

Geographic variation in density, demography, and life history traits of a harvested, sex-changing, temperate reef fish

Jennifer E. Caselle, Scott L. Hamilton, Donna M. Schroeder, Milton S. Love, Julie D. Standish, Jorge A. Rosales-Casián, and Oscar Sosa-Nishizaki

Abstract: Geographic variation in ecological and environmental factors may lead to intraspecific differences among populations. For the California sheephead (*Semicossyphus pulcher*), an important predator in kelp forests and a target of commercial and recreational fisheries, we evaluated the degree to which different populations exhibited variation in density, demography, and life history traits. We assessed biogeographic patterns of abundance through underwater visual census at 39 sites spanning a major portion of the species range (southern California, USA, to Baja California, Mexico) and made collections from seven focal sites to investigate geographic differences in demography and life histories. California sheephead densities were significantly greater in the southern part of their range and at offshore islands than along the mainland coast. At the focal sites, we found significant spatial variation in density, fecundity, size structure, growth rates, annual survivorship, and the timing of maturation and sex change. Density- and temperature-dependent effects helped to explain the intraspecific differences in these parameters. Studies such as this one will allow for demographic plasticity to be incorporated into future stock assessments. Management of temperate reef fishes may best be achieved on smaller spatial scales as we increase our understanding of geographic variation among populations.

Résumé : La variation géographique des facteurs écologiques et environnementaux peut mener à des différences intraspécifiques entre les populations. Nous avons évalué le degré de variation dans la densité, la démographie et les traits du cycle biologique chez différentes populations du labre californien (*Semicossyphus pulcher*), un important prédateur dans les forêts de varech et la cible des pêches commerciales et sportives. Nous avons évalué les patrons biogéographiques d'abondance par des inventaires visuels sous-marins à 39 sites couvrant une partie importante de l'aire de répartition de l'espèce (sud de la Californie, É.-U., à la Basse-Californie, Mexique); nous avons aussi fait des prélèvements à sept sites choisis afin d'étudier les différences géographiques de démographie et de cycle biologique. Les densités de labres californiens sont significativement plus grandes dans la partie sud de l'aire de répartition et près des îles du large que le long de la côte du continent. Aux sites choisis, il existe une variation significative de la densité, de la fécondité, de la structure en taille, des taux de croissance, de la survie annuelle et du calendrier de la maturation et du changement de sexe. Des effets dépendants de la température et de la densité aident à expliquer les différences intraspécifiques de ces variables. Des études comme la nôtre permettront d'incorporer la plasticité démographique dans les évaluations futures des stocks. La gestion des poissons des récifs tempérés se fait de façon optimale à des échelles spatiales plus restreintes à mesure que s'accroît notre compréhension de la variation géographique entre les populations.

Introduction

Many species exhibit geographic variation in their ecology over a range of spatial scales (e.g., Brown 1995), which may affect plasticity in demography and life history traits. Often, this biogeographic variation occurs naturally in response to changes in environmental conditions, such as temperature, habitat, predation pressure, and resource

availability (Reznick et al. 1990; Jennings and Beverton 1991; DeMartini et al. 2005). Different life history strategies within a species may have evolved as an adaptation to these variable environmental pressures (Stearns 1992). In addition, recent studies have shown that selective fishing practices may influence demography and life histories by altering growth rates, size structure, longevity, and the timing of maturation and sex change (Law 2000; Hawkins and Roberts

Received 15 October 2009. Accepted 4 October 2010. Published on the NRC Research Press Web site at cjfas.nrc.ca on 4 February 2011. J21470

J.E. Caselle,¹ S.L. Hamilton, and M.S. Love. Marine Science Institute, University of California, Santa Barbara, CA 93106-6150, USA.
D.M. Schroeder. Bureau of Ocean Energy, Management, Regulation and Enforcement, 770 Paseo Camarillo, 2nd Floor, Camarillo, CA 93010, USA.

J.D. Standish. Department of Ecology, Evolution, and Marine Biology, University of California, Santa Barbara, CA 93106-9610, USA.
J.A. Rosales-Casián. Departamento de Ecología Marina, Centro de Investigación Científica y de Educación Superior de Ensenada, B.C. (CICESE), Apartado Postal 2732, Ensenada, Baja California, México.

O. Sosa-Nishizaki. Departamento de Oceanografía Biológica, Centro de Investigación Científica y de Educación Superior de Ensenada, B.C. (CICESE), Apartado Postal 2732, Ensenada, Baja California, México.

¹Corresponding author (e-mail: caselle@msi.ucsb.edu).

2003; Hamilton et al. 2007). Describing biogeographic scales of variation among populations and understanding the processes that create such variation are important for interpreting ecological and evolutionary patterns and for managing natural resources in many systems.

Temperature- and density-dependent effects on physiological and ecological processes may provide proximate mechanisms to explain observed geographic patterns in demography and life histories. Latitudinal differences in temperature have been shown to influence growth, reproductive output, and the timing of maturation in fishes (Robertson et al. 2005; Ruttenberg et al. 2005; Ormseth and Norcross 2009), as well as average lifespans (Robertson et al. 2005; Munch and Salinas 2009). Studies of countergradient variation in growth have revealed that some species have adapted to seasonal differences in prey availability and the length of the growing season by growing faster in colder temperature regimes (Conover and Present 1990). Species abundance patterns also differ dramatically across their range, and geographic variation in densities can have important ecological consequences. Density dependence mediated by competition for limiting resources, such as prey and shelter, have been shown to influence growth, mortality, and the timing of maturation (Jones 1987; Samhuri 2009). For sex-changing species, additional life-history events such as the timing of sexual transformation are governed by local environmental conditions that affect densities, sex ratios, growth rates, and mortality (Warner 1988; Cowen 1990; Hamilton et al. 2007).

Intraspecific differences in demography may indicate geographic isolation among populations, and this type of information has been used previously in stock identification and for fisheries management (Begg et al. 1999). However, in many instances, stock assessments rely on population parameters from one or a few locations and seldom incorporate spatial variation among populations. In particular, nearshore, temperate reef fishes pose problems for traditional fisheries management, because emerging evidence suggests that adults have relatively small home ranges (Topping et al. 2005; Jorgenson et al. 2006) and more limited larval exchange than previously thought (Buonaccorsi et al. 2004; Miller and Shanks 2004). This evidence raises the possibility that reef fishes in temperate regions commonly exhibit variation in their demography and life histories. Thus, management of these temperate-region resources may need to occur over relatively small spatial scales (Gunderson et al. 2008). In addition, the increased adoption of place-based management such as marine reserves or other forms of spatial zoning will be informed by knowledge of the degree to which populations vary geographically in terms of abundance, size structure, demographics, and life history traits, and how those parameters are influenced by environmental conditions and fishing pressure.

Prior studies that have assessed spatial variation in demography and life histories in marine fishes have tended to focus on species that compose major fisheries in temperate regions, such as cod (Ormseth and Norcross 2009), herring (Jennings and Beverton 1991), and flatfishes (Brodziak and Mikus 2000). Recently, researchers have turned their attention to addressing these questions for coral-reef fishes, and they have documented spatial differences in growth rates,

mortality, and the timing of life history events at multiple spatial scales for both fished and unfished species (Williams et al. 2003; Gust 2004; DeMartini et al. 2005). Despite comprising many economically important commercial and recreational fisheries, spatial scales of intraspecific demographic variation have seldom been assessed for temperate reef fishes. However, previous research from a few populations of California sheephead (*Semicossyphus pulcher*) along the Pacific coast of North America has indicated significant geographic structuring of life history traits (Warner 1975; Cowen 1990).

California sheephead are large temperate wrasses that are common in kelp beds and rocky reefs from southern California through Baja California, Mexico. They 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 1975). California sheephead are ecologically important predators on sea urchins and other benthic invertebrates, and may help to prevent the phase transition from kelp forests to urchin barrens (Cowen 1986). Important commercial and recreational fisheries exist for this species throughout its range (Rosales-Casián and Gonzalez-Camacho 2003; Alonzo et al. 2004). Commercial landings increased dramatically in southern California throughout the 1990s with the advent of a trap fishery for live caught fish (Alonzo et al. 2004). A stock assessment, based largely on data from the 1970s–1980s from a few relatively unfished locations, explicitly called for more current information on spatial variation in the status of different populations (Alonzo et al. 2004). This information is of great importance to fisheries management, because intense harvest has recently been shown to significantly alter life histories of those specific populations that were used in the stock assessment (Hamilton et al. 2007).

The goals of this study were to describe natural variation in densities of the California sheephead across a large portion of the species range, both at mainland and offshore island sites in southern California and Baja California, Mexico. In addition, we investigated the geographic variation in demographic variables and life history characteristics, in relation to density and sea surface temperature, for seven focal populations. This work builds off of a previous study by Cowen (1990) that assessed life history differences in four historically unfished locations, almost 20 years previously. Understanding the degree to which populations (or subpopulations) vary in demographic and life history traits across their range is critical to interpreting results from studies of the species at single locations, and to assess the changes in populations through time, owing to increased harvest pressure and selective fishing practices.

Materials and methods

Study locations and survey techniques

On research cruises from May to November 1998 we recorded the abundance of *S. pulcher* at 39 sites (i.e., from Point Conception, California, USA, to Isla Asunción, Baja California, Mexico) throughout a major portion of the species range and studied life history traits at seven focal locations (sometimes combining multiple sites on one island; see Fig. 1). Sites were located both at offshore islands and along

the mainland coast. All study locations were characterized by rocky substrate and giant kelp, *Macrocystis pyrifera*. Using SCUBA, experienced fish counters estimated densities of *S. pulcher* on 24 belt-transects at each site. Transects were stratified by depth at each site, covering depths from 3 to 24 m. Each transect covered a volume of 80 m³ (20 m × 2 m × 2 m).

Field collections, measurements, and aging techniques

At seven focal locations (San Nicolas Island, Catalina Island, San Clemente Island, Isla San Martin, Punta Canoas, and Isla Cedros; indicated in Fig. 1), individual *S. pulcher* were collected by spear, similar to methodology reported in Warner (1975) and Cowen (1990). To ensure an unbiased collection of particular size classes, we pursued and speared each fish encountered, regardless of size or sex, before proceeding to another individual ($n = 57\text{--}122$ fish per site). However, at each site, one diver targeted one or several of the largest individuals observed at the site to estimate maximum age. We recorded the standard length (SL, mm), total length (TL, mm), wet weight (mass, g), and coloration (male or female color phases) of each individual. We found a strong positive relationship between mass (M) and length (L) for *S. pulcher* across the seven focal populations ($n = 629$, $r^2 = 0.98$, $P < 0.0001$; using a power function $M = 3.6 \times 10^{-5} \cdot L^{2.95}$, SL in mm). 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 1975; 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., in the process of sex change and identified by intermediate morphological coloration), of which few were collected, were categorized as male for presentation and analysis.

For age determination, the first three dorsal spines were removed, cleaned, and frozen, using methods modified from Warner (1975). To age a random sample of approximately 40 fish from each site, we prepared cross sections of the first dorsal spine (occasionally the second spine was used if the first spine yielded poor resolution of annual bands). 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 Crystalbond® (Electron Microscopy Sciences) and polished using a lapping wheel (South Bay Technologies) with 15, 9, and 3 µm polishing films, to improve ring clarity. Three observers counted annual rings using an image analysis system (Image Pro 4.5) connected to a compound microscope at 40× power (Fig. 2). To determine the maximum age of *S. pulcher* at each location, we also aged the dorsal spines of the two or three largest individuals, if not already in the random sample.

Data analysis

To examine spatial variation in the abundance of *S. pulcher*, we categorized sites into four regions (Northern Bight, Southern Bight, Northern Baja, and Southern Baja, Fig. 1) and considered whether the site was located on an offshore island or situated along the mainland coast (near-

Fig. 1. Map of the study area in the Southern California Bight, USA, and Baja California, Mexico. Each point represents a sampling location for estimates of *Semicossyphus pulcher* population density. The seven labeled locations represent collection areas for detailed life history studies. Collections from multiple sites on some islands were grouped for analysis of biogeographic patterns (e.g., Santa Catalina). Northern bight locations include San Nicolas Island and the Santa Barbara Channel, while Southern Bight locations include Santa Catalina and San Clemente islands and the San Diego area. Northern and Southern Baja locations are divided at Punta Canoas.

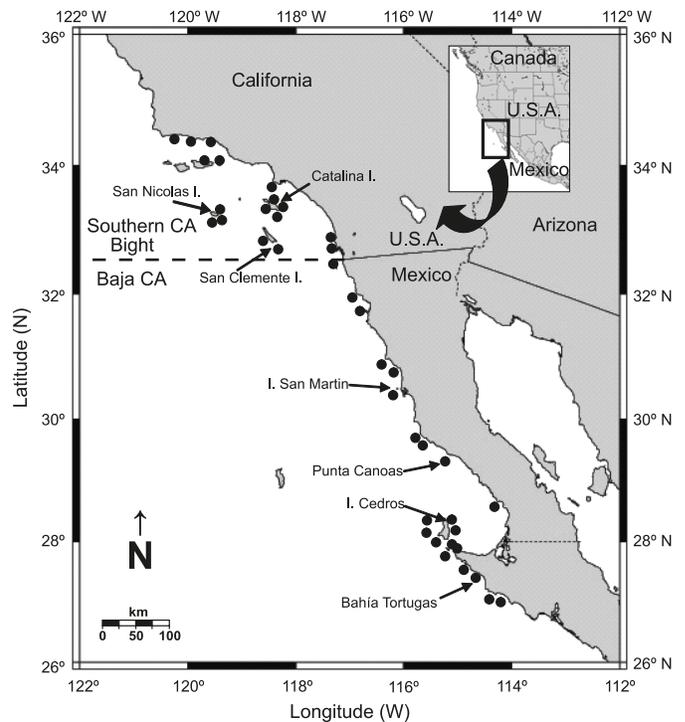
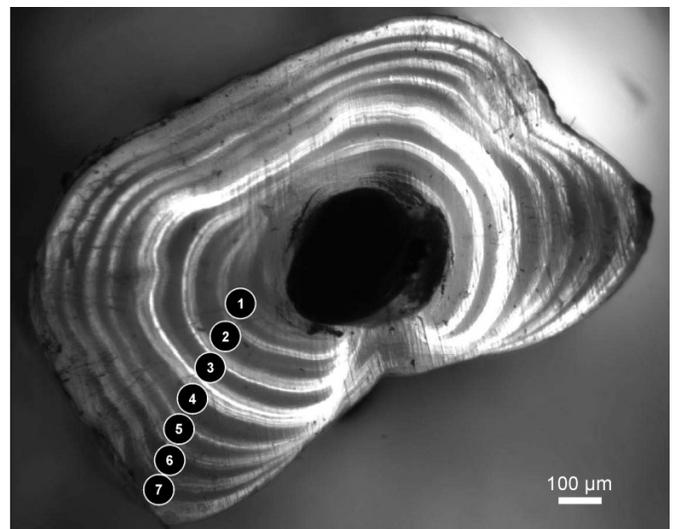


Fig. 2. Image of a sectioned dorsal spine used for aging. This fish was estimated to be 7-years-old, based on the count of alternating dark and light bands.



shore islets and rocks were included as mainland sites). Sites were grouped into regions on the basis of similarities in oceanographic conditions, whether they were located in the US or Mexico, and a desire to roughly balance sample sizes for statistical tests. We used nested analysis of variance (ANOVA) to examine spatial differences in densities among the study sites and as a function of region or island/mainland status. Sites were considered a random factor in the model. Densities were square-root transformed prior to analysis to improve normality and homogeneity of variances. We used Tukey's honestly significant difference (HSD) to perform post-hoc comparisons of statistical significance among various levels in the ANOVA. We also used a generalized linear mixed model with log-link and Poisson distribution, as is often appropriate for count data. The results were very similar to the ANOVA models, as the original data were not highly overdispersed. We present only the results of the ANOVA models.

Samples at the seven focal collection sites (Fig. 1) were used to assess variation in life history traits throughout the range of *S. pulcher*. We examined population-level differences in mean density, mean biomass, and size structure, as well as estimates of fecundity and egg production density (i.e., number of eggs produced per 80 m³). We calculated the fecundity of mature females using relationships between length, ovary mass, and egg production from Warner (1975), which reported minimal geographic variation in this fecundity relationship. First we estimated the ovary mass for each female by

$$(1) \quad \text{OM} = 1.31 \times 10^{-3} \text{SL}^{2.95} \quad (r^2 = 0.78)$$

where OM equals the ovary mass in grams and SL equals the standard length in centimetres. Ovary mass was then multiplied by oocyte density per gram of ovary, using the following equation:

$$(2) \quad \text{oocyte density} = 5377 \pm 499 \text{oocytes} \cdot (\text{g OM})^{-1}$$

to estimate the fecundity or number of oocytes contained with the gonads of female fish. Sites may differ further in egg production density, owing to spatial differences in sex ratios, which ranged from 0.8–4.0 (mature females:males) for the focal collections. Therefore, we estimated the egg production density of each focal site by multiplying the fecundity of the average female at each focal site by the density of mature females at that site. We examined spatial differences in density, average mass, and fecundity using ANOVA, with focal site as a fixed factor. Tukey's HSD was used to perform post hoc comparisons of statistical significance among focal sites. Data on biomass and egg production density are presented but not statistically compared, since they are functions of the other traits.

Spatial differences in size distributions of immature fish, mature females, and males, were compared among the focal sites using ANOVA. We also used the size, age, and sex data from the collections to estimate spatial differences in the timing of maturation and sex change among the focal populations. The size or age at maturity was defined as the size or age at which females began to predominate over immature fish 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 over mature females in the population (i.e., $L_{50\%}$ or $A_{50\%}$; length or age at 50% male). We used logistic regression to determine the predicted timing (L_{50} and A_{50}) of maturation and sexual transformation of each population. Statistical analyses were performed in JMP 7.0 (SAS Institute Inc., Cary, North Carolina).

To examine spatial differences in growth rates, we fit Von Bertalanffy growth curves to the size at age data from each focal population using least squares techniques and the following equation,

$$(3) \quad L_t = L_{\text{inf}} \{1 - \exp[-K(t - t_0)]\}$$

where L_t represents predicted length (L) at age (t), L_{inf} represents the predicted maximum asymptotic length (or length at time ∞), K is the coefficient of growth, t represents age, and t_0 represents the time at which fish length is zero. Because estimates of t_0 are sensitive to small sizes and ages, and because we had few new recruits (i.e., smallest size classes) in our collections, we fixed t_0 at zero for estimating L_{inf} and K (Robertson et al. 2005). We then extracted the Von Bertalanffy growth parameters from the best-fit model to generate growth curves for each population.

We used age-based catch curves to estimate annual mortality rates (Z) in each population following standard fisheries methods (e.g., Beverton and Holt 1957; Robertson et al. 2005). Mortality rates were calculated using log-linear regressions of the age-frequency data ($Z = \text{regression slope}$), excluding fish younger than the peak age mode. Estimates of annual survival rates (S) were then calculated according to the equation

$$(4) \quad S = \exp(-Z),$$

following Ricker (1975). Differences in mortality rates among sites may be attributed to differences in natural or fishing-induced mortality, or a combination of both.

For the seven focal populations, we examined correlations between densities and various demographic and life history traits. We hypothesized that density-dependent effects may influence demographic traits like fecundity and growth rates and life history variables such as the size at maturation and sex change. We also examined correlations between average sea surface temperature (SST) at each site, and these variables. Average SST values were calculated from monthly AVHRR satellite data from the years 1983–1998 for a 3 km × 3 km pixel extending offshore from each focal location. Because density and SST were positively correlated ($r = 0.60$) and influenced by biogeographic patterns, we also conducted partial correlations between these variables and all the demographic and life history variables, while controlling for the effects of SST and density, respectively.

Results

Geographic variation in density throughout the species range

Densities of *S. pulcher* varied dramatically on rocky reefs throughout the species' range, with a low of zero fish at Hollister Ranch and San Telmo, to a high of 7.0 fish per 80 m³ at a site on Isla Cedros (Fig. 3). Densities differed significantly among sites, and tended to be significantly

higher at offshore islands than along the mainland (Table 1a, island mean = 2.84 ± 0.33 fish·80 m⁻³; mainland mean = 1.49 ± 0.27 fish·80 m⁻³). We also detected significant spatial variation in *S. pulcher* densities among four geographic regions (Table 1b). A Tukey's post hoc HSD test indicates that southern Baja and the Southern Bight were not significantly different than northern Baja, which was in turn, not significantly different than the Northern Bight (southern Baja 3.33 ± 0.52 fish·80 m⁻³; Southern Bight, 2.19 ± 0.34 fish·80 m⁻³; northern Baja, 1.99 ± 0.37 fish·80 m⁻³; Northern Bight, 1.01 ± 0.19 fish·80 m⁻³; Fig. 3). In general, densities peaked in the southern part of the species range, particularly around the offshore islands.

Geographic variation in demography and life history traits among focal populations

The seven focal populations differed in density (ANOVA, $F_{[6,161]} = 4.01$, $P < 0.001$; Fig. 4a), with highest densities at Isla Cedros and lowest densities at San Nicolas Island. Average fish mass also differed among the locations (ANOVA, $F_{[6,612]} = 14.85$, $P < 0.0001$; Fig. 4b) but in a different way: average fish mass was lowest at Catalina Island and Isla Cedros, and greatest at Punta Canoas. This resulted, for example, in similar estimates of biomass for Isla Cedros and Punta Canoas, despite a 2.5-fold difference in population density (Fig. 4c). Biomass of *S. pulcher* was greatest at Isla Cedros and Punta Canoas, and lowest at Catalina Island and San Nicolas Island. Fecundity (i.e., the number of eggs produced per female) varied significantly among the focal locations (ANOVA, $F_{[6,252]} = 5.75$, $P < 0.0001$) showing a pattern opposite to that of density, with the highest fecundity at San Nicolas Island and lowest fecundity at Isla Cedros and Bahía Tortugas (Fig. 4d). In estimating egg production per unit area — after accounting for differences in the density of mature females — we estimated the highest egg output for San Nicolas Island (the site with the lowest density but the most female biased sex ratio) and the lowest egg output for Catalina Island (Fig. 4e).

Size frequency distributions of each sexual type, differed significantly among the seven focal populations of *S. pulcher* (Fig. 5). We found significant differences in the sizes of immature individuals among the populations (ANOVA, $F_{[6,163]} = 5.87$, $P < 0.0001$), although collections of immature fish were limited in some places. Immature fish were largest at Isla San Martin and smallest at Catalina Island, but were similarly sized at other locations. Mature males and mature females also differed significantly in size among the populations (ANOVA, males: $F_{[6,173]} = 10.45$, $P < 0.0001$; females: $F_{[6,252]} = 8.92$, $P < 0.0001$), being largest at San Nicolas Island and Punta Canoas, and smallest at Bahía Tortugas and Isla Cedros.

The geographic variation we observed in size structure was reflected in spatial differences in the timing of maturation and sexual transformation among populations. The size at maturation ($L_{50♀}$) varied from 159–212 mm SL among populations (Table 2), with fish maturing at the largest size at Isla San Martin and San Nicolas Island, and the smallest sizes at Bahía Tortugas. We detected greater spatial variation in the size at sex change ($L_{50♂}$) among focal populations, with $L_{50♂}$ ranging from 213–302 mm SL (Table 2). $L_{50♂}$ was largest at San Nicolas Island and smallest at Isla

Cedros. In general, there was a weak, albeit positive relationship between $L_{50♀}$ and $L_{50♂}$ ($r = 0.45$, $P = 0.31$), so that populations with individuals that matured at small sizes also changed sex at small sizes. Despite considerable spatial variation in size at maturation ($L_{50♀}$), the age at maturation ($A_{50♀}$) varied little among the focal populations (Table 3), ranging between 3.9 and 4.5 years. The age at sex change ($A_{50♂}$), however, showed more geographic variation, ranging from 5.3 to 8.0 years (Table 3). *Semicossyphus pulcher* changed sex at younger ages on Isla Cedros, and older ages at Punta Canoas and Isla San Martin. Because of the small range of variation in $A_{50♀}$ we did not find a relationship between $A_{50♀}$ and $A_{50♂}$ ($r = 0.20$, $P = 0.67$). There was however, a slight positive correlation between $L_{50♂}$ and $A_{50♂}$ ($r = 0.58$, $P = 0.17$), so that populations with individuals that changed sex at older ages tended to be larger in size.

To examine geographic variation in lifetime growth trajectories, we fit the Von Bertalanffy growth equation to the size at age data (Table 4). We observed distinct spatial differences in size at age predicted from the Von Bertalanffy fits (Table 4; Fig. 6a), with the largest size at age seen at San Nicolas Island and Punta Canoas, intermediate sizes at Isla San Martin, San Clemente Island, Catalina Island, and Bahía Tortugas, and the smallest size at age at Isla Cedros. A significant lack of overlap in parameter space of L_{inf} and K growth values highlights geographic differences in *S. pulcher* demography among populations (Fig. 6b).

Catch curve analyses of age-frequency data revealed substantial variation in instantaneous mortality rates (Z) and survivorship (S) among the seven focal populations (Table 5); however, the regression slopes were only marginally different among locations indicated by a significant interaction term (Fig. 7; analysis of covariance (ANCOVA), age × site: $F_{[6,40]} = 1.89$, $P = 0.10$; age: $F_{[1,40]} = 85.2$, $P < 0.001$; site: $F_{[6,40]} = 1.81$, $P = 0.11$). Estimated mortality rates were highest at Catalina and San Nicolas islands and lowest at Punta Canoas. In general, mortality rates were higher in southern California and lower in Baja California, with the exception of a relatively high mortality rate at Isla Cedros.

Correlations between density and temperature and life history traits

We used correlation analysis to explore relationships between density, SST, and various life history traits of *S. pulcher* among the seven focal populations (Table 6a). Interestingly, we observed a number of potentially density-dependent effects on sheephead populations (Fig. 8), including negative correlations between density and asymptotic size (L_{inf}), fecundity, and the size and age at sex change ($L_{50♂}$ and $A_{50♂}$, respectively). There was a positive correlation between density and growth to asymptotic size (K) mostly owing to the negative correlation between L_{inf} and K ($r = -0.85$, $P = 0.016$); a common result due to the mathematical constraints of the Von Bertalanffy growth equation. These correlations remained statistically significant (except for fecundity) after controlling for the effects of SST (Table 6b). These results suggest that high-density populations quickly reach a smaller asymptotic size, produce fewer eggs per female, and change sex at smaller sizes and earlier

Fig. 3. Changes in population density of *Semicossyphus pulcher* across a large portion of its biogeographic range. At each of 39 sampling sites, densities were estimated on 24 linear belt transects covering 80 m³ (20 m × 2 m × 2 m). Sites are roughly aligned from north to south and grouped into four geographic regions for spatial comparison of densities. Error bars represent ±1 SE.

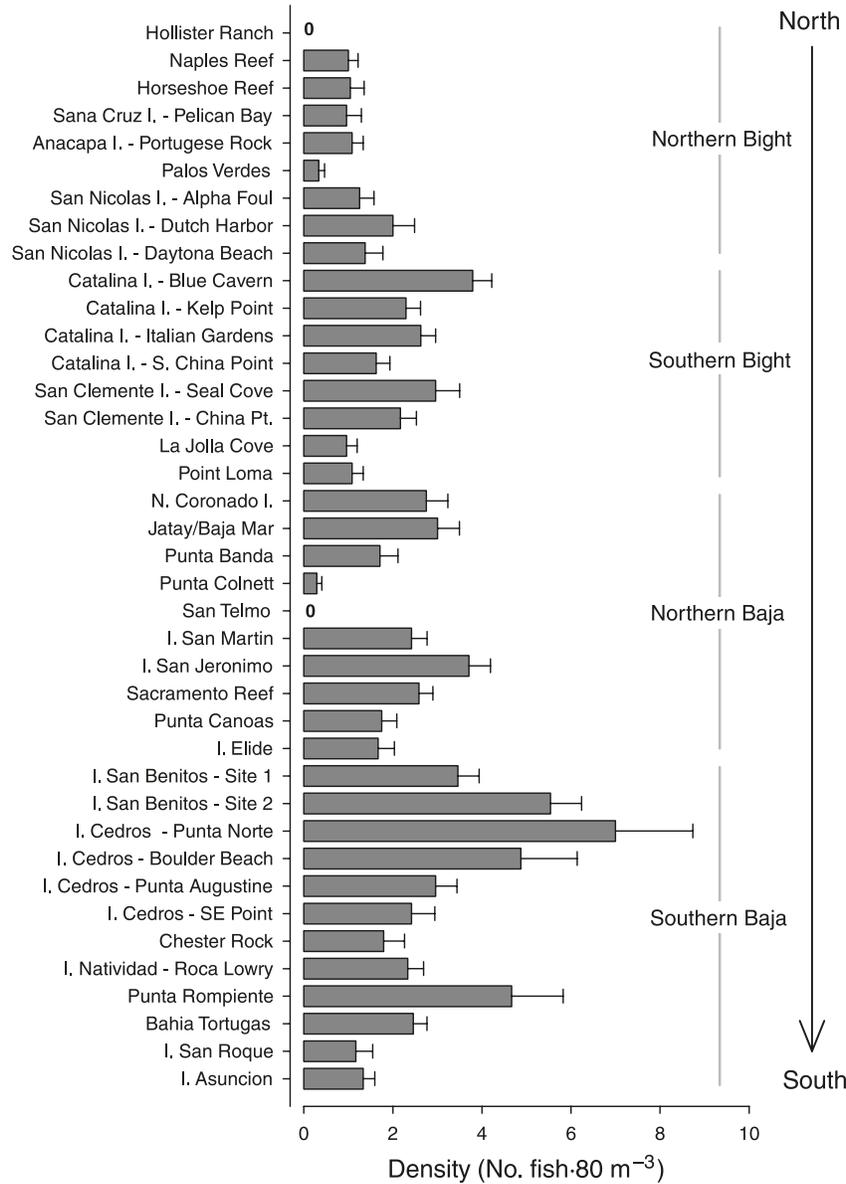
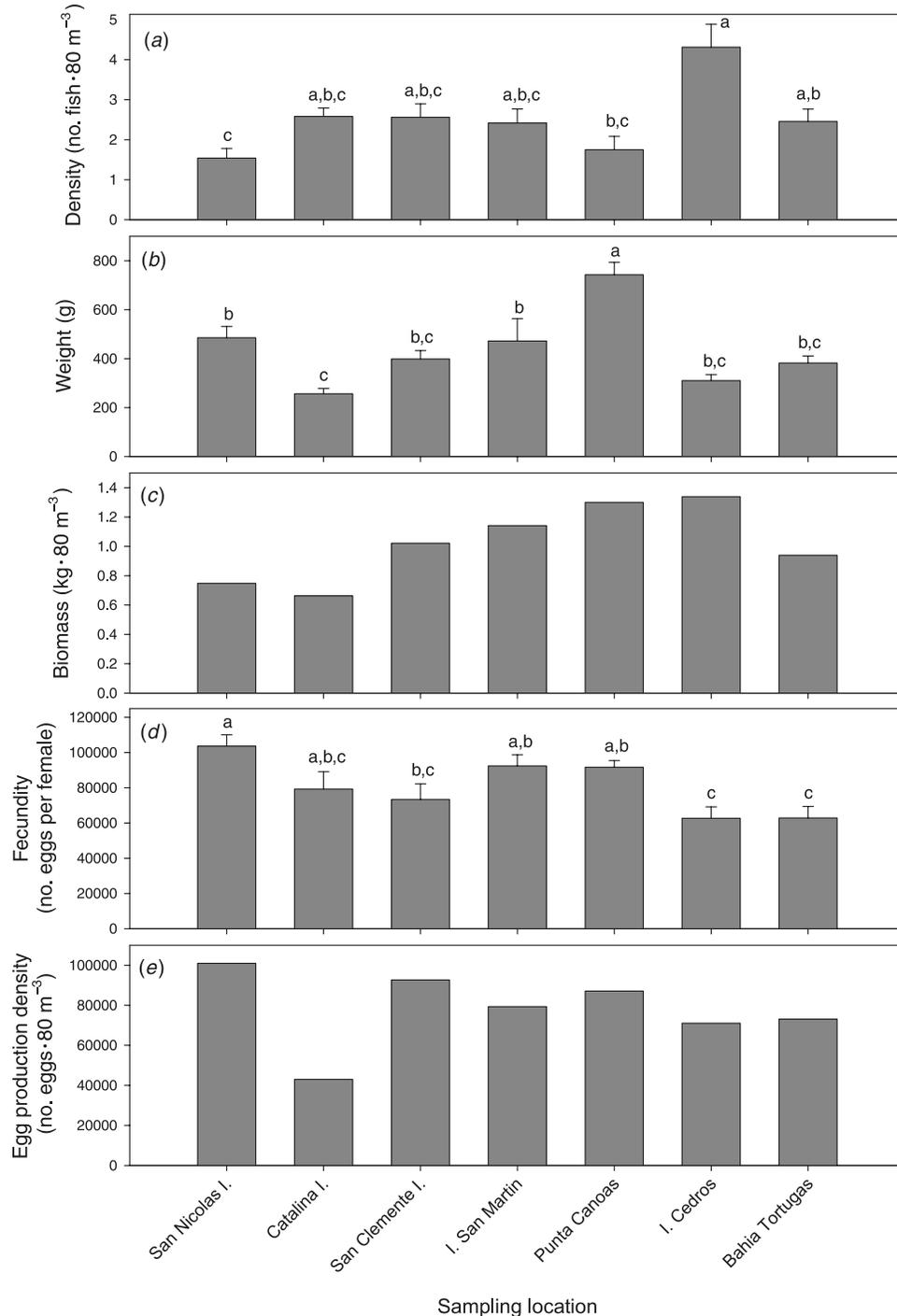


Table 1. Spatial variation in density of *Semicossyphus pulcher*.

Source	df	SS	F	p
(a)				
Site(island/mainland)	37	200.4	8.36	<0.0001
Island/mainland	1	65.4	12.08	0.0013
Error	897	581.5		
(b)				
Site(Region)	35	177.4	7.82	<0.0001
Region	1	88.5	5.82	0.0025
Error	897	581.5		

Note: Two-way nested analysis of variance (ANOVA) comparing among (a) sites and island/mainland locations and (b) sites and geographic regions.

Fig. 4. Spatial variation in life history traits of *Semicossyphus pulcher* at the seven focal sampling locations. Shown are (a) density, (b) average wet weight, (c) biomass, (d) average fecundity per female, and (e) egg production density. Biomass estimates were made by combining information on density and size. Fecundity was estimated using the relationship between body size, ovary size, and egg production following Warner (1975). Estimates of egg production density were made by combining information on fish density, the proportion of each population that was a sexually mature female, and average female fecundity. Error bars represent ± 1 SE. Statistical significance is indicated by the lack of overlap of letters above error bars. Biomass and egg production density were not statistically compared, since they are functions of the other parameters.

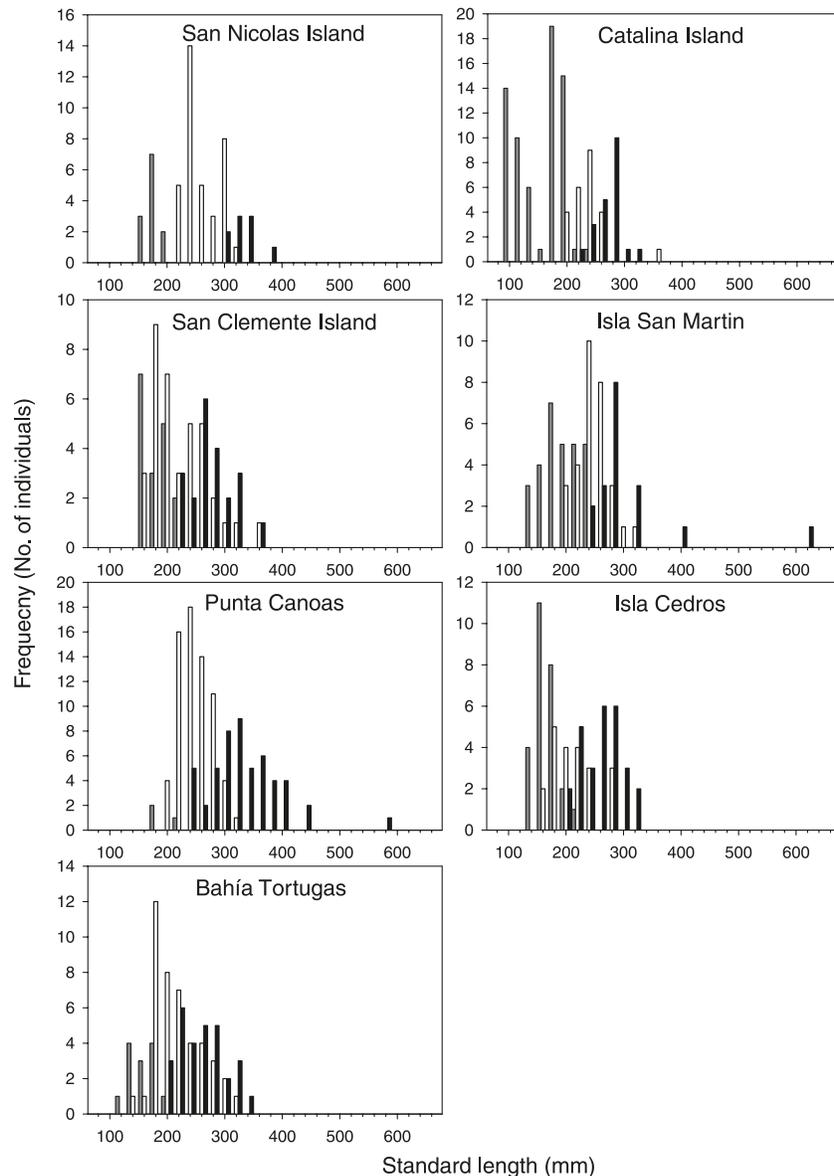


ages, thereby limiting the number of years the average female contributes to egg production.

In assessing the relationships between SST and various demographic and life history traits (Table 6a), we found negative relationships between SST and fecundity, sex ratio,

and the size at sex change. After removing the effects of density (Table 6b), only the relationship between SST and the size at sex change remained significant. However, in controlling for the effects of density, we also detected significant partial correlations between SST and the age at sex

Fig. 5. Size frequency histograms by sex for each of the seven focal populations of *Semicossyphus pulcher*. Shown are the numbers of individuals identified as immature, female, or male in each population. Determinations of sex were made by visual gonad inspection, as well as examinations of color pattern (initial vs. terminal phase) and external morphological characters. Black bars represent males, white bars represent females, and grey bars represent immature fish.



change and K , which differed greatly from the patterns that occurred when density effects were not accounted for (Table 6). Overall, *S. pulcher* from colder locations have increased fecundity, skewed sex ratios, and change sex at larger sizes. With density effects removed, we found that *S. pulcher* will change sex at older ages in colder locations and that they reach asymptotic size faster in colder locations.

Numerous other life history traits were correlated with one another. Of note, we detected a significant positive relationship between fecundity and the size at maturation ($L_{50\%}$; $r = 0.75$, $P = 0.05$), the size at sex change ($L_{50\%}$; $r = 0.90$, $P = 0.0065$), and L_{inf} ($r = 0.85$, $P = 0.016$), as might be expected for allometric relationships between size and egg production. We also detected significant positive relationships between the size at sex change ($L_{50\%}$) and sex ratio ($r = 0.81$, $P = 0.026$) and L_{inf} ($r = 0.92$, $P = 0.0033$).

Discussion

California sheephead showed significant spatial structuring in the geographic pattern of abundance measured across their range. Densities were highest in the southern portion of their range and lowest near the northern range limit at Point Conception (*S. pulcher* has been recorded as far north as Monterey Bay). Cowen (1990) reported similar patterns across a small number of sites for this species. Fish community surveys conducted during these cruises revealed that a number of other fish species showed similar biogeographic patterns in abundance (e.g., rock wrasse, scissortail damselfish, kelp bass; M.S. Love and D.M. Schroeder, unpublished data). Many species with these abundance distributions have subtropical affinities and differences in abundance may be related to latitudinal differences in temperature require-

Table 2. Size at maturity and size at sex change for seven focal populations of *Semicossyphus pulcher* calculated using logistic regression.

N (mean standard length [mm], SD)			Size at maturity (mm, SL)	95% CI	Logistic regression parameters	Size at sex change (mm, SL)	95% CI	Logistic regression parameters
I	F	M						
San Nicolas I.								
12 (169.0, 14.9)	36 (249.2, 30.8)	9 (318.4, 43.3)	201.5	NA*, NA*	$a = -11.91,$ $b = 2400.6$	302.8	289.2, 339.3	$a = -0.10,$ $b = 30.88$
Catalina I.								
67 (146.5, 41.4)	24 (225.7, 33.7)	21 (260.1, 22.7)	202.3	195.2, 211.9	$a = -0.13,$ $b = 23.35$	244.1	225.8, 266.3	$a = -0.047,$ $b = 11.54$
San Clemente I.								
19 (176.3, 22.6)	37 (216.3, 46.2)	19 (269.8, 34.5)	173.8	137.7, 192.1	$a = -0.037,$ $b = 6.39$	265.6	242.2, 310.2	$a = -0.029,$ $b = 7.59$
San Martin I.								
29 (184.0, 31.8)	30 (238.6, 27.9)	18 (295.2, 86.9)	212.5	198.5, 224.6	$a = -0.067,$ $b = 14.40$	268.6	251.2, 305.6	$a = -0.042,$ $b = 11.39$
Punta Canoas								
3 (177.7, 23.7)	68 (239.6, 26.8)	51 (320.4, 61.6)	184.3	NA [†] , 197.8	$a = -0.14,$ $b = 26.16$	275.6	265.6, 287.9	$a = -0.055,$ $b = 15.08$
Isla Cedros								
26 (158.2, 19.1)	21 (201.0, 35.6)	28 (245.9, 38.9)	177.8	165.3, 197.7	$a = -0.065,$ $b = 11.61$	213.2	180.4, 238.7	$a = -0.030,$ $b = 6.47$
Bahía Tortugas								
14 (152.7, 21.6)	43 (209.1, 41.2)	34 (254.0, 43.3)	159.6	137.9, 171.1	$a = -0.074,$ $b = 11.81$	239.9	217.6, 269.5	$a = -0.024,$ $b = 5.87$

Note: Size at maturity is defined as the predicted standard length (SL) at which 50% of the population is female. Size at sex change is defined as the predicted standard length at which 50% of the population is male. 95% CI is the confidence interval around the predicted size at maturity and size at sex change based on the logistic regression model. I, immature fish; F, females; M, males.

*95% CI could not be estimated because of lengths of immatures and females did not overlap.

[†]95% CI could not be estimated because of small sample size of immature class ($n = 3$).

ments. Spatial differences in levels of replenishment and (or) fishing may also help to explain these biogeographic patterns of abundance (Cowen 1985; Hamilton et al. 2007). In addition, densities of California sheephead were significantly higher at offshore islands than along the mainland coast. Many of those offshore islands are remote and may receive less fishing pressure than the mainland sites. Alternatively, these patterns may reflect differences in recruitment, environmental conditions (e.g., sedimentation), habitat, or prey availability at islands versus the mainland (Pondella et al. 2005).

Detailed investigations of the seven focal populations revealed that California sheephead exhibit geographic variation in demographic and life history variables. We observed significant spatial differences in population densities, growth rates, size structure, and the timing of maturation and sex change. Interestingly, Isla Cedros, the site with the highest density, was composed of smaller fish and therefore had lower reproductive output than sites with lower densities (e.g., San Nicolas Island, Punta Canoas). San Nicolas Island, with a highly skewed sex ratio showed the highest egg production density of any site. Not surprisingly, the amount of fish biomass and not density is a better predictor of the reproductive potential of different populations. Differences in

growth rates among the focal populations may reflect differences in prey availability and diet composition, which have been shown to differ significantly among populations in southern California and Baja California (Cowen 1986). Significant differences in the timing of maturation and sex change across populations have been suggested to be influenced by differences in growth rates and survivorship (Cowen 1990). Fish from populations that grow more slowly and experience higher mortality rates mature and change sex at smaller sizes. Previous evidence has also suggested that fish that mature and change sex at small sizes arise from high-density populations that turn over rapidly (Cowen 1990). Geographic variation in sex ratios have been linked to the average number of years that fish spend as mature females in each population (Cowen 1990; Hamilton et al. 2007). Fish from populations with sex ratios skewed towards females spend longer as mature females before changing sex. These patterns are likely related to how local densities and size structure influence the abilities of males to guard mating territories and harems of females.

A number of studies of fished and unfished species from seas in tropical and temperate regions, have documented geographic variation in demographic and life history traits. Spatial variation in growth rates and predicted asymptotic

Table 3. Age at maturity and age at sex change for seven focal populations of *Semicossyphus pulcher* calculated using logistic regression.

N (mean age [years], SD)			Age at maturity	Logistic regression parameters	Age range (years)		Age at sex change	Logistic regression parameters	Age range (years)	
I	F	M	(years)		I	F	(years)		F	M
San Nicolas I.										
8 (2.9, 0.6)	22 (5.1, 1.0)	9 (6.4, 1.0)	3.9	$a = -14.78,$ $b = 56.96$	2–4	4–7	6.7	$a = -1.14,$ $b = 7.47$	4–7	5–8
Catalina I.										
17 (2.8, 1.2)	19 (5.3, 1.3)	15 (6.6, 1.4)	4.0	$a = -12.44,$ $b = 49.75$	1–4	4–8	6.1	$a = -0.93,$ $b = 5.68$	4–8	5–10
San Clemente I.										
13 (3.1, 0.9)	14 (6.2, 1.6)	18 (7.4, 1.8)	4.1	$a = -12.71,$ $b = 51.52$	2–4	4–9	6.3	$a = -0.45,$ $b = 2.80$	4–9	5–12
San Martin I.										
12 (3.8, 0.8)	16 (5.9, 1.8)	11 (9.2, 4.9)	4.5	$a = -2.51,$ $b = 11.23$	3–5	4–11	7.5	$a = -0.54,$ $b = 4.04$	4–11	6–22
Punta Canoas										
3 (3.3, 0.6)	24 (6.3, 1.6)	21 (10.0, 3.8)	3.9	$a = -13.52,$ $b = 53.46$	3–4	4–10	8.0	$a = -0.95,$ $b = 7.56$	4–10	6–25
Isla Cedros										
12 (2.6, 0.7)	13 (6.1, 1.5)	19 (6.8, 1.5)	4.0	$a = -14.26,$ $b = 56.33$	2–4	4–8	5.3	$a = -0.34,$ $b = 1.80$	4–8	5–9
Bahía Tortugas										
11 (3.0, 0.8)	15 (6.3, 1.6)	14 (7.7, 1.6)	4.0	$a = -13.61,$ $b = 54.86$	2–4	4–10	7.1	$a = -0.55,$ $b = 3.96$	4–10	5–11

Note: Age at maturity is defined the predicted age at which 50% of the population is female. Age at sex change is defined as the predicted age at which 50% of the population is male. Range is the minimum and maximum age reported in that category (sample sizes were too small to calculate reliable 95% confidence interval, CI). I, immature; F, female; M, male. N, approximately 30 randomly chosen fish per site.

sizes have been recorded at a number of spatial scales: among local populations separated by hundreds of metres (Robertson et al. 2005), among different reefs and islands in one region (Gust et al. 2002; Kritzer 2002; Ruttenberg et al. 2005) or across multiple regions (hundreds of kilometres) (Cowen 1990; Williams et al. 2003), among spatially separate stocks (Brodziak and Mikus 2000; Ormseth and Norcross 2009; Brunel and Dickey-Collas 2010), and across oceanographic basins (thousands of kilometres) (Meehan et al. 2001; Robertson et al. 2005). Often these demographic differences are attributed to environmental variation in habitat, predation pressure, productivity, resource availability, and temperature. Geographic variation in the timing of life history events, such as the timing of maturation, has been reported for different stocks of sole along the Pacific coast (Brodziak and Mikus 2000), cod in Alaska (Ormseth and Norcross 2009), and Atlantic herring (Jennings and Beverton 1991). These differences in the timing of maturation have been attributed to differences in environmental and fishing pressures among locations. For tropical parrotfishes, the size at sex change has been shown to be influenced by population-specific natural mortality rates (Gust 2004; DeMartini et al. 2005). At locations characterized by high predator abundance, fish are selected to change sex at smaller sizes. Warner (1975) and Cowen (1990) reported similar patterns for California sheephead at Guadalupe Island and shifts in the timing of sex change might also be related to human-induced fishing mortality in this species (Hamilton et al. 2007). Increased predation pressure can also lead to pheno-

typic plasticity in the timing of maturation among populations (Reznick et al. 1990).

Density and temperature effects on demography and life histories

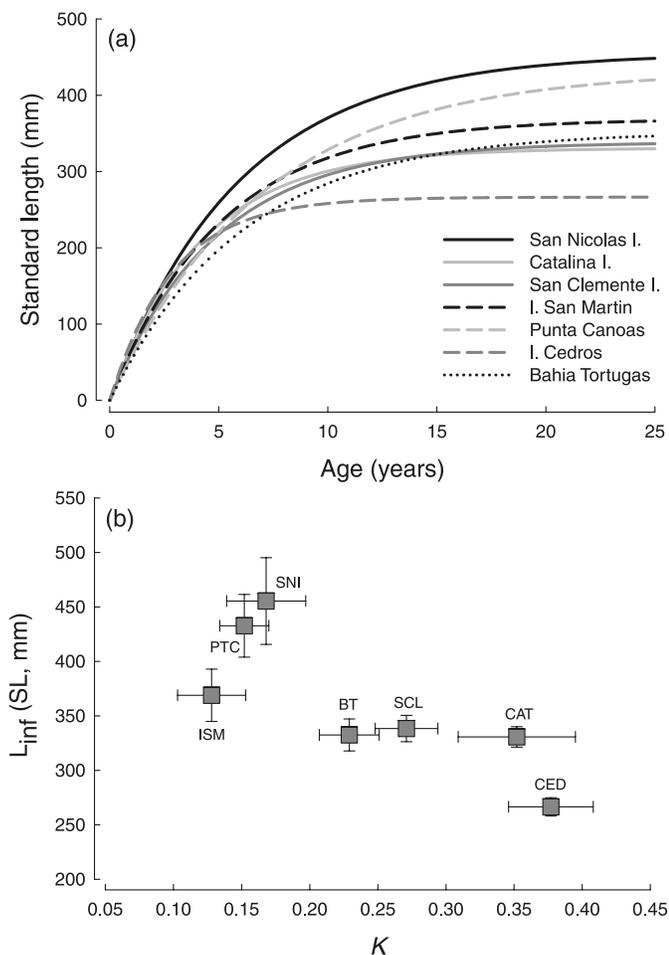
Few studies have looked at the effects of conspecific density on geographic patterns in demography and life histories. We found strong density-dependent patterns at the population level with negative relationships between density and asymptotic size, fecundity, and the timing of life history events, after controlling for the effects of temperature. In locations with elevated densities of *S. pulcher*, fish are smaller in size, have lower reproductive output, and change sex at smaller sizes and younger ages. These density-dependent effects on life histories may be influenced by resource competition and differences in prey quantity and quality among populations. Previous gut content work showed strong geographic differences in diet along with differences in prey availability (Cowen 1986). Fish from high-density and slow-growing populations in Baja California had diets composed of bryozoan encrusted algae, arguably poor food resources compared with the lower density populations at San Nicolas Island, where diets were dominated by brachyuran crabs and urchins. San Nicolas Island is also a highly productive location that receives strong upwelling, and supports a higher standing stock of preferred food resources, such as crabs (S.L. Hamilton and J.E. Caselle, unpublished data). Cowen (1986) concluded that at high density locations, *S. pulcher* consume a higher percentage of the annual pro-

Table 4. Von Bertalanffy growth parameters and estimates of annual survivorship for a random subsample of *Semicossyphus pulcher* taken from seven focal sites throughout their biogeographic range and for all sites combined.

Site	<i>N</i>	Avg. size (SL, mm; \pm SD)	L_{inf} (\pm SD)	<i>K</i> (\pm SD)
San Nicolas I.	39	251.7 (57.1)	455.4 (39.8)	0.168 (0.029)
Catalina I.	51	216.5 (55.0)	330.7 (9.4)	0.352 (0.043)
San Clemente I.	45	227.6 (52.1)	338.4 (12.1)	0.271 (0.023)
San Martin I.	39	250.3 (76.6)	368.9 (24.0)	0.128 (0.025)
Punta Canoas	48	280.1 (75.7)	432.7 (28.8)	0.152 (0.018)
Cedros I.	44	213.9 (47.7)	266.5 (8.4)	0.377 (0.031)
Bahía Tortugas	40	210.4 (55.2)	332.5 (14.7)	0.229 (0.022)
All sites	305	235.3 (64.6)	332.2 (5.7)	0.243 (0.008)

Note: L_{inf} represents the asymptotic length (SL in mm) while *K* (growth coefficient) represents the rate of approach to that maximum size, for each population for the Von Bertalanffy equation. The average size is for the subsample of fish randomly selected for aging analysis.

Fig. 6. Spatial variation in *Semicossyphus pulcher* lifetime growth curves in the seven focal populations. (a) Shown are fits to the size-at-age data for each population, using the Von Bertalanffy growth equation. (b) Von Bertalanffy growth parameters for each population and estimates of variation in L_{inf} and *K*. Error bars represent ± 1 SD.



duction of preferred prey and switch to alternative low quality prey, which has effects on demography and life histories. Competitive interactions in coral-reef fishes have been shown to lead to density-dependent effects that reduce

growth and the timing of maturation (Jones 1987; Caselle et al. 2003). For example, at elevated densities, aggressive interactions among female bicolor damselfish have been shown to result in density-dependent reductions in growth and reproductive output (Samhoury 2009). Similar effects may occur in populations of California sheephead, as females compete for resources and to mate with males during the reproductive season.

We also detected temperature-dependent effects on demography and life history traits, such as negative relationships between SST and fecundity, sex ratios, the size at maturation and sex change, and the predicted asymptotic size of populations. Fish from populations exposed to colder annual temperatures had higher fecundities, sex ratios more skewed towards females, and were larger at maturation and sex change, in addition to growing to larger sizes. After controlling for the effects of density on these patterns, only the negative relationships between temperature and the size at sex change and growth to asymptotic size were significant. Countergradient variation in growth and other demographic traits (i.e., faster growth and larger sizes at higher latitudes) has been documented in numerous fish species, but most famously for the Atlantic silverside, *Menidia menidia* (Conover and Present 1990). Often, fish from colder regions are genetically adapted to shorter growing seasons, and therefore show greater growth potential, possibly owing to greater food conversion efficiency. Across the range of California sheephead, variation in temperature and its effects on growth and other life history and demographic characteristics is likely to be complex, as temperature does not vary simply with latitude (Pondella et al. 2005). Northern Baja is characterized by areas of upwelling and colder waters than those to the north and the south. For California sheephead, differences in growth may be more related to local differences in productivity and resource availability (Cowen 1986, 1990) as this species has a long larval duration (approx. 60 d, Cowen 1985) and population genetic studies suggest little geographic differentiation among distant populations (Bernardi et al. 2003). In a study that isolated temperature effects by controlling for latitudinal differences, Ruttenberg et al. (2005) showed that growth, longevity, and reproductive output in the damselfish *Stegastes beebei* was strongly related to regional differences in temperature and the avail-

Table 5. Estimates of annual mortality and survivorship rates from log-linear regression of age-frequency data (catch curves) for a random subsample of *Semicossyphus pulcher* taken from seven focal sites throughout their biogeographic range and for all sites combined.

Site	<i>N</i>	Max. age (years)	Min. age (years)	Mortality (<i>Z</i>)	Survivorship (<i>S</i>)
San Nicolas I.	39	8	2	0.357	0.698
Catalina I.	51	10	1	0.500	0.607
San Clemente I.	45	12	3	0.293	0.748
San Martin I.	39	22	3	0.219	0.811
Punta Canoas	48	25	3	0.188	0.829
Cedros I.	44	9	2	0.312	0.726
Bahía Tortugas	40	11	2	0.224	0.803
All sites	305	25	1	0.376	0.690

ability of preferred algal prey. Robertson et al. (2005) reported strong negative relationships between temperature and longevity, survivorship, and the asymptotic size of populations across the species range for the ocean surgeonfish *Acanthurus bahianus* in the Caribbean. These temperature-dependent effects appear to be generally explained by the metabolic theory of ecology (Munch and Salinas 2009) and have been described for other fishes (Meekan et al. 2001; Choat and Robertson 2002; Brunel and Dickey-Collas 2010). Unlike Robertson et al. (2005), we did not detect significant relationships between survivorship and temperature, potentially because these patterns were obscured by spatial differences in fishing pressure.

Implications for fisheries management

Fishing pressure differs significantly across the range of *S. pulcher*, with the highest fishing pressure in southern California and lower fishing pressure in Baja California. These patterns are reflected in the survivorship results calculated from age frequency data, with lower survivorship in southern California and higher survivorship in Baja California. Our collections were made in 1998, during the year of peak landings for the live fish fishery in southern California (Alonzo et al. 2004). Despite lower fishing pressure in Baja California, *S. pulcher* comprises 25% of the catch of the artisanal fishery (Rosales-Casián and Gonzalez-Camacho 2003) and catches have likely increased, although catch records were not available from Baja California sites. Punta Canoas, the most isolated site in Baja California, showed the highest survivorship, potentially reflecting limited exploitation. In contrast, survivorship estimates were lowest at San Nicolas and Catalina Islands, where commercial and recreational fishing pressure were greatest, respectively (Wright et al. 2000). San Clemente Island is fished relatively heavily by both commercial and recreational interests (Wright et al. 2000). We have previously demonstrated that size-selective harvesting can alter life history traits in *S. pulcher* (Hamilton et al. 2007), so the currently reported biogeographic patterns in demography and life histories are likely to differ from the pre-exploitation patterns. In particular, size structure, growth rates, and the timing of maturation and sex change decreased at San Nicolas and Catalina Islands as a response to increased exploitation, but did not change at Bahía Tortugas where fishing pressure remained light. Therefore, the impacts of fishing on these populations may

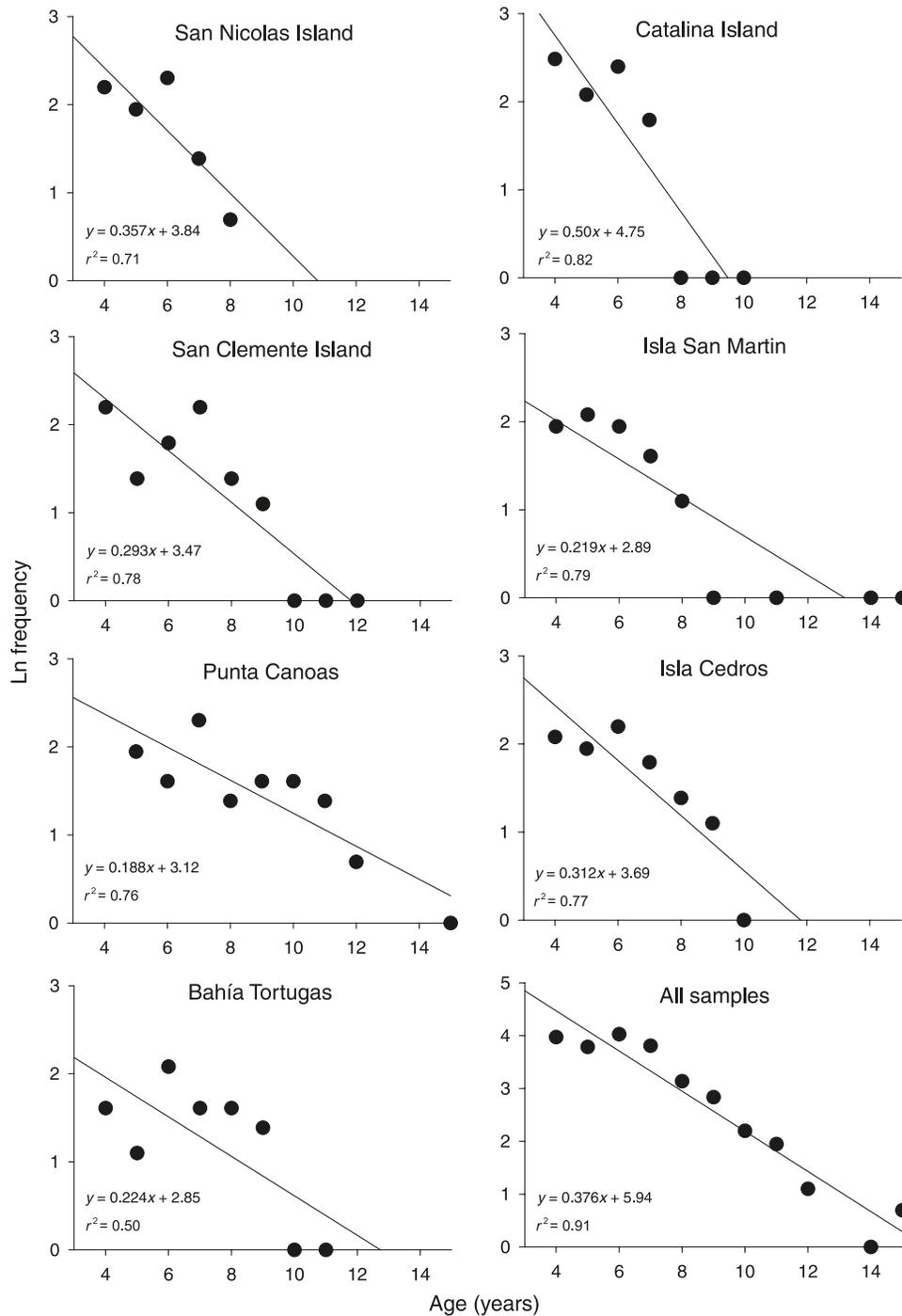
obscure biogeographic patterns in demography (e.g., island vs. mainland, latitudinal).

Numerous studies have reported fishing-induced changes to demographic and life history traits in fishes (McGovern et al. 1998; Law 2000; Hawkins and Roberts 2003). Hawkins and Roberts (2003) reported decreases in the size of sex change of parrotfishes across numerous Caribbean islands spanning a gradient in fishing pressure, similar to our findings for *S. pulcher*. Heavily exploited protogynous hermaphrodites, such as gag *Myctoperca microlepis*, show shifts in the timing of maturation but no change in the size at sex change, which appears fixed in this species (McGovern et al. 1998). As a consequence of the fishery targeting large individuals (primarily males), sex ratios have become heavily female biased with the potential for sperm limitation. Similar shifts in sex ratios of *S. pulcher* have been observed at San Nicolas Island (Hamilton et al. 2007). Shifts in the timing of maturation to younger ages and smaller sizes are a common response to size-selective exploitation (Rijnsdorp 1993; Law 2000; Hutchings 2005).

As more studies continue to report significant geographic variability in demographic and life history traits among fish populations, these sources of variation should be considered when making management recommendations. Even small variation in life history parameters may influence model results and in such cases, and where data exist, they should be incorporated into fisheries models. Size and catch limits tuned to average demographic parameters or those from only one population may, in some cases, give a false impression of the optimal regulations required to achieve sustainable harvest throughout the range of a species. For *S. pulcher*, a 2004 stock assessment recognized that population parameters differed between southern California and Baja California using data from historically unfished locations (Alonzo et al. 2004). However, size and catch limits were ultimately based on data from the Catalina population reported in Warner (1975) and that population has changed dramatically due to fishing in the past few decades (Hamilton et al. 2007). Future stock assessments for this species should consider using more current population-specific information (Alonzo et al. 2004).

For reef fishes with geographically variable demography and life histories, spawning biomass and optimal yields could potentially be improved by setting different size and catch limits across the species range (S.L. Hamilton, unpub-

Fig. 7. Age based catch curve estimates of annual mortality rates from log-linear regressions of age frequency data for *Semicossyphus pulcher*.



lished data). Size limits should be increased for populations that mature at larger sizes, to allow more individuals an opportunity to reproduce and contribute to future generations. For sex-changing species, variation in size at sex change can also influence predicted spawning biomass and yields and should be taken into account by fisheries managers (Alonzo and Mangel 2005). The approach of incorporating demographic plasticity into fisheries management advocates for smaller scale and more localized management (Gun-

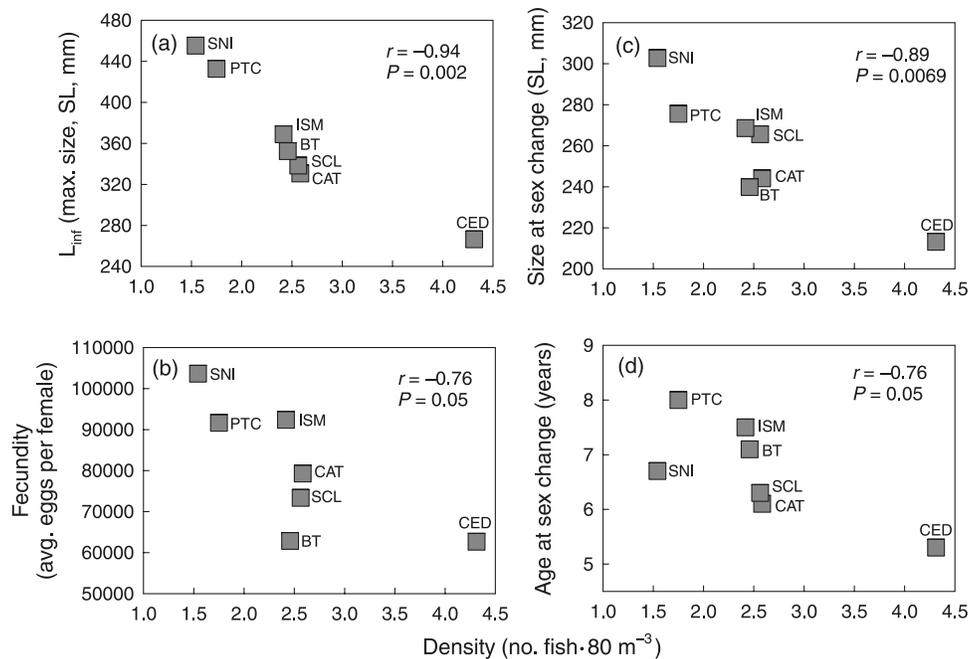
derson et al. 2008). While this approach may be logistically difficult for some fisheries, small-scale co-management schemes have been successfully implemented for several coastal reef-based organisms (Orensanz et al. 2005; Gonzales et al. 2006). Smaller scale management may require moving beyond traditional stock assessments in addition to the development of new modeling and management tools (Holland 2003). Spatial management through marine protected areas may be one effective management strategy for

Table 6. Pearson’s correlation coefficients of the relationships between density, temperature (sea surface, SST), and various life history traits of *Semicossyphus pulcher* sampled at seven focal populations throughout their geographic range.

	Density	Fecundity	Sex ratio	$L_{50♀}$	$L_{50♂}$	$A_{50♀}$	$A_{50♂}$	L_{inf}	K	Survivorship
(a) Pairwise correlations										
Density	—	-0.76*	-0.64	-0.29	-0.89**	0.12	-0.75*	-0.94**	0.94**	-0.17
Temperature	0.60	-0.77*	-0.82*	-0.60	-0.82*	0.04	-0.05	-0.60	0.32	0.39
(b) Partial correlations										
Density	—	-0.58	-0.31	-0.09	-0.88**	0.11	-0.90**	-0.90**	0.98**	-0.54
Temperature	—	-0.61	-0.72	-0.54	-0.79*	-0.03	-0.76*	-0.15	-0.85*	0.62

Note: $L_{50♀}$, size at maturation; $L_{50♂}$, size at sex change; $A_{50♀}$, age at maturation; $A_{50♂}$, age at sex change; L_{inf} , asymptotic length parameter of the Von Bertalanffy equation; K , the rate of approach to that asymptotic length; (a) pairwise correlations between variables; (b) partial correlations after controlling for the effects of temperature or density on the correlations between the other variables. *, $P < 0.05$; **, $P < 0.01$.

Fig. 8. Density-dependent effects on selected life history traits. Shown are relationships between density and (a) L_{inf} (max. predicted size; standard length, mm) from the Von Bertalanffy growth fits, (b) predicted fecundity (average number of eggs per female), (c) $L_{50♂}$ (size at sex change), and (d) $A_{50♂}$ (age at sex change).



this species and others with high levels of demographic variation over relatively small spatial scales. For California sheephead, regional management based on biogeographic patterns may not only improve spawning biomass and yields, but also preserve their important ecological role in kelp forests.

Acknowledgements

The authors would like to thank J. Figurski, M. Paddock, M. Nishimoto, E. Hessell, W. Golden, L. MacDonald, J. Harding, J. Roller, M. Meeker, D. Pondella, D. Richards, and the captain and the crew of the dive vessel “Horizon”. We send a sincere thank you to J. Cope for estimating the Von Bertalanffy growth parameters using the size at age data. B. Kinlan provided SST data from AVHRR satellite imagery. T. Silvas, C. Lee, E. Kondo, C. Lantz, T. Eglhoff, S. Hammond, and A. Erickson prepared dorsal spines for aging. We extend our gratitude to R. Warner for stimulating discussion and helpful insights. The authors appreciate the insightful comments of two anonymous reviewers. Funding

was provided by the California Department of Fish and Game, the Biological Resource Division USGS, California Sea Grant, and PISCO, the Partnership for Interdisciplinary Studies of Coastal Oceans, which is supported primarily by the Gordon and Betty Moore Foundation and the David and Lucile Packard Foundation. This is PISCO contribution number 366.

References

Alonzo, S.H., and Mangel, M. 2005. Sex-change rules, stock dynamics, and the performance of spawning-per-recruit measures in protogynous stocks. *Fish. Bull.* (Wash. D. C.), **103**: 229–245.
 Alonzo, S.H., Key, M., Ish, T., and MacCall, A. 2004. Status of the California sheephead (*Semicossyphus pulcher*) stock (2004). California Department of Fish and Game. Available from www.dfg.ca.gov/marine/sheephead2004.
 Begg, G.A., Hare, J.A., and Sheehan, D.D. 1999. The role of life history parameters as indicators of stock structure. *Fish. Res.* **41**: 141–163. doi:10.1016/S0165-7836(99)00071-5.

- Bernardi, G., Findley, L., and Rocha-Olivares, A. 2003. Vicariance and dispersal across Baja California in disjunct marine fish populations. *Evolution*, **57**(7): 1599–1609. PMID:12940364.
- Beverton, R.J.H., and Holt, S.J. 1957. On the dynamics of exploited fish populations. Fish and Fisheries Series II. Chapman & Hall, London, UK.
- Brodziak, J., and Mikus, R. 2000. Variation in life history parameters of Dover sole, *Microstomus pacificus*, off the coasts of Washington, Oregon, and northern California. *Fish. Bull.* (Wash. D. C.), **98**: 661–673.
- Brown, J.H. 1995. Macroecology. University of Chicago Press, Chicago, Ill.
- Brunel, T., and Dickey-Collas, M. 2010. Effects of temperature and population density on von Bertalanffy growth parameters in Atlantic herring: a macro-ecological analysis. *Mar. Ecol. Prog. Ser.* **405**: 15–28. doi:10.3354/meps08491.
- Buonaccorsi, V.P., Westerman, M., Stannard, J., Kimbrell, C., Lyann, E., and Vetter, R.D. 2004. Molecular genetic structure suggests limited larval dispersal in grass rockfish, *Sebastes rastrelliger*. *Mar. Biol.* (Berl.), **145**: 779–788.
- Caselle, J.E., Hamilton, S.L., and Warner, R.R. 2003. The interaction of retention, recruitment, and density-dependent mortality in the spatial placement of marine reserves. *Gulf Caribb. Res.* **14**: 107–117.
- Choat, J.H., and Robertson, D.R. 2002. Age-based studies on coral reef fishes. In *Coral reef fishes: dynamics and diversity in a complex ecosystem*. Edited by P.F. Sale. Academic Press, New York, N.Y. pp. 57–80.
- Conover, D.O., and Present, T.M.C. 1990. Countergradient variation in growth rate: compensation for length of the growing season among Atlantic silversides from different latitudes. *Oecologia* (Berl.), **83**: 316–324.
- Cowen, R.K. 1985. Large scale pattern of recruitment by the labrid, *Semicossyphus pulcher*: causes and implications. *J. Mar. Res.* **43**: 719–742. doi:10.1357/002224085788440376.
- Cowen, R.K. 1986. Site-specific differences in the feeding ecology of the California sheephead, *Semicossyphus pulcher* (Labridae). *Environ. Biol. Fishes*, **16**: 193–203. doi:10.1007/BF00005171.
- Cowen, R.K. 1990. Sex change and life history patterns of the labrid *Semicossyphus pulcher*, across an environmental gradient. *Copeia*, **3**: 787–795. doi:10.2307/1446444.
- DeMartini, E.E., Friedlander, A.M., and Holzwarth, S.R. 2005. Size at sex change in protogynous labroids, prey body size distributions, and apex predator densities at NW Hawaiian atolls. *Mar. Ecol. Prog. Ser.* **297**: 259–271. doi:10.3354/meps297259.
- Gonzales, J., Stotz, W., Garrido, J., Orensanz, J.M., Parma, A.M., Tapia, C., and Zuleta, A. 2006. The Chilean TURF system: how is it performing in the case of the loco fishery? *Bull. Mar. Sci.* **78**: 499–527.
- Gunderson, D.R., Parma, A.M., Hilborn, R., Cope, J.M., Fluharty, D.L., Miller, M.L., Vetter, R.D., Heppell, S.S., and Greene, H.G. 2008. The challenge of managing nearshore rocky reef resources. *Fisheries*, **33**: 172–179. doi:10.1577/1548-8446-33.4.172.
- Gust, N. 2004. Variation in the population biology of protogynous coral reef fishes over tens of kilometers. *Can. J. Fish. Aquat. Sci.* **61**: 205–218. doi:10.1139/f03-160.
- Gust, N., Choat, J.H., and Ackerman, J.L. 2002. Demographic plasticity in tropical reef fishes. *Mar. Biol.* (Berl.), **140**: 1039–1051. doi:10.1007/s00227-001-0773-6.
- Hamilton, S.L., Caselle, J.E., Standish, J.D., Schroeder, D.M., Love, M.S., Rosales-Casian, J.A., and Sosa-Nishizaki, O. 2007. Size-selective harvesting alters life histories of a temperate sex-changing fish. *Ecol. Appl.* **17**(8): 2268–2280. doi:10.1890/06-1930.1. PMID:18213967.
- Hawkins, J.P., and Roberts, C.M. 2003. Effects of fishing on sex-changing Caribbean parrotfishes. *Biol. Conserv.* **115**: 213–226. doi:10.1016/S0006-3207(03)00119-8.
- Holland, D.S. 2003. Integrating spatial management measures into traditional fishery management systems: the case of the Georges Bank multispecies groundfish fishery. *ICES J. Mar. Sci.* **60**: 915–929. doi:10.1016/S1054-3139(03)00097-3.
- Hutchings, J.A. 2005. Life history consequences of overexploitation to population recovery in Northwest Atlantic cod (*Gadus morhua*). *Can. J. Fish. Aquat. Sci.* **62**: 824–832. doi:10.1139/f05-081.
- Jennings, S., and Beverton, R.J.H. 1991. Intraspecific variation in the life history tactics of Atlantic herring (*Clupea harengus* L.) stocks. *ICES J. Mar. Sci.* **48**: 117–125. doi:10.1093/icesjms/48.1.117.
- Jones, G.P. 1987. Competitive interactions among adults and juveniles of a coral reef fish. *Ecology*, **68**: 1534–1547. doi:10.2307/1939237.
- Jorgenson, S.J., Kaplan, D.M., Klimley, A.P., Morgan, S.G., O'Farrell, M.R., and Botsford, L.W. 2006. Limited movement in blue rockfish *Sebastes mystinus*: internal structure of home range. *Mar. Ecol. Prog. Ser.* **327**: 157–170. doi:10.3354/meps327157.
- Kritzer, J.P. 2002. Variation in the population biology of stripey bass *Lutjanus carponotatus* within and between two island groups on the Great Barrier Reef. *Mar. Ecol. Prog. Ser.* **243**: 191–207. doi:10.3354/meps243191.
- Law, R. 2000. Fishing, selection, and phenotypic evolution. *ICES J. Mar. Sci.* **57**: 659–668. doi:10.1006/jmsc.2000.0731.
- McGovern, J.C., Wyanski, D.M., Pashuk, O., Manooch, C.S., and Sedberry, G.R. 1998. Changes in the sex ratio and size at maturity of gag, *Mycteroperca microlepis*, from the Atlantic coast of the southeastern United States during 1976–1995. *Fish. Bull.* (Wash. D. C.), **96**: 797–807.
- Meekan, M.G., Ackerman, J.L., and Wellington, G.M. 2001. Demography and age structure of coral reef damselfishes in the tropical eastern Pacific Ocean. *Mar. Ecol. Prog. Ser.* **212**: 223–232. doi:10.3354/meps212223.
- Miller, J.A., and Shanks, A.L. 2004. Evidence for limited larval dispersal in black rockfish (*Sebastes melanops*): implications for population structure and marine-reserve design. *Can. J. Fish. Aquat. Sci.* **61**: 1723–1735. doi:10.1139/f04-111.
- Munch, S.B., and Salinas, S. 2009. Latitudinal variation in lifespan within species is explained by the metabolic theory of ecology. *Proc. Natl. Acad. Sci. U.S.A.* **106**(33): 13860–13864. doi:10.1073/pnas.0900300106. PMID:19666552.
- Orensanz, J.M., Parma, A.M., Jerez, G., Barahona, N., Montecinos, M., and El'as, I. 2005. What are the key elements for the sustainability of 'S-fisheries'? Insights from South America. *Bull. Mar. Sci.* **76**: 527–556.
- Ormseth, O.A., and Norcross, B.L. 2009. Causes and consequences of life-history variation in North American stocks of Pacific cod. *ICES J. Mar. Sci.* **66**: 349–357. doi:10.1093/icesjms/fsn156.
- Pondella, D.J., Gintert, B.E., Cobb, J.A., and Allen, L.G. 2005. Biogeography of the nearshore rocky-reef fishes at the southern and Baja California islands. *J. Biogeogr.* **32**: 187–201. doi:10.1111/j.1365-2699.2004.01180.x.
- Reznick, D.A., Bryga, H., and Endler, J.A. 1990. Experimentally induced life-history evolution in a natural population. *Nature*, **346**: 357–359. doi:10.1038/346357a0.
- Ricker, W.E. 1975. Computation and interpretation of biological statistics of fish populations. *Bulletin 191*. Fisheries Research Board of Canada, Ottawa, Ontario.
- Rijnsdorp, A.D. 1993. Fisheries as a large-scale experiment on life-

- history evolution: disentangling phenotypic and genetic effects in changes in maturation and reproduction of North-sea plaice, *Pleuronectes platessa*. *Oecologia (Berl.)*, **96**: 391–401. doi:10.1007/BF00317510.
- Robertson, D.R., Ackerman, J.L., Choat, J.H., Posada, J.M., and Pitt, J. 2005. Ocean surgeonfish *Acanthurus bahianus*. I. The geography of demography. *Mar. Ecol. Prog. Ser.* **295**: 229–244.
- Rosales-Casián, J.A., and Gonzalez-Camacho, J.R. 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.
- Ruttenberg, B.I., Haupt, A.J., Chiriboga, A.I., and Warner, R.R. 2005. Patterns, causes and consequences of regional variation in the ecology and life history of a reef fish. *Oecologia (Berl.)*, **195**: 394–403. doi:10.1007/s00442-005-0150-0.
- Samhuri, J.F. 2009. Food supply influences offspring provisioning but not density-dependent fecundity in a marine fish. *Ecology*, **90**(12): 3478–3488. doi:10.1890/08-1732.1. PMID:20120815.
- Stearns, S.C. 1992. *The evolution of life histories*. Oxford University Press, Oxford, UK.
- Topping, D.T., Lowe, C.G., and Caselle, J.E. 2005. Home range and habitat utilization of adult California sheephead, *Semicossyphus pulcher* (Labridae), in a temperate no-take marine reserve. *Mar. Biol. (Berl.)*, **147**: 301–311. doi:10.1007/s00227-005-1573-1.
- Warner, R.R. 1975. The reproductive biology of the protogynous hermaphrodite *Pimelometopon pulchrum* (Pisces: Labridae). *Fish. Bull. (Wash. D. C.)*, **73**: 262–283.
- Warner, R.R. 1988. Sex change and the size-advantage model. *Trends Ecol. Evol.* **3**: 133–136. doi:10.1016/0169-5347(88)90176-0.
- Williams, A.J., Davies, C.R., Mapstone, B.D., and Russ, G.A. 2003. Scales of spatial variation in demography of a large coral-reef fish — an exception to the typical model? *Fish. Bull. (Wash. D. C.)*, **101**: 673–683.
- Wright, N., Kum, J., King, C., Knaggs, E., Leos, B., and Perez, C. 2000. California sheephead, *Semicossyphus pulcher* 1993–1999 Commercial catch by ports and blocks. *Marine Fishery Profiles, Vol. 1: Nearshore*. California Department of Fish and Game Marine Region, Sacramento, Calif.