Abstract — Fecundity was estimated for shortspine thornyhead (*Sebastolobus alascanus*) and longspine thornyhead (*S. altivelis*) from the northeastern Pacific Ocean. Fecundity was not significantly different between shortspine thornyhead off Alaska and the West Coast of the United States and is described by $0.0544 \times FL^{3.978}$, where FL=fish fork length (cm). Fecundity was estimated for longspine thornyhead off the West Coast of the United States and is described by $0.8890 \times FL^{3.249}$. Contrary to expectations for batch spawners, fecundity estimates for each species were not lower for fish collected during the spawning season compared to those collected prior to the spawning season. Stereological and gravimetric fecundity estimation techniques for shortspine thornyhead provided similar results. The stereological method enabled the estimation of fecundity for samples collected earlier in ovarian development; however it could not be used for fecundity estimation in larger fish.

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Fecundity of shortspine thornyhead (*Sebastolobus alascanus*) and longspine thornyhead (*S. altivelis*) (Scorpaenidae) from the northeastern Pacific Ocean, determined by stereological and gravimetric techniques*

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Shortspine thornyhead (*Sebastolobus alascanus*) is distributed from the Bering Sea to Baja California (Orr et al., 2000). Longspine thornyhead (*S. altivelis*) is distributed from the Gulf of Alaska to Baja California (Orr et al., 2000), and a few specimens have recently been collected in the eastern Bering Sea (Hoff and Britt, 2003). Both species are commercially important (Piner and Methot, 2001; Gaichas and Ianelli, 2003) and inhabit deep waters over the continental shelf and slope. Both shortspine and longspine thornyhead are determinate spawners (Wakefield, 1990; Pearson and Gunderson, 2003), and spawn pelagic, gelatinous egg masses (Pearcy, 1962; Best, 1964; Wakefield, 1990; Wakefield and Smith, 1990). Shortspine thornyhead spawn between April and July in Alaska, and between December and May along the West Coast of the United States, whereas longspine spawn between January and April along the West Coast (Pearson and Gunderson, 2003).

Annual fecundity is used as a measure of reproductive output in fishery population models and life history studies. Accurate annual fecundity estimates require identifying oocytes to be spawned in the current spawning season. For iteroparous spawners, developing oocytes are often distinguished from reserve oocytes by diameter or yolk presence (Macer, 1974). Collection date for samples is important. If samples are collected too early in oocyte development, some developing oocytes will be indistinguishable from reserve oocytes, and fecundity will be underestimated.

In shortspine thornyhead, oocyte stages 4–8 are maturing to be spawned in the current spawning season, whereas oocyte stages 1–3 are reserve oocytes to be spawned in future spawning seasons (Pearson and Gunderson, 2003). Early vitellogenic oocytes (stage 4) overlap in size with late perinucleus (stage 3) reserve oocytes (Pearson and Gunderson, 2003). Late vitellogenic oocytes (stage 5) are easily distinguished from reserve oocytes. In whole oocytes, neither oocyte size nor appearance can be relied on to distinguish stage-3 and early stage-4 oocytes; however stage-3 and stage-4 oocytes can be visually distinguished from histological samples (Pearson and Gunderson, 2003). Emerson et al. (1990) developed a stereological method to estimate fecundity

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from histological sections. Unlike gravimetric methods (e.g., Hunter et al., 1992) where whole oocytes are used to estimate fecundity, stereological methods do not rely on oocyte diameter or other proxies for vitellogenesis. A collection of shortspine thornyhead ovaries from Alaska contained few specimens considered suitable for a gravimetric fecundity method because too few of the specimens contained all developing oocytes in stage 5 or beyond. However, enough samples were suitable for the stereological method.

This study provides a fecundity estimate based on stereological and gravimetric techniques for shortspine thornyhead off Alaska. Benefits and limitations of the stereological method in this case are discussed. A gravimetric technique is also used to estimate fecundity for longspine thornyhead and shortspine thornyhead from samples off the West Coast of the United States. In addition, we examine the hypothesis that thornyheads are batch spawners, and that fecundity consequently declines over the course of the spawning season (Wakefield, 1990).

Materials and methods

Ovaries were collected from a large geographic area in Alaska, including the Gulf of Alaska, the Aleutian Islands, and the Bering Sea. National Marine Fisheries Service (NMFS) observers aboard commercial fishing vessels collected ovaries from April through June 2000. Length and somatic weight (ovaries and stomach contents removed) (±5 g) were recorded at sea. Ovaries were excised and placed in 10% formalin solution buffered with sodium bicarbonate.

Ovaries from shortspine thornyhead and longspine thornyhead were also collected during the 1999 NMFS West Coast trawl survey. Samples were collected between Northern California and Washington (34°57′N lat. 121°33′W long. to 48°04′ lat. 125°58′W long.). Length and somatic weight (±2 g) were recorded at sea.

Additional West Coast longspine and shortspine thornyhead ovaries were collected from commercial fishing vessels by the Oregon Department of Fish and Wildlife in Astoria. Ovaries were collected off Oregon and Washington from February through May 2000, during December 2000, and during January 2001. After shipment to the NMFS Alaska Fisheries Science Center in Seattle, length, somatic weight (±2 g), and ovary weight (±0.001 g) were recorded. Ovaries were excised and placed in 10% formalin buffered with sodium bicarbonate.

A cross section was removed from one ovarian lobe (middle or middle posterior region) for histological processing. When a whole cross section was too large to fit on a microscope slide, a wedge was cut from the cross section that included both the ovarian wall and the center of the ovary. Samples were processed through a dehydration series, embedded in paraffin, and sectioned at 4 µm. Slides were stained with hematoxylin and eosin.

Gravimetric fecundity estimation

Histological ovary sections were examined at 100× magnification to select samples for the gravimetric method. Oocytes were identified to one of eight developmental stages as described by Pearson and Gunderson (2003). To differentiate between oocytes to be spawned in the current year and reserve oocytes for future years, only ovaries with all maturing oocytes in stage-5 (late vitellogenesis) and beyond were used. By definition, yolk fills more than 50% of the cytoplasm within stage-5 oocytes, and the dark yolk made it easy to distinguish these oocytes. Stage-4 oocytes would also be spawned in the current year but overlapped significantly in size with nonmature stage-3 oocytes, and early stage-4 oocytes did not always have enough yolk (0–50%) to differentiate them from stage-3 oocytes with the gravimetric method. Specimens containing any stage-4 oocytes were omitted as a result. Ovaries with stage-8 oocytes were also omitted because the increased amount of gelatinous material which surrounds the oocytes in *Sebastolobus* could not be contained within the ovaries during subsampling.

Ovaries were weighed (±0.001 g) after they had been stored in formalin. Subsamples were cut from the ovaries and weighed (±0.001 g). For smaller ovaries, an entire cross section was taken. For larger ovaries, a pie-piece–shaped wedge was cut from the cross section to ensure a representative sample of outer ovarian wall. When cut correctly, a wedge starting at the center of the cross section would have the same weight ratio of ovarian wall to wedge subsample as the original cross section. Subsamples usually contained approximately 1000 oocytes (mean=1133), but this number varied according to stage of development and the amount of gelatinous material in the ovary (range: 108–3711).

Gelatinous material could not be subsampled by cutting at room temperature; therefore ovaries were briefly frozen before subsampling. This procedure enabled the gelatinous material to be cut, and also made it easier to obtain a representative sample of the ovarian wall. Initially, parts of three ovaries were frozen, and no effects of the freezing were detected with a light microscope. Only samples for gravimetric fecundity estimates were briefly frozen.

No difference in oocyte density was found among the different regions of the ovaries (see "Results" section); however, gravimetric subsamples were still taken randomly along the length of the ovaries to minimize potential bias from any location.

The oocytes in the subsamples were counted under a stereomicroscope, and fecundity was estimated by

$$Fec = \frac{W}{w} N,$$

where Fec = estimated fecundity;
W = total ovary weight;
w = subsample weight; and
n = number of oocytes in the subsample.

Stereological fecundity estimation

The majority of oocytes within an ovary were found to be at the same developmental stage; however development was not completely synchronous. Some ovaries containing stage-5 and -6 oocytes (late vitellogenesis to migratory nucleus) also contained a few stage-4 oocytes, which although unsuitable for fecundity estimation with the gravimetric method, could be used with the stereological method described by Emerson et al. (1990). Fecundity was estimated from ten of these samples by using the stereological method to complete the shortspine thornyhead collection from Alaska.

Fecundity was estimated per unit of volume and then multiplied by the volume of both ovaries. The formula used to estimate fecundity per unit of volume is

$$N_v = \frac{k}{\beta} \frac{N_a^{3/2}}{V_i^{1/2}},$$

where N_v = the number of oocytes per unit of volume;
k = an oocyte size correction coefficient;
β = an oocyte shape correction coefficient;
N_a = the average number of vitellogenic oocytes per unit of area; and
V_i = the average fractional volume of vitellogenic oocytes per unit of area.

The method for estimating the parameter k is given in Emerson et al. (1990) and the parameter k was estimated for six shortspine thornyhead samples. The resulting k values had a small range (1.0088–1.022), and a small standard deviation (0.0066), and a mean k value of 1.017 was used for all samples as a result. β was calculated by using the method given in Weibel and Gomez (1962). The β parameter was calculated from one shortspine thornyhead sample (53 oocytes) to be 1.565.

Exact volume of sample ovaries was impossible to determine because portions of the ovaries had already been removed for histological study (Pearson and Gunderson, 2003). Volume was estimated by dividing whole ovary weight by an average density of 1.052 g/mL. This was the average density from six samples (SD=0.0297) estimated by water displacement in a graduated cylinder.

Values for N_a and V_i were estimated by using a simplified Weibel grid for particulate structures (Weibel et al., 1966) instead of a Weibel multipurpose grid. A square containing 13 rows of 13 points was created and printed out on a clear acetate sheet. This overlay was taped to the front of a monitor. A video camera mounted to a stereomicroscope sent the image of the histology section to the computer monitor. The number of vitellogenic oocytes per grid and the number of points falling on vitellogenic oocytes were recorded and used to estimate N_a and V_i, respectively. The Weibel grid was used at 25× magnification, and 50× magnification was used to help distinguish borderline vitellogenic oocytes.

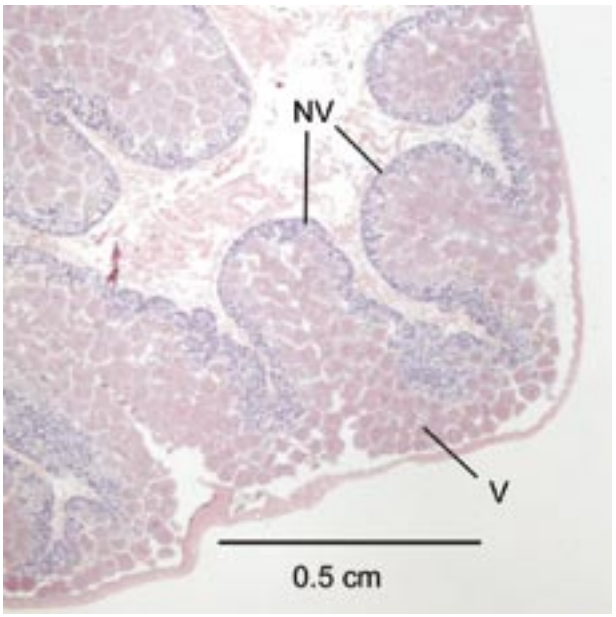

Figure 1

Partial cross section of shortspine thornyhead rockfish (*Sebastolobus alascanus*) ovary showing bands of vitellogenic (V) and nonvitellogenic (NV) oocytes.

A sampling grid was placed under the ovary histological section. The corner of the Weibel grid was aligned with corners of the sampling grid in order to systematically sample the ovary cross section. Two histological sections were sampled per ovary.

The number of Weibel grid counts per ovary depended on the size of the ovary cross section. An average of 55.9 (range: 29–103) Weibel grid counts were taken per ovary. This number was greater than the average number of Weibel grid counts used by Emerson et al. (1990), but the extra counts were made because shortspine thornyhead vitellogenic oocytes develop on peduncles (Erickson and Pikitch, 1993; Pearson and Gunderson 2003) and are distributed in a band around the central part of the ovary (Fig. 1). Because the vitellogenic oocytes are not uniformly distributed, the Weibel grid was applied systematically at more points across the entire ovary, and the counts were averaged. Because the whole cross section could not be systematically sampled and averaged, cross sections of larger fish were not used for stereological estimates.

Statistical methods

Length-fecundity relationships were estimated by using the following equation:

$$Fec = al^b,$$

Table 1
Fecundity estimates (number of oocytes) by ovary location and method.

	Stereological method				Gravimetric method			
	Sample location in ovary				Sample location in ovary			
Species	Mid	Posterior	Anterior	CV	Mid	Posterior	Anterior	CV
Shortspine	122,180	87,504	111,758	0.166	131,934	110,456	111,425	0.103
Shortspine	313,131	257,378	304,348	0.103	269,453	230,992	257,427	0.078
Shortspine	184,802	199,572	203,014	0.049				
Shortspine	474,432		458,877	0.024				
Longspine	38,061	26,179	28,424	0.204	38,968	33,207	33,653	0.091
Longspine	36,152	23,127	19,411	0.335				
			Mean CV	0.147			Mean CV	0.091

where Fec = estimated fecundity;
l = fork length; and
parameters a and b were estimated by nonlinear regression with SPSS software (version 11.0, SPSS Inc., Chicago, IL).

Weight-fecundity relationships were estimated by using the following equation

$$Fec = m(Wt_{somatic}) + b1,$$

where Fec = estimated fecundity;
$Wt_{somatic}$ = somatic weight; and
m and $b1$ were estimated by using linear regression in EXCEL (Microsoft, Redmond, WA).

Reduction in variance F tests (Quinn and Deriso, 1999) were used to compare fecundity relationships between areas, studies, and before and during spawning season.

Results

Ovary location differences

We tested for difference in oocyte density between middle, posterior, and anterior sections of six ovary pairs with the stereological method (ovaries from the migratory nucleus to late hydration phase) and did not find a significant difference in ovary location (two-way ANOVA, P=0.148) (Table 1).

Stereological method versus gravimetric method

The gravimetric method and the stereological method provided similar results. For shortspine thornyhead, the average ratio of gravimetric to stereological estimates for ten pairs of data was 0.993 (Table 2), and a plot of the gravimetric versus stereological estimates showed that they follow a 1:1 trend line (Fig. 2). The gravimetric method gave a somewhat lower coefficient of variation than the stereological method, based on multiple samples of the same ovaries (Table 1). An F test (Quinn and Deriso, 1999) did not show a significant difference (P=0.84) between the gravimetric (n=16) and stereological (n=10) methods in the length-fecundity relationships obtained for Alaskan shortspine thornyhead, and the data were therefore combined (Fig. 3).

Shortspine thornyhead

Shortspine thornyheads from Alaska (n=26) and the West Coast (n=30) had similar fecundity at length (Fig. 3). An F test did not indicate fecundity at length for the two areas was significantly different (P=0.53); therefore the data were combined to obtain the relationships (Figs. 3 and 4):

$$Fec = 0.0544\left(Fork\,Length(cm)\right)^{3.978} \quad (r^2=0.792,\ n=56)$$

$$Fec = 0.223\left(Wt_{somatic}(g)\right) - 63.079 \quad (r^2=0.781,\ n=53).$$

A majority of the shortspine thornyhead fecundity at length data points obtained in this study fell below the regression line reported by Miller (1985) (Fig. 3). The raw data from Miller (1985) were not published; therefore no statistical test was possible.

The data were also separated into months preceding the start of spawning and those after the start of spawning (Pearson and Gunderson, 2003) to look for evidence of batch spawning. Shortspine collected between October and November were grouped as specimens before the start of spawning. Shortspine collected from April through June in Alaska and from March through May off the West Coast were grouped as specimens after the start of spawning. Fish collected after spawning had begun (n=41) did not show a significant

Table 2

Paired fecundity estimates (number of oocytes) by method and by section of the ovary (middle, posterior, anterior) where oocyte samples were taken.

Specimen	Position in the ovary	Gravimetric	Stereological	Ratio of gravimetric to stereological
Shortspine 1	Middle	150,448	184,853	0.814
Shortspine 2	Middle	195,356	187,037	1.044
Shortspine 3	Middle	427,717	307,771	1.390
Shortspine 4	Middle	414,594	561,258	0.739
Shortspine 5	Middle	131,934	122,180	1.080
	Posterior	110,456	87,504	1.262
	Anterior	111,425	111,758	0.997
Shortspine 6	Middle	269,453	313,131	0.861
	Posterior	230,992	257,378	0.897
	Anterior	257,427	304,348	0.846
			Mean ratio	0.993

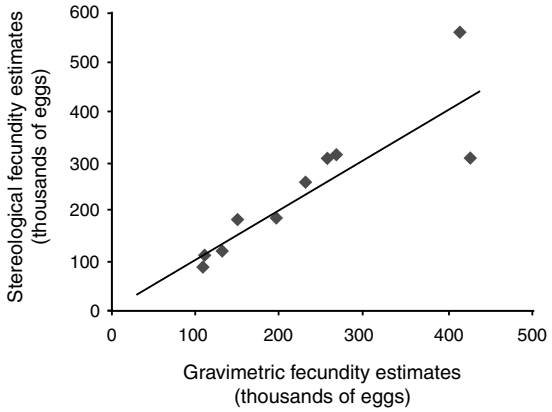

Figure 2

Plot of gravimetric versus stereological fecundity estimates for ten shortspine thornyhead rockfish (*Sebastolobus alascanus*) data pairs. Line = 1:1 ratio.

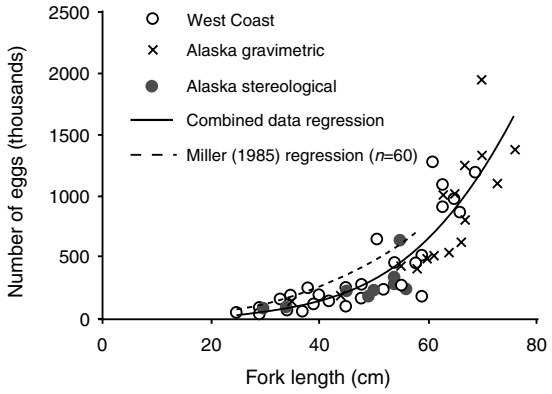

Figure 3

Shortspine thornyhead (*Sebastolobus alascanus*) fecundity-at-length estimates by location and method, and regression of combined data (our study) and by regression of data from Miller's study (1985).

decrease in fecundity at length when compared to fish collected before spawning had begun (n=11) (F test, P=0.71) (Fig. 5).

Longspine thornyhead

Longspine thornyhead fecundity data conformed more closely to a linear regression on somatic weight (Fig. 6):

$$Fec = 183.81\left(Wt_{somatic}(g)\right) - 4617 \qquad (r^2=0.536,\ n=29)$$

than to a nonlinear regression on length (Fig. 7):

$$Fec = 0.8890\left(Fork\,Length(cm)\right)^{3.249} \qquad (r^2=0.442,\ n=29).$$

A majority of the predicted fecundity values at somatic weight were higher than those derived from Wakefield's (1990) regression line on somatic weight (Fig. 6), but Wakefield's (1990) raw data were not published.

Wakefield (1990) estimated spawning to begin in February and created separate fecundity-at-weight relationships for fish collected in October–November and in February–March). He noted a decline in fecundity as the spawning season progressed but did not test this fecundity difference for statistical significance. Similar groupings (October–December, n=17; and February–March, n=11) in our study did show a statistically significant difference in fecundity as the spawning season progressed (F test, P=0.004) (Fig. 7); however, the

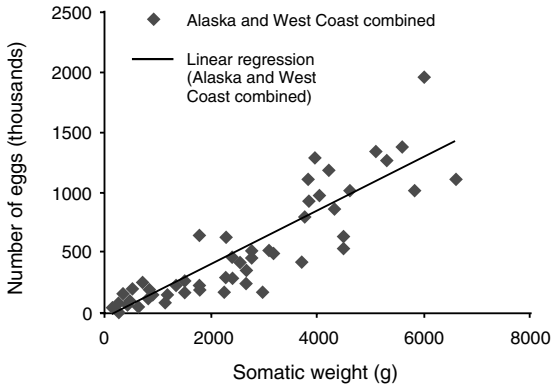

Figure 4

Fecundity at somatic weight for combined Alaska and West Coast shortspine thornyhead rockfish (*Sebastolobus alascanus*).

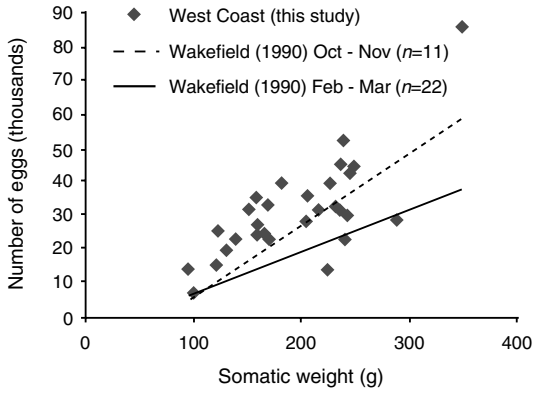

Figure 6

West Coast longspine thornyhead rockfish (*Sebastolobus altivelis*) fecundity data at somatic weight (our study), compared to fecundity data of Wakefield (1990).

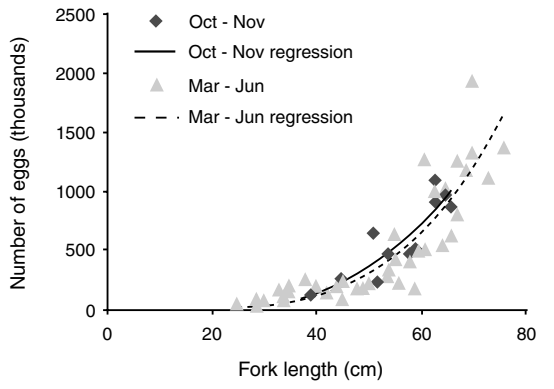

Figure 5

Shortspine thornyhead rockfish (*Sebastolobus alascanus*) fecundity at length separated by October–November and March–June collection dates.

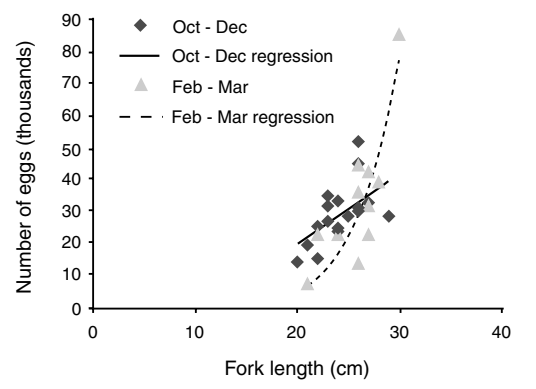

Figure 7

Longspine thornyhead rockfish (*Sebastolobus altivelis*) fecundity at length separated by October–December and February–March collection dates.

regression lines intersected, and the February–March group was not lower than the October–December group. The February–March group did have lower fecundity than the October–December group for lengths smaller than 27 cm; however the sample size was very small. No significant difference existed between the two groups when the single, large fecundity observation late in the spawning season was ignored (P=0.34).

Discussion

Emerson et al. (1990) cited the ability to distinguish borderline vitellogenic oocytes from nonvitellogenic oocytes as an advantage of the stereological method, and this was a clear benefit in our study. The stereological method allowed us to differentiate between vitellogenic and nonvitellogenic oocytes at an earlier stage of ovary development than was possible with the gravimetric method. However, the use of ovaries in earlier stages of development increases the potential magnitude of fecundity overestimates due to atresia. Atresia, or the resorption of oocytes, is a potential source of error for fecundity estimates (Hunter et al., 1992). Although atretic oocytes can be identified with the stereological method, oocytes that are destined for atresia will be counted, causing fecundity to be overestimated. The amount of atresia will determine the magnitude of this overestimate. Samples

collected at later ovarian development stages would avoid this potential error (Tuene et al., 2002).

Because of a nonrandom distribution of vitellogenic and nonvitellogenic oocytes in the ovary, it was necessary to average Weibel grid counts over an entire ovary cross section. Larger ovaries that did not fit on a single slide could not be used, so that fecundity of larger fish had to be determined with the gravimetric method. This was a major limitation because few fish greater than 60 cm had ovaries small enough to be suitable for the stereological method. This limitation, however, might not apply to fish species with vitellogenic oocytes randomly distributed throughout the ovary.

The number of Weibel grid counts required was larger in our study than in Emerson et al. (1990), and the extra counts increased the amount of time involved with computation of fecundity estimates. In addition to the time required to prepare histological sections, the time to obtain stereological estimates took approximately twice as long as those obtained with the gravimetric method. Our estimates of shortspine thornyhead fecundity at length (Fig. 3) appeared lower than the regression published by Miller (1985), but our longspine thornyhead fecundity estimates were higher than those published by Wakefield (1990) (Fig. 6). Several potential explanations exist for the differences. Temporal or geographic differences in fecundity could exist. Samples from different decades were used in the two studies, and Wakefield (1990) used longspine samples taken from off Point Sur, California, whereas we used samples collected off Oregon and Washington. However, the differences may also be explained by methodological differences between authors, including different criteria to include oocytes in fecundity estimates, and differences in the ovarian development of samples. Relatively small sample sizes from our study and from Wakefield (1990) may add uncertainty to these fecundity estimates. The length range of samples could also affect comparisons for shortspine thornyhead fecundity. The fecundity estimates from Miller (1985) did not include any fish greater than 60 cm, whereas we used fish approaching 80 cm.

Wakefield (1990) grouped fecundity data by date, that is to say before the start of spawning and after the start of spawning. His data indicated a decline in fecundity after spawning begins, which he attributed to batch spawning. Similar temporal groupings in our study did not necessarily show a decrease in fecundity that was indicative of batch spawning in longspine or shortspine thornyhead. An important caveat regarding these comparisons is that the combination of small sample sizes and high variability in fecundity at length would cause only large differences in fecundity to be detected. However, the sample sizes used for comparison before and during spawning season (shortspine thornyhead n=11, 41) (longspine thornyhead n=17,11) were close to the sample sizes Wakefield (1990) used as evidence for batch spawning (n=11,22). Larger sample sizes for both species would help answer the question of whether these are batch-spawning species. Pearson and Gunderson (2003) did not find any hydrated oocytes or postovulatory follicles co-occurring with vitellogenic oocytes in histological sections of either species used in our study. They concluded that batch spawning does not occur from off Northern California to Alaska for shortspine thornyhead, and from off Northern California to Washington for longspine thornyhead, and the results of the present study support this conclusion.

Ovaries are often opportunistically collected during commercial fishing seasons or scheduled fisheries surveys and may not provide oocyte samples from the optimum time of year for estimating fecundity with gravimetric techniques. Nevertheless, the stereological technique enabled us to make fecundity estimates for a greater number of the available samples. The technique could be used in similar instances where the logistics of sampling require collections to be made earlier than the optimal date for gravimetric estimates.

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