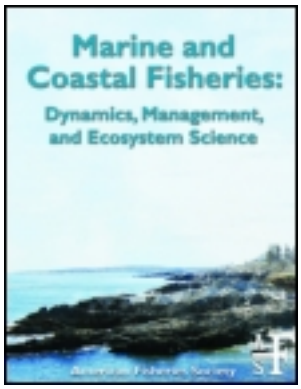

Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science

Publication details, including instructions for authors and subscription information:
http://www.tandfonline.com/loi/umcf20

Reassessment of the Fecundity of California Sheephead

Kerri A. Loke-Smith [a a c], Alyssa J. Floyd [a], Christopher G. Lowe [a], Scott L. Hamilton [b d], Jennifer E. Caselle [b] & Kelly A. Young [a]

[a] Department of Biological Sciences, California State University Long Beach, 1250 Bellflower Boulevard, Long Beach, California, 90840, USA

[b] Marine Science Institute, University of California Santa Barbara, Santa Barbara, California, 93106, USA

[c] California Department of Fish and Game, 4665 Lampson Avenue, Suite C, Los Alamitos, California, 90720, USA

[d] Moss Landing Marine Laboratories, 8272 Moss Landing Road, Moss Landing, California, 95039, USA

Version of record first published: 01 Oct 2012.

To cite this article: Kerri A. Loke-Smith, Alyssa J. Floyd, Christopher G. Lowe, Scott L. Hamilton, Jennifer E. Caselle & Kelly A. Young (2012): Reassessment of the Fecundity of California Sheephead, Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science, 4:1, 599-604

To link to this article: http://dx.doi.org/10.1080/19425120.2012.707167

Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science 4:599–604, 2012

ISSN: 1942-5120 online
DOI: 10.1080/19425120.2012.707167

ARTICLE

Reassesment of the Fecundity of California Sheephead

Kerri A. Loke-Smith,*[1] Alyssa J. Floyd, and Christopher G. Lowe
Department of Biological Sciences, California State University Long Beach, 1250 Bellflower Boulevard, Long Beach, California 90840, USA

Scott L. Hamilton[2] and Jennifer E. Caselle
Marine Science Institute, University of California Santa Barbara, Santa Barbara, California 93106, USA

Kelly A. Young
Department of Biological Sciences, California State University Long Beach, 1250 Bellflower Boulevard, Long Beach, California 90840, USA

Abstract

Fecundity estimates used in a 2004 stock assessment to evaluate the overall health of the population of California sheephead *Semicossyphus pulcher* were based primarily on two studies. The first estimated the total fecundity of only nine individuals captured near Santa Catalina Island, California, and the second estimated batch fecundity of individuals taken from only one artificial reef. In order to develop a current and more comprehensive estimate of fecundity, we collected California sheephead from seven locations off southern California throughout the spawning season (July through September). To estimate both total fecundity and batch fecundity, we categorized and counted oocytes from ovarian subsamples of 28 and 24 (respectively) mature females (stage 3, spawning capable; determined by histological analysis). Total and batch fecundity increased with somatic mass, standard length, and ovary mass. We found total fecundity to increase with somatic mass to a power of 5.5, which is considerably greater than the value (2.95) reported previously. Our observations therefore highlight the importance of large females in the reproductive potential of the California sheephead stock. Regression analysis indicates that ovary mass is the most accurate biological indicator of fecundity for California sheephead and should be used for subsequent stock analyses.

California sheephead *Semicossyphus pulcher* are protogynous sequential hermaphrodites. The dominant female in a group changes sex in response to removal of the dominant male (Warner 1975; Cowen 1990). Although this is not a novel mechanism among wrasses, it is rare among exploited temperate fish species and may make California sheephead particularly susceptible to overfishing. California sheephead are targeted by both recreational and commercial fisheries. Landings have increased since the 1980s and there is concern about sustainability of current levels of exploitation. Indeed, the average maximum sizes of both females and males have been decreasing, with concomitant reductions in size and age at sex change, and reduction in size at maturation in at least one population (Hamilton et al. 2007). A 2004 stock assessment concluded abundance has declined 50% from the unfished state (Alonzo et al. 2004).

Alonzo et al. (2004) created models of the California sheephead population to best manage the fisheries. Those models used data from previously published fecundity estimates (Warner

Subject editor: Richard Brill, Virginia Institute of Marine Science, USA

*Corresponding author: kerriloke@gmail.com
[1]Present address: California Department of Fish and Game, 4665 Lampson Avenue, Suite C, Los Alamitos, California 90720, USA.
[2]Present address: Moss Landing Marine Laboratories, 8272 Moss Landing Road, Moss Landing, California 95039, USA.
Received January 27, 2012; accepted June 19, 2012

TABLE 1. Parameters of previous and current California sheephead fecundity studies, including total fecundity per gram somatic mass (F_{TO}; yolky eggs/g ovary), batch fecundity (F_B; hydrated oocytes/batch), and batch fecundity per gram somatic mass (F_{BS}; hydrated eggs/g somatic mass).

Study	*n*	Number of populations sampled	Size	F_{TO} (SD)	F_B (SD)	F_{BS} (SD)
Warner (1975)	9	1	209–359 mm	5,378 (648)		
DeMartini et al. (1994)	26	1 (artificial reef)	379 g (average)		5,755 (3,557)	15 (8.7)
Jirsa et al. (2007)	11	1 (captive)	369–430 mm		12,000–35,000[a]	11–33[b]
Current study	28	7	196–432 mm	5,685 (1,896)	48,418 (56,021)	38 (28.5)

[a]Derived from the average to maximum number of eggs spawned per day by 11 females/11.
[b]Derived from the average to maximum number of eggs spawned per day for 11 females/total biomass of same 11 females.

1975; Cowen 1990; DeMartini et al. 1994; Jirsa et al. 2007; Sundberg et al. 2009). Female California sheephead are serial batch spawners and spawn almost daily (Adreani et al. 2004). They may, therefore, have multiple stages of oocytes within the ovary at any given time during the breeding season. Moreover, fecundity itself can be assessed in a number of ways. Total fecundity is an estimate of the total number of yolky oocytes and usually includes the total number of eggs that may be released in the next two to three spawning events. Batch fecundity is an estimate of the number of eggs that may be released in the next batch and maybe a more useful estimate of reproductive potential (Hunter et al. 1985). Batch fecundity can be used to estimate annual fecundity (the total number of hydrated oocytes spawned over a reproductive season) if both spawning frequency and length of the spawning season are known.

Warner (1975) reported that total fecundity in California sheephead increases exponentially with standard length (exponent 2.95). Due to the small size (<359 mm SL) and low number ($n = 9$) of individuals, however, the fecundity relationship was truncated, and caution was issued by the author against extrapolating the fecundity curve beyond the size range sampled. The two previous estimates of batch fecundity have included 26 individuals collected at a single artificial reef (DeMartini et al. 1994; Table 1) and 11 captive females (Jirsa et al. 2007). We argue a more complete fecundity estimate using females representative of the entire California sheephead stock is needed. We therefore reevaluated fecundity using a wide size-range of fish collected from multiple locations across southern California. We estimated total and batch fecundity using methods similar to those of previous studies to make our data directly comparable with those used in the 2004 stock assessment (Alonzo et al. 2004).

METHODS

California sheephead were collected off the coast of southern California during the spawning seasons (July–September) of 2005 and 2007. Collection sites included the oil platform Edith and the following Channel Islands: Santa Rosa, Santa Cruz, Anacapa, San Nicolas, Santa Catalina, and San Clemente (Table 2). Specimens collected at Santa Catalina in 2005 were a subset of those used in the Sundberg et al. (2009) and Loke-Smith et al. (2010) studies.

All fish were collected by hook and line or by spear. Those collected by hook and line were euthanized in an ice slurry prior to dissection. The gonads were removed, weighed, fixed in 10% formalin for 7–10 d, subsequently washed in phosphate-buffered saline, and stored in 70% ethanol. Small cross sections of tissue from throughout the gonad were embedded in paraffin wax for histological analysis. In cases where the gonad was too large for a cross section to fit onto a single slide, pie-shaped wedges were taken to maximize gonadal structures examined. Sections (6 μm thick) were cut on a microtome, mounted on slides, and stained using hemotoxylin and eosin. Gonads were staged according to Sundberg et al. (2009) and only females identified as stage 3 (i.e., those with vitellogenic and hydrated oocytes and capable of spawning) were included in our study.

Oocytes were categorized into five developmental stages (Figure 1): two stages of previtellogenic oocytes (chromatin nucleolar oocytes, perinucleolar oocytes), two stages of vitellogenic oocytes (yolk vessicle oocytes and yolk globular oocytes), and hydrated oocytes (the final stage of oocyte development typified by large transparent sacs to be released in the next spawning event). Total fecundity was determined by estimating the total number of vitellogenic or yolked oocytes

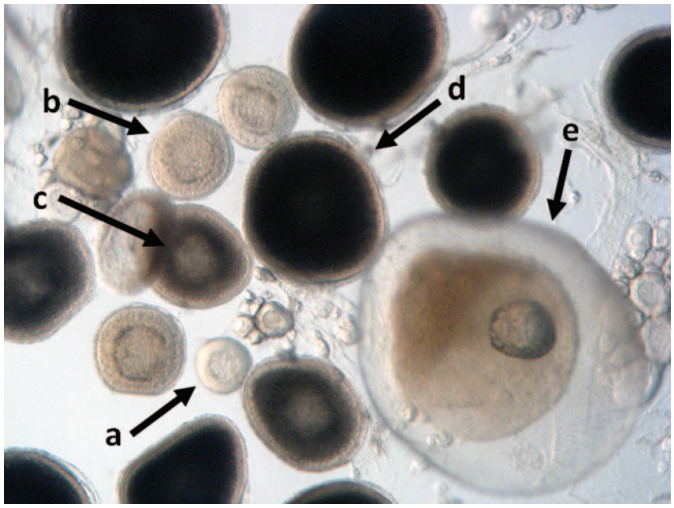

FIGURE 1. Oocytes of each developmental stage: **(a)** chromatin nucleolar oocytes, **(b)** perinucleolar oocytes, **(c)** yolk vesicle (cortical alveolar) oocytes, **(d)** yolk globular oocytes, and **(e)** hydrated.

TABLE 2. Summary of data and estimates of total fecundity (F_T), total fecundity per gram somatic mass (F_{TO}), batch fecundity (F_B), and batch fecundity per gram somatic mass (F_{BS}) for all stage 3 females. The F_B and F_{BS} of females estimated to have fewer than 50 oocytes present in the ovary were omitted and are denoted by a blank cell.

Capture date	Capture Site	Somatic mass (g)	Standard Standard (mm)	Ovary Ovary (g)	F_T (number of yolky oocytes)	F_{TO} (number of yolky oocytes/ gram ovary)	F_B (number of hydrated oocytes)	F_{BS} (number of hydrated oocytes/ gram somatic mass
Sep 9, 2007	San Clemente Island	200	196	5	24,232	5,245	2,518	13
Aug 2, 2007	Santa Catalina Island	316	215	4	29,087	6,730	2,788	9
Aug 2, 2007	Santa Catalina Island	351	216	19	111,400	6,020	12,954	37
Jul 20, 2005	Santa Catalina Island	212	221	3	11,379	4,230		
Sep 11, 2007	San Clemente Island	405	226	5	17,231	3,245	1,460	4
Jul 20, 2005	Santa Catalina Island	288	233	2	9,058	3,653		
Jul 20, 2005	Santa Catalina Island	361	237	9	40,790	4,770		
Aug 07, 2005	Santa Catalina Island	337	238	13	68,535	5,105	9,398	28
Sep 11, 2007	San Clemente Island	427	238	13	83,757	6,595	1,334	3
Jul 21, 2005	Santa Catalina Island	454	243	6	9,576	1,710	924	2
Aug 7, 2005	Santa Catalina Island	394	244	16	97,790	6,175	17,341	44
Jul 01, 2005	Santa Catalina Island	480	256	9	77,712	8,488	3,594	7
Jul 01, 2005	Santa Catalina Island	459	260	11	80,609	7,513	3,165	7
Jul 27v05	Platform Edith	718	260	22	108,256	4,975	1,414	2
Jul 23, 2007	Santa Cruz Island	701	284	79	528,316	6,685	65,595	94
Jul 23, 2007	Santa Cruz Island	809	298	91	686,975	7,580	33,533	41
Jul 23, 2007	Santa Cruz Island	806	303	84	634,177	7,530	61,060	76
Jul 25, 2007	Santa Rosa Island	993	316	47	138,558	2,960	41,427	42
Sep 7, 2007	San Nicholas Island	1,131	324	69	486,539	7,053	40,698	36
Jul 19, 2007	Anacapa Island	1,229	335	71	487,596	6,855	47,301	38
Sep 8, 2007	San Nicholas Island	986	348	54	335,070	6,205	61,560	62
Aug 30, 2005	Platform Edith	1,216	350	60	420,044	7,015	71,255	59
Jul 25, 2007	Santa Rosa Island	1,594	368	106	307,400	2,900	81,620	51
Sep 08, 2007	San Nicholas Island	2,021	414	129	459,662	3,555	109,259	54
Jul 18, 2007	Anacapa Island	2,194	415	156	1,301,979	8,330	118,007	54
Jul 25, 2007	Santa Rosa Island	2,250	423	200	614,000	3,070	217,000	96
Sep 8, 2007	San Nicholas Island	2,403	428	147	1,167,787	7,933		
Jul 19, 2007	Anacapa Island	2,661	432	239	1,686,925	7,045	156,840	59

(yolk vessicle oocytes and yolk globular oocytes at the time of capture; Sundberg et al. 2010) present in the ovary. Batch fecundity was determined by estimating the total number of hydrated oocytes in the ovary. To estimate the total number of oocytes in the whole ovary, subsamples (0.20–0.30 g) were cut from the center of the ovary to the ovarian wall from ovaries removed from 28 spawning-capable females (stage 3; Sundberg et al. 2009). Each subsample was placed in a sieve made from PVC piping with 80-μm mesh, and flowing water was used to gently separate the oocytes from each other and from the protective ovarian membrane. Any remaining oocytes were individually teased from the tissue under a dissecting microscope. All of the yolked oocytes and hydrated oocytes in the subsample were then counted. The total number of oocytes (yolked or hydrated) was then divided by the subsample mass and multiplied by the whole ovary mass to determine the total and batch fecundities, respectively. Individuals with an estimated batch fecundity of less than 50 hydrated oocytes were assumed to have recently spawned and were omitted from batch fecundity curve calculations.

Oocytes were classified by developmental stages: chromatin nucleolar oocytes, perinucleolar oocytes, yolk vesicle (cortical alveolar) oocytes, yolk globular oocytes, and hydrated oocytes. The diameter of 40 oocytes in each stage were measured for 27 individuals to the nearest 0.5 μm at 500 × magnification (10 μm) using a micrometer in an Olympus SZX12 microscope.

Regressions were used to describe the relationships of total and batch fecundities versus standard length, somatic weight, and ovary weight (SigmaPlot 11.0, Systat Software, San Jose, California). Because egg diameters were not normally distributed and had unequal variances, data were analyzed using

Kruskal–Wallis analysis of variance (ANOVA) with Mann–Whitney pairwise comparisons.

RESULTS

Individuals sampled for fecundity ranged from 196 to 432 mm standard length and from 200 to 2,661 g wet weight. The smallest females (≤459 g, 13 of 28 individuals) were caught primarily at Santa Catalina and San Clemente islands and the largest (≥718 g, 15 of 28 individuals) at the oil platform on the San Pedro Shelf or at the more northern Channel Island sites (Table 1). As expected, mean ± SD egg sizes differed significantly across egg stages with average diameters of 69 ± 11 μm for chromatin nucleolar oocytes, 266 ± 23 μm for perinucleolar oocytes, 336 ± 30 μm for yolk vesicle oocytes, 483 ± 42 μm for yolk globular oocytes, and 878 ± 70 μm for hydrated oocytes ($H = 98.90$, $df = 4$, $P < 0.0001$). All egg stages were significantly different from each other in post hoc comparisons.

Total and batch fecundity increased in a power relationship with somatic mass, standard length, and ovary mass (Figure 2a–c). Regression analysis suggests that ovary mass is the most accurate indicator of total and batch fecundity for California sheephead ($r^2 = 0.94$ and $r^2 = 0.86$, respectively; Figure 2c).

DISCUSSION

The relationship between total fecundity and standard length scaled to the power of 5.5. The increases in fecundity with California sheephead length are, therefore, much larger than would be predicted by simple ontogenetic allometry and the square-cube law. Our results suggest that management regulations that protect large females (e.g., increased minimum size limits, slot limits to prevent fishing of large individuals) may increase reproductive output of California sheephead.

California sheephead are batch spawners with indeterminate fecundity that may vary geographically across their range. Therefore, batch fecundity may give a more accurate indicator of reproductive potential than total fecundity. DeMartini et al. (1994) reported batch fecundity of 15 eggs/g body weight. In contrast, we observed 38 eggs/g (Table 1). The average size in both studies was similar, and the different results remain unexplained.

It is likely that the inclusion of two stages of development for the total fecundity measure (yolk vessicle oocytes and yolk globular oocytes), as opposed to batch fecundity which includes only hydrated oocytes, explains the different scaling exponents. Warner (1975) noted a loss in the number of eggs prior to hydration, and the difference in the fecundity measurements may reflect this reduction. While using total fecundity as a measurement of reproductive potential has been debated, the difference between the total and batch fecundity numbers suggests that a reserve level of yolked oocytes may be required for successful reproduction, and calculating both total and batch fecundity is useful. Regardless, the difference between the nature of the total and batch fecundity curves highlights the importance of the method used for fecundity determination and particularly for their incorporation into stock assessments.

Jirsa et al. (2007) determined the average number of eggs spawned daily by a group of 11 captive California sheephead to be 130,000, with a maximum of 375,000 eggs spawned in 1 d. Batch fecundity for this captive group was estimated at 12,000–35,000 hydrated oocytes per individual, lower than our calculated value of 41,418 hydrated oocytes (Table 1). This discrepancy may be explained by captive fish not spawning daily due to greater interfemale competition or dominance than in the wild. This would result in an underestimate of batch fecundity in captive fish.

California sheephead have been increasingly exploited for three decades, and changes in life history and reproductive biology have been reported (Hamilton et al. 2007; Loke-Smith et al. 2010; Caselle et al. 2011). Similar effects (reduced size and age at sexual maturity and reduced fecundity) have been reported in other species subjected to intense fishing pressure (reviewed by Rochet 1998). At the population level, reducing size at sexual maturity can equate to a reduction in fecundity such that the reproductive output of the population is diminished. Indeed, early maturation results in lower maximum size in Atlantic herring (Jennings and Beverton 1991), and such a cycle may be reducing the overall fecundity in California sheephead near Santa Catalina and San Clemente islands where females and males now mature at smaller sizes than elsewhere (Hamilton et al. 2007; Caselle et al. 2011).

The reproductive biology of California sheephead is complicated by a hermaphroditic mating system and skewed sex ratios in most populations. Divergence across populations, including geographical variation and differences in fishing pressure, are likely to influence fecundity. Indeed, due to natural variability in fecundity, a much larger sample size would be necessary to identify differences across the California sheephead range. However, our use of individuals from several populations provides a more complete picture than if all the data were collected from a single population. By determining the fecundity of California sheephead sampled from multiple sites, we were able to develop the relationships of fecundity to somatic mass, standard length, and ovary mass, which incorporated a greater sample size, a broader size range, and a greater spatial sampling area than previous studies. We argue, therefore, that our data provide a better estimate of fecundity for California sheephead in southern California. We also measured egg diameter, and the observed low variability indicates that this parameter could be used to assign correct oocyte staging when determining fecundity.

Because California sheephead are exhibiting biological adaptations in response to fishing pressure that may negatively affect the sustainability of the species, it is also vital that the reproductive potential continue to be monitored and that the most current models of fecundity are used to optimize management strategies.

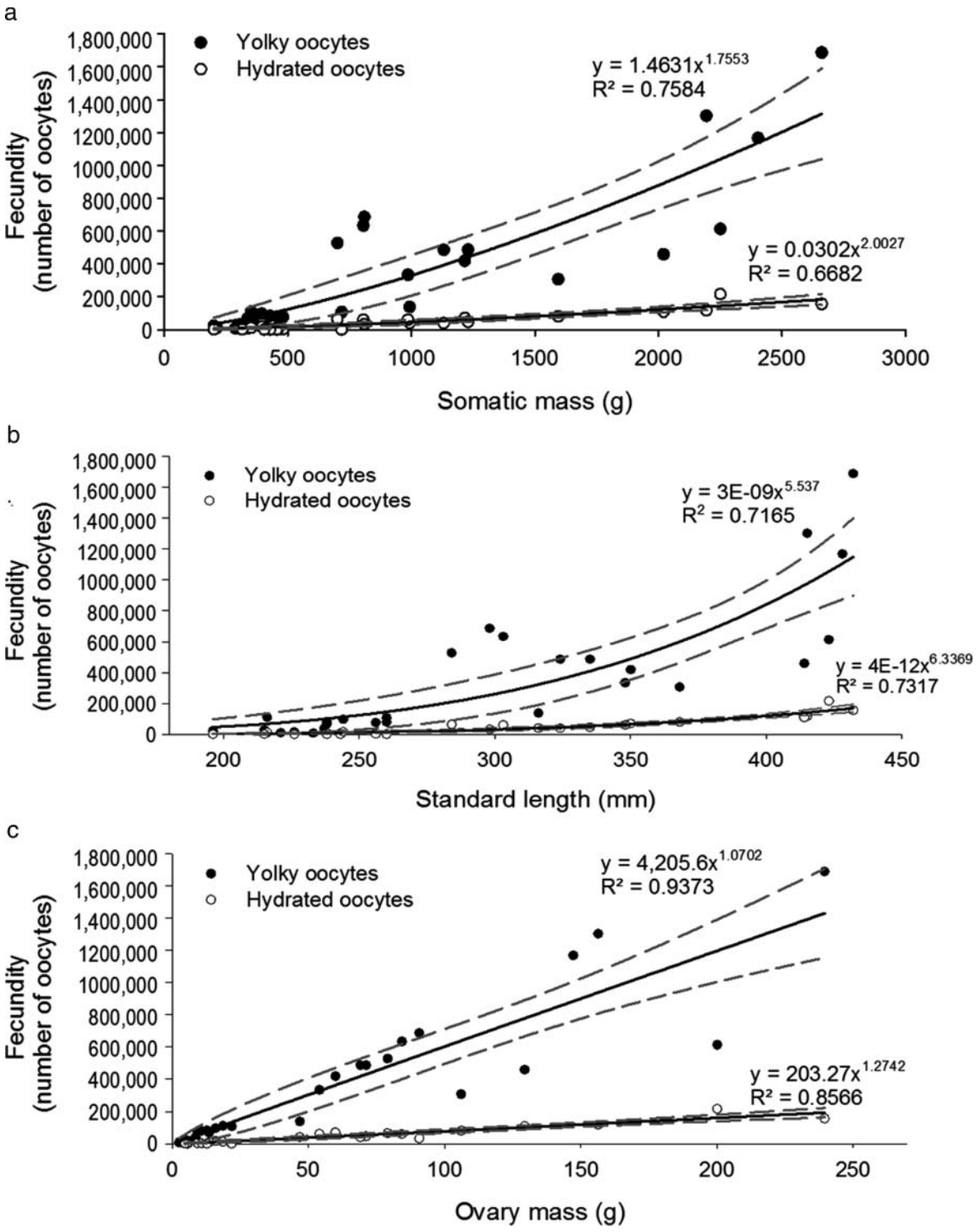

FIGURE 2. Total and batch fecundity in relation to **(a)** somatic mass (g), **(b)** standard length (mm), and **(c)** ovary mass (g). Solid black lines indicate the best fit relationship and broken grey lines indicate 95% confidence intervals.

ACKNOWLEDGMENTS

The research presented here was funded by the California Department of Fish and Game (Contract Number S0470012 to C. G. Lowe and K. A. Young) and California SeaGrant College Program (project no. R/OPCFISH05) through the National Oceanic and Atmospheric Administration's National Sea Grant College Program, U.S. Department of Commerce. Additional financial support was provided by the SCTC Marine Biology

Foundation and the Los Angeles Rod and Reel Club Marine Biology Foundation. Support was also provided by the Channel Islands National Marine Sanctuary and the Partnership for Interdisciplinary Studies of Coastal Oceans. We would like to thank G. McMichael, J. Barr, K. Davis, P. Carlson, A. Parsons-Field, A. Ray, L. Bellquist, K. Anthony, C. Mireles, B. Rogers, H. Zemel, C. Mull, S. Trbovich, C. Martin, T. Farrugia, M. Espinoza, M. Donovan, H. Gliniak, T. Mason, E. Jarvis, and C. Aime for help with field collections and fish dissections. We would also like to thank the editor, Dr. R.W. Brill and two anonymous reviewers for their valuable comments and suggestions.

REFERENCES

Adreani, M. S., B. E. Erisman, and R. R. Warner. 2004. Courtship and spawning behavior in the California sheephead, *Semicossyphus pulcher* (Pisces: Labridae). Environmental Biology of Fishes 71:13–19.

Alonzo, S. H., M. Key, T. Ish, and A. D. MacCall. 2004. Status of the California sheephead (*Semicossyphus pulcher*) stock (2004). California Department of Fish and Game, Stock Assessments, Sacramento. Available: www.dfg.ca.gov/marine/sheephead2004/index.asp. (January 2012).

Caselle, J. E., S. L. Hamilton, D. M. Schroeder, M. S. Love, J. D. Standish, J. A. Rosales-Casián, and O. Sosa-Nishizaki. 2011. Geographic variation in density, demography, and life history traits of a harvested, sex-changing, temperate reef fish. Canadian Journal of Fisheries and Aquatic Sciences 68:288–303.

Cowen, R. K. 1990. Sex change and life history patterns of the labrid, *Semicossyphus pulcher,* across an environmental gradient. Copeia 1990:787–795.

DeMartini, E. E., A. M. Barnett, T. D. Johnson, and R. F. Ambrose. 1994. Growth and production estimates for biomass-dominant fishes on a southern California artificial reef. Bulletin of Marine Science 55:484–500.

Hamilton, S. L., J. E. Caselle, J. D. Standish, D. M. Schroeder, M. S. Love, J. A. Rosales-Casián, and O. Sosa-Nishizaki. 2007. Size-selective harvesting alters life histories of a temperate sex-changing fish. Ecological Applications 17:2268–2280.

Hunter, J. R., N. C. H. Lo, and R. J. H. Leong. 1985. Batch fecundity in multiple spawning fish. NOAA Technical Report NMFS 36:66–77.

Jennings, S., and R. J. H. Beverton. 1991. Intraspecific variation in the life history tactics of Atlantic herring (*Clupea harengus* L.) stocks. ICES Journal of Marine Science 48:117–125.

Jirsa, D., M. Drawbridge, and K. Stuart. 2007. Spawning of a captive population of California sheephead, *Semicossyphus pulcher*. Journal of the World Aquaculture Society 38:122–128.

Loke-Smith, K. A., M. A. Sundberg, K. A. Young, and C. G. Lowe. 2010. Use of morphology and endocrinology to predict sex in California sheephead: evidence of altered timing of sex change at Santa Catalina Island, California. Transactions of the American Fisheries Society 139:1742–1750.

Rochet, M. J. 1998. Short-term effects of fishing on life history traits of fishes. ICES Journal of Marine Science 55:371–391.

Sundberg, M. A., K. A. Loke, C. G. Lowe, and K. A. Young. 2009. Gonadal restructuring during sex transition in California sheephead (*Semicossyphus pulcher*): a reclassification three decades after initial studies. Bulletin, Southern California Academy of Sciences 108:16–28.

Warner, R. R. 1975. The reproductive biology of the protogynous hermaphrodite *Pimelometopon pulchrum* (Pisces: Labridae). U.S. National Marine Fisheries Service Fishery Bulletin 73:262–282.