transformation. The hook-and-line commercial fishery, which dominated the catch in the early 1990s (Alonzo et al. 2004), may also have removed many of the large individuals at SNI prior to the development of the trap fishery.

The selective harvesting practices of most fisheries have been shown routinely to affect size distributions and life history traits of fishes (e.g., Ricker 1981, Rijnsdorp et al. 1996). Further evidence for the effects of exploitation on size distributions is witnessed by the general increase in fish size following the removal of size-selective harvest pressures through the implementation of nonextractive marine reserves (Paddack and Estes 2000; reviewed in Halpern 2003). Comparisons across space, i.e., between fished and closed areas, reveal trends similar to those observed through time. For both hermaphroditic and gonochoristic species, fish size distributions in exploited areas are generally shifted left relative to size distributions of populations in areas closed to fishing (Buxton 1993, Schroeder and Love 2002, Hawkins and Roberts 2003).

Exploitation effects on sex-related traits

As predicted, the size and age (SNI only) at maturation decreased at exploited sites relative to the unexploited location in this study. Declines in the size and age at which fish mature is a common outcome following selective harvesting in many marine fisheries (reviewed in Law 2000). In several cases, this phenotypic shift appears to have a genetic basis rather than being a growth-compensatory response to changes in abundance following exploitation (Jørgensen 1990, Rijnsdorp 1993, Olsen et al. 2004, Hutchings 2005). Genetic changes may be hard to reverse after fishing pressures relax because

natural agents of selection operate slowly and in some cases may not exert sufficient pressure in the reverse direction (Law 2000, Conover et al. 2005). Following the harvest moratorium for cod Gadus morhua, declines in size-at-age have not reversed (Sinclair et al. 2002); however, the trend toward earlier maturation may show signs of reversing (Olsen et al. 2005). Natural predation creates selective pressures comparable to harvesting and can influence the timing of maturation among populations experiencing different predation regimes (e.g., parrotfish [Gust 2004]). In addition, experimental manipulations of size-selective predation often find evidence of rapid evolutionary change, selecting for maturation at earlier ages and smaller sizes (e.g., guppies [Reznick and Ghalambor 2005]). Potential predators as well as rates of natural predation on S. pulcher are unknown (Stephens 2001). However, given the loss of large predators throughout this ecosystem, it appears unlikely that increases in natural predation rates are responsible for the dramatic loss of the largest size classes and the shifts in life history traits observed in this study.

Historically, in unexploited locations with naturally slow rates of growth and high natural mortality, sex change in S. pulcher occurred at smaller sizes and earlier ages (see Catalina–Guadalupe Island comparison in Warner [1975b], Cowen [1990]). Therefore, it is not surprising that the timing of sex change has shifted to smaller sizes and earlier ages in exploited sheephead populations (CAT and SNI), which experience high levels of fishing-induced mortality. These changes in the timing of sexual transformation for S. pulcher are predicted to occur (1) when large males are selectively removed (e.g., CAT), thereby opening vacancies in territories which stimulate females to undergo sexual transformation or (2) when high mortality rates and corresponding shorter mean life spans favor strategies for earlier maturation and sex change (e.g., SNI). Similar patterns have been observed for other sex-changing species as a result of elevated natural predation rates in the absence of fishing (Gust 2004, DeMartini et al. 2005) and due to increased fishery-induced mortality (shrimp [Hannah and Jones 1991], fishes [Platten et al. 2002, Hawkins and Roberts 2003]).

Compensating for selective harvesting by changing sex at a smaller size will only ensure population persistence if individuals live long enough to attain a size at which sex change can occur. Although the *mean* size at sexual transformation has been reduced at CAT and SNI, interestingly the *minimum* size at which males first appear in each population has not changed (see Fig. 3). This result is unexpected: the size advantage hypothesis coupled with the observed variability in the mean size at sex change among populations (Warner 1975b, Cowen 1990) would predict a smaller size for the first appearance of males, following removal of the largest size classes. This result is especially surprising at SNI where sizes of both sexes changed most abruptly

and males first appeared at a relatively large size (~300 mm) compared to CAT (~240 mm) and BT (~220 mm). The minimum size of sexual transformation may be fixed and to some extent determined locally by rates of growth to a size or age at which individuals are competent to undergo sexual transformation and by the composition of local mating groups. It remains unclear whether sex change is fixed or socially mediated in *S. pulcher*, though the rules governing sex change have been shown to influence the response of this species to size-selective fishing (Alonzo and Mangel 2005). If the minimum size at sex change is invariant on a local scale, the possibility remains that intensive harvest could potentially remove all males, resulting in reproductive failure through sperm limitation (Armsworth 2001, Alonzo and Mangel 2004), unless harvest rates are reduced or provisions made to limit fishing of some male size classes. Minimum size limits for *S. pulcher* were not implemented until the year after we made our collections and were set at 30 cm (Alonzo et al. 2004), the minimum size of males observed at SNI. Sex-selective fishing has similar negative effects on the availability of males and ensuing reproductive success in both tropical hermaphroditic fishes (McGovern et al. 1998, Hawkins and Roberts 2003) and simulated crab fisheries (Sato and Goshima 2006).

The positive relationship between the mean time spent as a mature female and the operational sex ratio (i.e., mature female : male) has not changed through time, even though some of the collection sites were not identical between historical and recent comparisons (see Fig. 6). These results indicate that local mating conditions, mortality rates, and size-dependent expected reproductive success influence the timing of sex change and resulting population sex ratios for *S. pulcher*. In unexploited locations, where natural mortality is greater and individuals spend less time on average as females, sex ratios in *S. pulcher* are closer to 1:1 (Cowen 1990). Contrary to this result, fishing mortality has increased and individuals are spending four fewer years as mature females at SNI in 1998 compared to historical means, yet the operational sex ratio increased from 3:1 in the early 1980s to 4:1 in 1998. Recent models predict fishing will induce shifts in population sex ratios; however, the direction of change depends on the rules governing sexual transformation (Alonzo and Mangel 2005). This study, combined with the model results, gives testable predictions for future work on mating systems for this species.

Management implications

Properly managing a sex-changing species when the commercial and recreational fisheries selectively target different segments of the population in different locations remains a challenge. Models examining the effects of different management strategies on harvested sex-changing fish suggest that closed areas (spawning or other marine protected areas) and reduced fishing mortality (sometimes on specific size classes) may help maintain sex ratios, preserve age structure, prevent sperm limitation, enhance yield, and limit evolutionary changes in response to fishing, such as shifts to earlier maturation (Buxton 1992, Alonzo and Mangel 2004, Baskett et al. 2005, Heppell et al. 2006). Heppell et al. (2006) explored the effects of different management strategies on population recovery of gag grouper (*Mycteroperca microlepis*), a species with a fixed size at sex change and a highly female-biased sex ratio following years of intense exploitation. For fisheries managers, a noteworthy result is that the success of a particular management strategy depended on the objective. Population growth rates were highest for scenarios that reduced mortality of females (e.g., nearshore closures), while improved sex ratios and fertility rates were accomplished through offshore spawning reserves that protected males.

Other complementary models have demonstrated the capacity for sex change rules (i.e., endogenous and exogenous cues) to influence stock dynamics, spawning-per-recruit measures, and fertilization rates (Alonzo and Mangel 2005; for an exception, see Armsworth [2001]). Consequently, whenever possible, rules governing sex change should be considered in management scenarios of hermaphroditic species. More importantly, even stocks with a plastic pattern of sex change are predicted to have dynamics distinctly different from otherwise identical dioecious populations (Alonzo and Mangel 2005). Models demonstrate further that the intensity of exploitation and the selectivity of the fishery relative to the size at maturation and size at sex change can dramatically influence population size, spawning stock biomass, and fecundity (Alonzo and Mangel 2004, 2005, Heppell et al. 2006). For protogynous fish stocks, nonlinear dynamics are possible when fishing targets a wide range of reproductive sizes. Therefore, in addition to minimum size limits, which are used to prevent recruitment overfishing (i.e., the take of fish before maturation), managers should consider slot limits (i.e., minimum and maximum size limits) for sex-changing fisheries. For protogynous fish, slot limits will not only help prevent sperm limitation by preventing the removal of large males, but will help ensure that large females, with exponentially greater fecundity, continue contributing to future generations.

For *S. pulcher*, we suggest that (1) reduced harvest rates (through the use of MPAs or reduced quotas), (2) slot limits and/or (3) minimum size limits well above the size at sex change for any given population may help prevent further erosion of size-frequency distributions, life history traits, and reproductive output. Future stock assessments should be based on current life history parameters and not those from unfished populations measured 20–30 years in the past. Current regulations should be updated to reflect the severe changes that have occurred to populations of *S. pulcher*. The most recent data used in this study are now nearly 10 years old. Since

that time, commercial fishing pressure in Southern California has been greatly reduced due to stricter harvest controls enacted in 1999, the year after our study (Alonzo et al. 2004). We are currently in the process of assessing whether those management efforts have initiated a recovery in these populations. A recent promising sign of the efficacy of management is that densities and biomass of adult *S. pulcher* are higher at sites inside than outside of an MPA on Catalina Island (Froeschke et al. 2006). It is critical that basic life history data continue to be collected and used for management. Future research should also address the potential for sperm limitation and focus on determining whether current management solutions are successful at reversing the disturbing trends reported here. In particular, future modeling efforts should aim at predicting the effects of different management strategies (e.g., slot limits, MPAs, reduced effort; see Heppell et al. 2006) on *S. pulcher* population size, age structure, sex ratio, and fertilization success, given the current fishery-induced changes in life history traits.

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