National Marine
Fisheries Service
NOAA

Fishery Bulletin
established in 1881

Spencer F. Baird
First U.S. Commissioner
of Fisheries and founder
of *Fishery Bulletin*

Reproductive biology and age at maturity of shortspine thornyhead (*Sebastolobus alascanus*) in Alaska

Todd T. TenBrink (contact author)

Email address for contact author: todd.tenbrink@noaa.gov

Resource Ecology and Fisheries Management Division
Alaska Fisheries Science Center
National Marine Fisheries Service, NOAA
7600 Sand Point Way NE
Seattle, Washington 98115-6349

Abstract—Ovaries from female shortspine thornyhead (*Sebastolobus alascanus*) collected in the Aleutian Islands and Gulf of Alaska from 2014 through 2016 were used to investigate aspects of the reproductive biology of this species. Although this species is abundant in both geographical areas, published data on its reproduction remain limited. Ovaries were examined histologically to assess their development and to determine length and age at maturity. The seasonality of ovarian development was similar between geographical areas, with females spawning in May and June. Mature ovaries in early developing phases were observed in October. For females, length at 50% maturity was 23.0 cm in fork length (FL) (95% confidence interval [CI]: 22.3–23.8 cm FL), and age at 50% maturity was 12.8 years (95% CI: 12.00–13.51 years), with all of them maturing at ages between 11 and 14 years. Precision in age estimates between readers was acceptable (coefficient of variation=9.45; average percent error=6.69; percent agreement=25.9%), compared with that in estimates for difficult-to-age rockfish species (*Sebastes* spp.). This study resulted in additional knowledge of the reproductive biology of the shortspine thornyhead and greater understanding of its life history for fisheries management. Larger sample sizes and greater spatiotemporal coverage for sampling of specimens for aging are necessary to further identify maturity of this species and differences between geographical areas.

Manuscript submitted 2 May 2025.
Manuscript accepted 11 September 2025.
Fish. Bull. 123:235–250 (2025).
Online publication date: 26 November 2025.
doi: 10.7755/FB.123.4.3

The shortspine thornyhead (*Sebastolobus alascanus*) is a long-lived scorpaenid that inhabits deep, outer-continental-shelf and slope waters of the North Pacific Ocean and is 1 of 3 species that belong to the genus *Sebastolobus*. The shortspine thornyhead ranges from the Sea of Okhotsk and Japan to the Bering Sea and Aleutian Islands and to Isla Cedros and central Baja California in Mexico (Love et al., 2002). Along the coasts of the eastern North Pacific Ocean, higher densities of shortspine thornyhead are found at depths greater than 200 m in Alaska (von Szalay and Raring, 2020), greater than 400 m off the coast of California (Zahner et al., 2023), and between 150 and 450 m off British Columbia in Canada (Starr and Haigh, 2017).

In Alaska, the shortspine thornyhead is a commercially important species. There is no directed fishery for shortspine thornyhead, and catches occur mainly in the bottom-trawl fisheries for species of flatfish and rockfish (*Sebastes* spp.) and in the hook-and-line fishery for sablefish (*Anoplopoma fimbria*) (Sullivan et al., 2022a; Siwicke et al., 2024). Separate stocks of shortspine thornyhead are regionally managed in multispecies complexes in the Bering Sea and Aleutian Islands (*Other Rockfish complex*; Sullivan et al., 2022a) and in the Gulf of Alaska (*Thornyhead complex*; Echave et al., 2022; Siwicke et al., 2024). The shortspine thornyhead is the most abundant species within these complexes. In the Bering Sea and Aleutian Islands, the Other Rockfish complex is assessed in 2 groups, with shortspine thornyhead assessed separately from the other species and accounting for 95% of the estimated biomass of the entire complex (Sullivan et al., 2022a). Biomass for the Thornyhead complex in the Gulf of Alaska is currently modeled by using only shortspine thornyhead (Siwicke et al., 2024). Although the longspine thornyhead (*S. altivelis*) is also part of the complex in the Gulf of Alaska, it is rare and distributed in waters deeper than those in which the shortspine thornyhead occurs (>500 m; Siwicke et al., 2024).

Effective management of shortspine thornyhead has been hindered by a lack of biological information. Knowledge of life history attributes, such as age, growth, and reproduction (e.g., maturity) includes data that can be used to estimate population structure (Begg et al., 1999). Fishing reference points, such as overfishing levels, are calculated from reliable estimates of biomass and natural mortality in management regions in Alaska for species that have limited data (Sullivan et al., 2022a; Siwicke et al., 2024). Currently, the estimates of natural mortality for shortspine thornyhead are computed on the basis of historical age data from previous studies (Jacobson, 1990; Kline, 1996), but reproductive parameters are also routinely incorporated into estimation of mortality for similarly managed rockfish species (Sullivan et al., 2022b; Omori et al., 2023). Because of the inability to produce reliable age esimates, however, it has not been possible to model parameters, such as recruitment, as part of stock assessments for shortspine thornyhead. Fisheries management is based on the conservation of reproductive potential, which is determined by using inputs of maturity (and fecundity) in stock assessment models (Morgan, 2008). Maturity at age, the estimated proportion of females that are mature at a given age (maturity ogive), is a key component of reproductive biology and the calculation of spawning stock biomass, which is used as a proxy for reproductive potential for many stocks in Alaska (NPFMC, 2024).

Although mode of reproduction and spawning strategy have been previously described for this species (Erickson and Pikitch, 1993), reproduction and maturity of shortspine thornyhead have been explored in only a small number of studies, by using histological examination, which is the most accurate method (e.g., Brown-Peterson et al., 2011). Pearson and Gunderson (2003) studied the length at maturity for this species across broad areas of Alaska and off the West Coast of the United States, and Cooper et al. (2005) estimated fecundity and examined evidence of batch spawning for this species in the Gulf of Alaska, Bering Sea, and Aleutian Islands. Age determination for shortspine thornyhead has been described in even fewer studies, and to my knowledge, no female maturity ogive involving multiple age readers has been published. In studies on aging of shortspine thornyhead (e.g., Butler et al.[1]; Kline, 1996), age determination has been difficult, with poor and variable reader precision and irregular growth increments.

To update our knowledge of the biology of shortspine thornyhead, reproductive characteristics, such as ovarian development, spawning seasonality, and maturity of specimens from 2 geographical areas of Alaska are summarized herein on the basis of results from the use of histological techniques. Also presented is preliminary work on age determination methods used to estimate a maturity ogive for this species in Alaska.

Materials and methods

Field collections

By using a length-stratified sampling design, ovary samples were taken from shortspine thornyhead collected from both fishery-dependent (i.e., fishery observers) and fishery-independent (bottom-trawl survey of the NOAA Alaska Fisheries Science Center [AFSC]) sampling sources in the western and central Gulf of Alaska and in the western Aleutian Islands from 2014 through 2016 (Fig. 1, Table 1). Shortspine thornyhead were collected from fishery-dependent samples at inshore processing plants on Kodiak Island and aboard bottom-trawl vessels in the Gulf of Alaska and the Aleutian Islands. Sampling at processing plants was conducted in May 2016 during offloading of bottom-trawl vessels participating in rockfish fisheries. Additional specimens from the Gulf of Alaska were collected during the bottom-trawl survey conducted in 2015 by the AFSC. For collections in the Aleutian Islands, shortspine thornyhead were sampled during fishing operations targeting Atka mackerel (*Pleurogrammus monopterygius*) in October 2014 and April 2015 and during those targeting rockfish species in July 2015. Specimens also were collected during the AFSC bottom-trawl surveys conducted in June and July of 2014 and 2016.

For each specimen, sex was determined, fork length (FL) in centimeters and whole wet weight in grams (whenever possible) were measured, and a whole ovary and otoliths were collected. Ovaries were preserved in 10% formalin in the field prior to processing. Whole fish from a single haul of the AFSC bottom-trawl survey of the Aleutian Islands in 2016 (number of samples [*n*]=41), however, were stored frozen to be processed later because of time constraints and the known difficulty in field identification of sex for small fish (<18 cm FL; Fruh et al., 2010). Through initial histological analysis of frozen tissue, it was determined that any autolysis (cell destruction) present did not prevent any stage of oocyte development or anatomical marker from being distinguished. These frozen samples were all from immature individuals. The quality of histology from frozen tissue samples, however, was not comparable to that from fresh tissue fixed in 10% formalin, as there was partial degradation of features and less contrast between cellular features than that normally observed with fresh tissue (Suppl. Figure).

Histological analysis

Histological analysis of approximately 1.0 g of tissue (cross-sectioned) from the middle of one ovarian lobe was conducted (with ovarian wall). Ovarian cross sections were embedded in paraffin, cut into thin sections of up to 4 µm, mounted on slides, and stained with hematoxylin and eosin, following standard histological procedures (e.g., Feldman and Wolfe, 2014). The primary oocyte development stage and the associated histological features were established, following Brown-Peterson et al. (2011), with

---

[1] Butler, J. L., C. Kastelle, K. Rubin, D. Kline, H. Heijnis, L. Jacobson, A. Andrews, and W. W. Wakefield. 1995. Age determination of shortspine thornyhead *Sebastes alascanus*, using otolith sections and ^{210}Pb:^{226}Ra ratios. Natl. Mar. Fish. Serv., Southwest Fish. Sci. Cent., Admin. Rep. LJ-95-12, La Jolla, CA. [Available from Southwest Fish. Sci. Cent., Natl. Mar. Fish. Serv., NOAA, 8901 La Jolla Shores Dr., La Jolla, CA 92037-1508.]

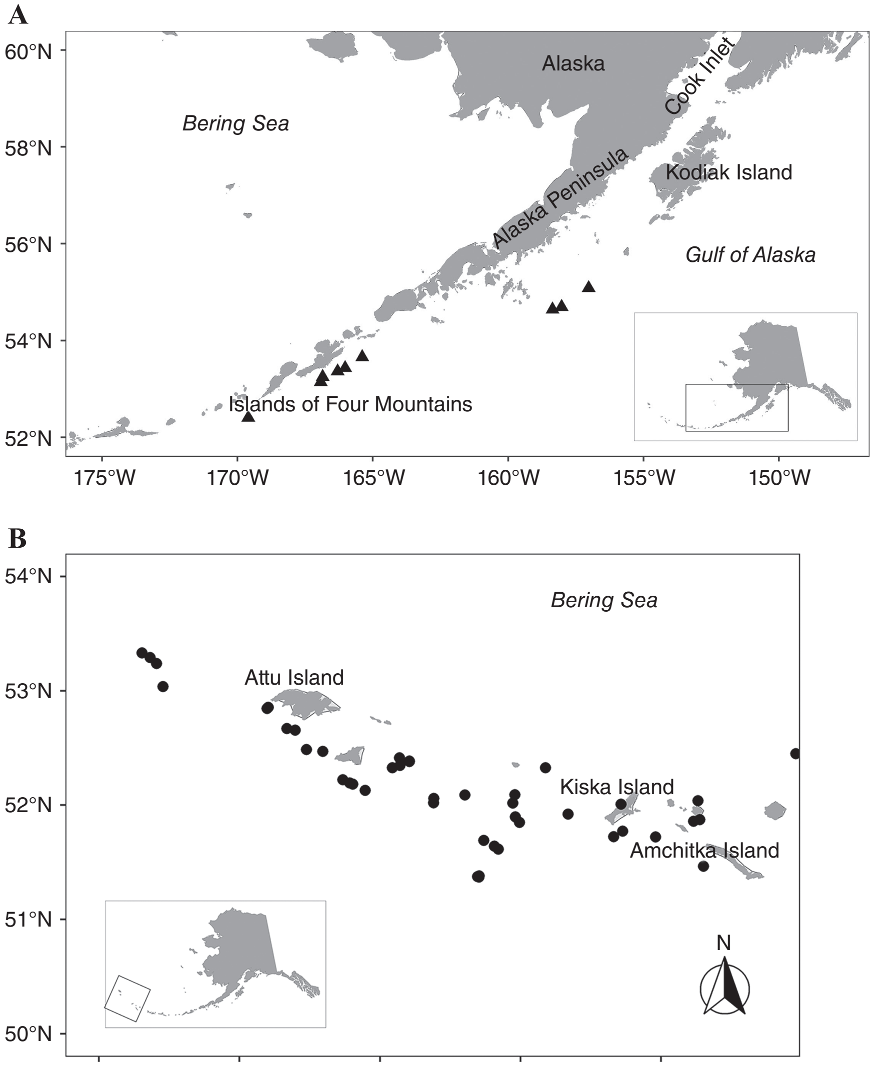

Figure 1

Maps of the locations in the (**A**) Aleutian Islands and (**B**) Gulf of Alaska at which female shortspine thornyhead (*Sebastolobus alascanus*) used in this study were captured from 2014 through 2016.

some descriptions following Erikson and Pikitch (1993) and updated terminology from Lowerre-Barbieri et al. (2023) (Table 2). A fish was considered mature if there was evidence that spawning would occur during the current reproductive year or evidence that the fish had spawned in the current or recent reproductive cycle (Lowerre-Barbieri et al., 2023). Many features that help to distinguish between an immature and mature fish remained visible after spawning; however, there was uncertainty regarding some features used to distinguish immature females from regenerating females, given that much of the sampling for this study occurred during non-spawning periods or when many fish did not exhibit spawning markers, such as postovulatory follicles. The features used to distinguish between an immature and mature fish included small ovarian cross sections, well-organized lamellar structure, a lack of muscle bundles or small blood vessels, and thin ovarian walls (Lowerre-Barbieri et al., 2023). To account for the uncertainty of assessing the maturity of those females that had moderate overlapping of the aforementioned features, specimens were classified as *unidentified mature* and evaluated separately.

Age determination

Age assignments were made to provide an initial maturity ogive for stock assessment, with the goal of establishing reasonable age precision between multiple readers. The establishment of methods for baseline age determination was essential given the known historical difficulties in aging shortspine thornyhead (e.g., Butler et al.[1]; Kline, 1996; Kastelle et al., 2020). Otoliths were aged through the use of the thin-section method (Smith et al., 1995) by 2 readers, including the author, with expertise in aging rockfish. Readers applied the same age determination protocol and independently assigned an age. A birthdate convention of 1 January was used to estimate ages (Matta and Kimura, 2012). Because of the general lack of clarity near the otolith edge in the thin sections, the timing of marginal growth was difficult to interpret. Samples for aging were collected in 4 different months (April, June, July, and October); therefore, observing increment growth and patterns across the calender year was not possible. There appeared to be little difference in edge growth between months, with most having a translucent zone or the beginning of an opaque zone (growth). Marginal increments were not measured, and edge growth generally was not counted.

Table 1

Total number of ovaries collected for histology (273), by month and year, from shortspine thornyhead (*Sebastolobus alascanus*) caught in the Gulf of Alaska (GOA) and the Aleutian Islands (AI) from 2014 through 2016. A blank cell indicates that no ovaries were collected from specimens in that location in that month and year.

	2014		2015		2016	
Month	GOA	AI	GOA	AI	GOA	AI
April				7		
May			20		5	
June		6	7	13		41
July		17		14		116
August						8
October		19				

Table 2

Descriptions of the histological features present at the primary stages of oocyte development in female shortspine thornyhead (*Sebastolobus alascanus*) collected in the Aleutian Islands and Gulf of Alaska during 2014–2016. Descriptions of oocyte development stages follow Brown-Peterson et al. (2011), with some following Erikson and Pikitch (1993). Reproductive phases follow Lowerre-Barbieri et al. (2023). PN=perinuclear; PG=primary growth; Vtg1–3=primary, secondary, and tertiary vitellogenesis; MN=migratory nucleus; POF=postovulatory follicles; and GM=gelatinous material.

Maturity status	Reproductive phase	Oocyte stage	Histological features
Immature	Immature	PN	Characterized by oogonia and PG (early and late perinuclear oocytes). Thin ovarian wall. Oocytes are generally organized and tightly clustered. If stroma branching exists, it appears well-defined, but a central stroma may be absent. Less lumen space present. Atresia generally absent. Ovary and oocyte sizes small.
	Developing (mature)	Oil vacuole	Small oil vacuoles appear, primarily closer to the nucleus. Peduncle formation begins at this secondary oocyte development stage, although incomplete. Thin ovarian wall. Secretory layer of ovarian wall incomplete. Ovary and oocyte size remains small. Atresia is minor.
Mature	Developing (mature)	Vtg1	Evidence of primary or early vitellogenesis along the periphery of the oocyte as small globules. Yolk globules largely remain along the edges. Protruding vascularized peduncles are prominent, and their length is increased relative to the previous reproductive phase.
	Late developing	Vtg2	Vitellogenesis is marked with large yolk globules filling approximately 50% of the cytoplasm space within the oocyte.
	Late developing	Vtg3	Oocyte cytoplasm completely filled with large yolk globules. Secretory cell layer of ovarian wall prominent; there might be signs of a gelatinous sheath surrounding the oocytes. Oocytes large in size.
	Late developing	MN	Nucleus appears toward the periphery of the oocyte. Large oil vacuoles may be present, obscuring much or all of the nucleus.
	Spawning	Hydration	Yolk globule fusion occurs within the oocyte. Ovarian wall is thick.
	Spawning	Ovulation	After hydration, empty follicles are observed. Ova are released into GM inside cavity.
	Regressing (postspawning)	POFs, Vtg3	POFs; remnant Vtg3 oocytes; late-stage atresia present; early-stage atresia also present, notably at ends of peduncles; lumen space prominent; thick ovarian wall. Lamella and stroma tissue disorganized from spawning. Peduncles become atretic, although not entirely absent. GM present.
	Regenerating	PG	An inactive state of development; PG oocytes present; ovarian wall thickness variable. Increase in the amount of muscle and stroma tissue present; muscle bundles, blood vessels, and POFs present; atresia present, including in peduncles; residual GM present.

All otoliths were embedded in resin and cut into thin sections with a thickness between 0.3 and 0.4 mm by using an IsoMet High Speed Pro[2] (Beuhler, Lake Bluff, IL). Multiple otoliths were mounted along each row with the proximal surface facing down cut transversely directly through the cores. From each otolith, 2–4 sections were taken for aging. Sections were mounted to glass slides. The section that was used to determine the age was marked for reading. No additional preparation was needed except to enhance the reading surface with mineral oil. Reflective light was preferable over transmitted light when examining the thin sections of otoliths. Images were annotated with estimates made during the aging process by using Photoshop Elements, vers. 18.0 (Adobe Systems, San Jose, CA).

Prior to conducting between-reader comparisons of pairs of age estimates, a set of whole otoliths from juvenile fish were surface-aged and then also cut into thin sections to help determine measurements of increments for the first 3 years. To establish age criteria for the early years, measurements were taken for 74 otoliths from the core to the third annual mark identified on the basis of the interpretation of the strong contiguous opaque and translucent zones around the otolith axes. Some samples were measured multiple times to establish consistent repeatability of annular marks and recognition of fast growing subannular marks or checks (irregular translucent growth zones, which are sometimes present in otoliths but are not annual marks). The following mean widths of the first 3 annual marks were established respectively: 1.05, 2.24, and 3.00 mm. Additionally, thin-section slides (n=428) prepared by using the same method from an earlier study of shortspine thornyhead in the Gulf of Alaska (Black[3]) were available and used to help establish age criteria and repeatability prior to estimation of ages for this study.

The precision of age assignments by readers was measured by using standard statistical tools. Each sample with an estimated age was aged by a second reader until a reasonable threshold of precision was achieved (coefficient of variation [CV] of approximately 9.0, with minimal reader bias), a level of precision similar to that reported for difficult-to-age rougheye rockfish (*Sebastes aleutianus*) and blackspotted rockfish (*S. melanostictus*), whose ages have been used in a biennial age-structured stock assessment (Spencer et al., 2024). Precision of aging was estimated and evaluated by using percent agreement (exact agreement between readers), average percent error (APE) (Beamish and Fournier, 1981), CV, and age-bias plots (Campana et al., 1995). A Bowker's test of symmetry was used to statistically assess bias between readers (Bowker, 1948; Evans and Hoenig, 1998). Specimens without agreement in age assignments between readers were reexamined, and any remaining discrepancies were resolved between reader and tester.

Length and age at maturity

Models were fitted by using single predictors, length or age, to describe biological maturity. Functional maturity was not assessed. There were not enough observations to fully explore adding other variables, such as depth or some spatiotemporal variable. Generalized linear models (GLMs) were fitted to maturity data to estimate length and age at 50% maturity. For logistic regression, the binomial data (0=immature; 1=mature) underwent a logit transformation through the use of the following formula:

$$\hat{P} = \frac{1}{1 + e^{-(\alpha + \beta x)}},$$

where $\hat{P}$ = the expected proportion of mature fish;
α and β = the coefficients of the logistic model; and
x = the size or age.

A weighted GLM for the proportion mature at age was incorporated because of possible bias introduced from length-stratified age sampling, given the possibility that a given age can include several length classes and that the probability of being mature at a given age is influenced by length at that age. Observations were weighted by the abundances of the size classes (Morgan and Hoenig, 1997). For the maturity ogives, 95% confidence intervals (95% CIs) were estimated by using bootstrapping methods with resampling of cases 10,000 times (Ogle et al., 2023). Cook's distance plots were constructed to assess outliers and influential data points, with a value greater than the threshold of 0.5 considered to be influential. To assess how the models fit the data, McFadden's pseudo R^2 was used, comparing the log-likelihood of the model in which the predictor variable was used with the log-likelihood of the null model (intercept only). A value greater than 0.2, on a scale between 0 and 1, is considered a good fit, according to McFadden (1974). An analysis of deviance was used to evaluate fits of logistic regression models and to measure the difference between models, with the full model maximizing the log-likelihood function. As a form of sensitivity analysis, separate logistic models were fitted with data from samples that were classified as *unidentifed mature*, with all samples treated as either *immature* or *mature*.

All statistical analyses were conducted in statistical software R, vers. 4.4.1 (R Core Team, 2024).

Results

Histological analysis

A total of 273 specimens were collected and examined for histology (Table 1). Females collected in the Aleutian Islands ranged in size from 13 to 58 cm FL (mean: 28.4 cm FL [standard deviation (SD) 7.9]), and females collected in the Gulf of Alaska ranged in size from 20 to 36 cm FL (mean: 29.2 cm FL [SD 3.8]) (Fig. 2). The timing of ovarian development appeared to be similar between geographical areas. Results of analysis of all data combined indicate a general annual pattern of oocyte seasonality,

---

[2] Mention of trade names or commercial companies is for identification purposes only and does not imply endorsement by the National Marine Fisheries Service, NOAA.

[3] Black, B. 2010. Unpubl. data. Hatfield Mar. Sci. Cent., Oregon State Univ., 2030 SE Marine Science Dr., Newport, OR 97365.

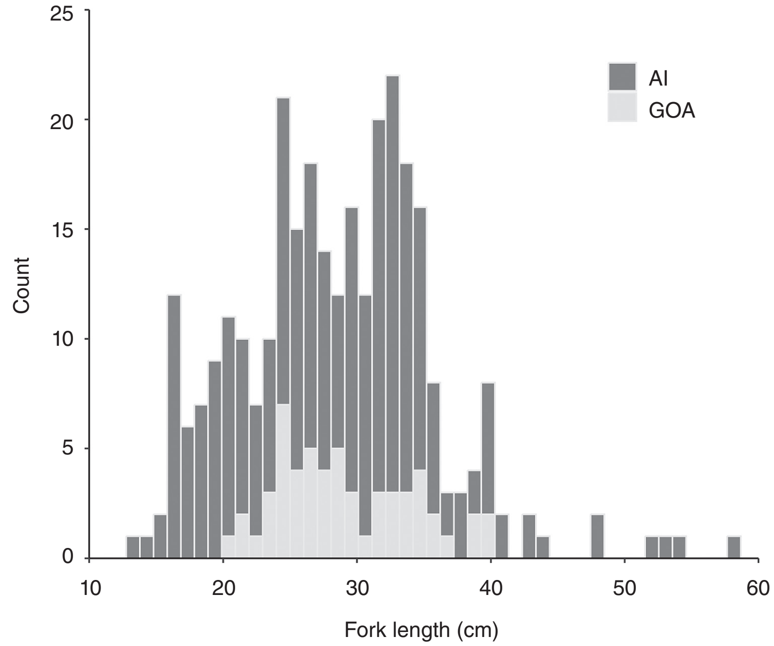

Figure 2

Number of female shortspine thornyhead (*Sebastolobus alascanus*), by fork length, collected in the Aleutian Islands (AI) and Gulf of Alaska (GOA) during 2014–2016.

with spawning females occurring in May and June and females in early phases of reproductive development occurring by October (Fig. 3). Immature females were characterized by the presence of primary growth oocytes, a thin ovarian wall, and no evidence of previous spawning (Fig. 4, A and B).

Observations of females in the imminent spawning and active spawning phases were found in May and June (Fig. 4, C, D, and E). Ovaries from active spawning females had hydrated oocytes mixed with tertiary vitellogenic oocytes (Fig. 4D). Gelatinous material was present (Fig. 4E) in all of the females sampled in May, and residual gelatinous material could be found in ovaries as late as October. Females in the regressing phase had postspawning characteristics, such as the presence of postovulatory follicles, remnant tertiary vitellogenic oocytes, and mid-to-late-stage atresia in their ovaries, indicating that these fish had already spawned (Fig. 5, A and B). Regenerating females were found throughout the study period, with the presence of primary growth oocytes, blood vessels, a thick ovarian wall, muscle bundles, postovulatory follicles, and residual gelatinous material indicating previous spawning (Fig. 5, C and D). Females in October also exhibited development of early primary vitellogenesis, a sign that oocyte progression for the next spawning cycle had begun (Fig. 5E). Peduncle formation was observed during initial stages of vitellogenesis (Fig. 5E). There was no evidence in samples of widespread atresia, which would have indicated abortive maturation or skip spawning in any female shortspine thornyhead analyzed.

Age determination

General observations of ages from otolith thin sections indicate clear growth patterns mixed with one or more localized or core-to-edge ambiguous areas. Under reflective light, patterns of fast and slow growth were distinguished by light and dark bands, respectively. The reading axis that produced the best repeatability and precision was near the sulcus or mid-proximal side (Fig. 6A). Ambiguous areas were defined as areas of compressed growth zones that did not conform to overall growth patterns on a consistent basis along a desired reading axis (Fig. 6B). These areas varied in size and location. Clearer growth patterns usually were limited to specimens with estimated ages of at least 20 years. Interpretations of annuli were difficult for large and old fish (>35 cm FL and >25 years old), given that old individuals appeared to have increasingly more areas that were difficult to interpret. Additionally, the interpretation of faint growth zones resulted in less precision, and these areas could be a source of under-aging if the growth zones were more compact.

Calculations of precision of age estimates for shortspine thornyhead (range: 4–47 years) fell within acceptable CV levels, relative to similarly difficult-to-age rockfish species (Table 3), and were similar to those from previous studies

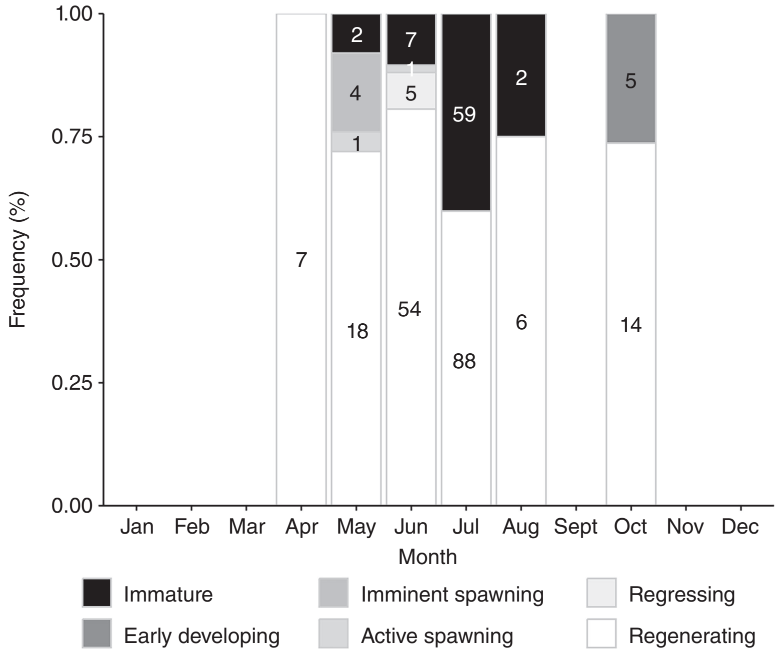

Figure 3

Proportion of female shortspine thornyhead (*Sebastolobus alascanus*), captured in both the Aleutian Islands and the Gulf of Alaska between 2014 and 2016, in each reproductive phase by month of collection. Numerals in bars indicate the sample sizes for reproductive phases.

involving multiple age readers for this species (Suppl. Table). Approximately 80% (85 of 107) of the ages were tested by a second reader for the maturity ogive (Fig. 7). Uncertainty of age estimation, assessed by comparing precision between readers, was low, with an overall percent agreement of 25.9% (Table 3). The absolute difference in age estimates between readers indicates that 80.0% of the ages assigned were within 2 years of the age estimate from the other reader. The largest deviations from the 1:1 equivalence line occurred mainly among those specimens with ages estimated at ≥25 years, a group that is few in number (n=5) (Fig. 7). No statistical reader bias was observed (Bowker's test of symmetry: X^2=35.0, P=0.563). Overall, mean ages for the first reader and second reader were 12.35 and 12.16 years, respectively (Table 3). Precision was better for specimens that were young to moderately old (≤20 years old) than for older specimens (21–47 years old), with a CV of 9.26 versus a CV of 10.77.

Length and age at maturity

In the analysis of deviance, no signficant difference was found in logistic model fits between the model in which data for only the Aleutian Islands were used and the model in which data for both the Aleutian Islands and the Gulf of Alaska combined were used (P>0.05). Therefore, for females from both regions combined, the estimated length and age at 50% maturity is 23.0 cm FL (95% CI: 22.3–23.8 cm FL; n=273) and 12.8 years (95% CI: 12.0–13.5 years; n=107) (Fig. 8, Table 4). McFadden's pseudo R^2 values are 0.66 and 0.95 for the length and age models, respectively, indicating good fits to the data. In Cook's distance plots, there are no identifiable outliers that influenced the model fits. The dataset used consists of information for 70 immature and 203 mature females. The size range of immature females was 13–33 cm FL, with only 4 immature specimens larger than 25 cm FL observed. The size range of mature females was 21–58 cm FL, with all females mature at lengths greater than 33 cm FL. All females ≤10 years old were immature, and all females ≥14 years old were mature. A total of 47 samples were classified as *unidentified mature*, and 5 of these samples were from specimens for which ages were determined. The treatment of these females as mature generated a length and age at 50% maturity of 21.0 cm FL and 11.4 years (Table 4). When these females were treated as immature, the model produced a length and age at 50% maturity of 25.4 cm FL and 13.1 years (Table 4).

Discussion

Effective management of shortspine thornyhead has been hindered by a lack of life history data, and this study

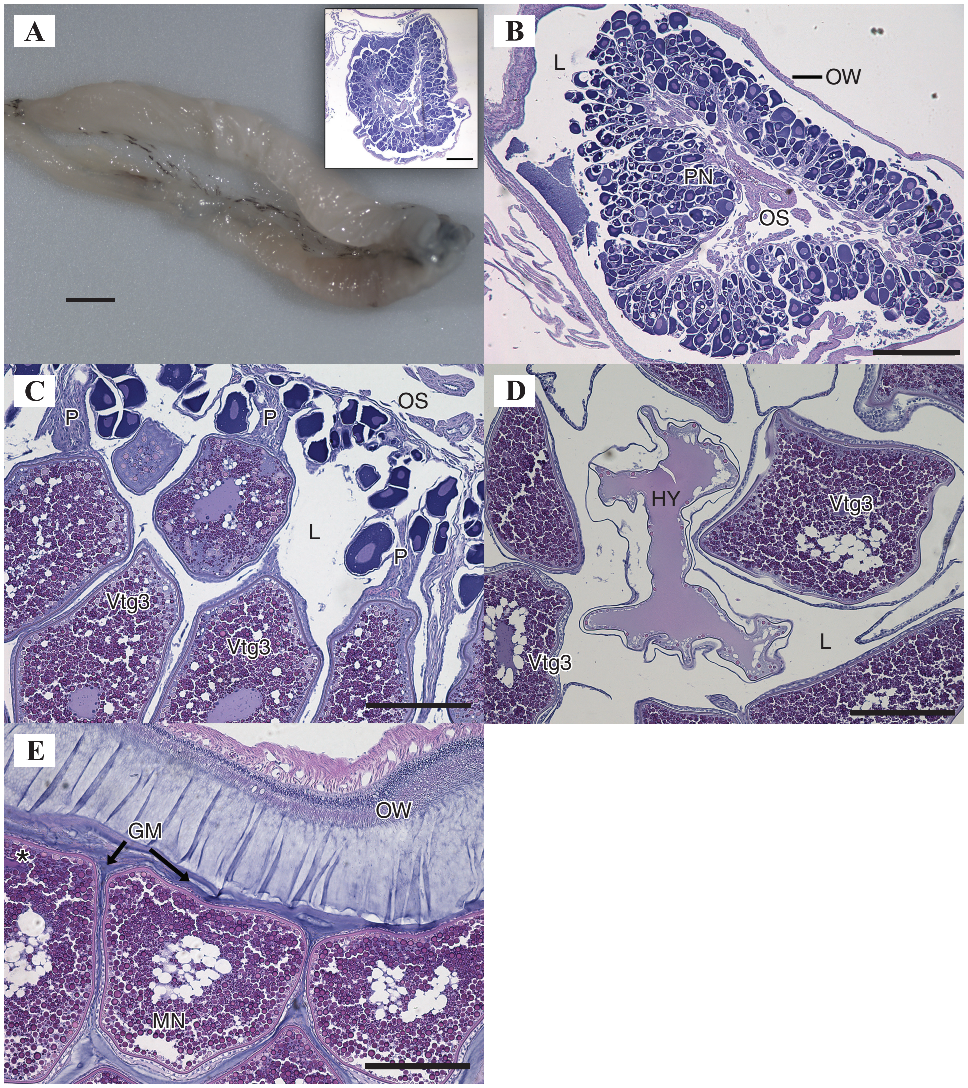

Figure 4

Histological images of ovarian tissue from shortspine thornyhead (*Sebastolobus alascanus*) collected in Alaska in 2015 and 2016, illustrating the immature and imminent and active spawning phases of reproduction. (**A**) The main image is of an ovary from an immature female with a fork length (FL) of 16 cm that was collected in July 2016 (scale bar: 1 mm), and the inset is a histological image of that ovary (scale bar: 0.25 mm). (**B**) This image shows tissue from a 21-cm-FL female collected in June 2016 and assigned to an immature phase (scale bar: 0.25 mm), given the presence of well-defined branching of the ovarian stroma (OS), a thin ovarian wall (OW), and early and late perinuclear (PN) oocytes. (**C**) The tissue in this image indicates that the 34-cm-FL female was in the imminent spawning phase, when it was caught in June 2015, with tertiary vitellogenic (Vtg3) oocytes attached to the terminal ends of peduncles (P) into the lumen cavity (L) (scale bar: 0.25 mm). (**D**) In this image of tissue from a 33-cm-FL female collected in June 2015, a hydrated oocyte (HY) is surrounded by Vtg3 oocytes indicative of active spawning (scale bar: 0.25 mm). (**E**) The advanced oocytes (migratory nucleus [MN] oocytes, with the nucleus indicated by an asterisk near the left edge of the image) embedded in gelatinous material (GM) in this sample indicate that this 40-cm-FL female, collected in May 2015, was in the imminent spawning phase (scale bar: 0.25 mm).

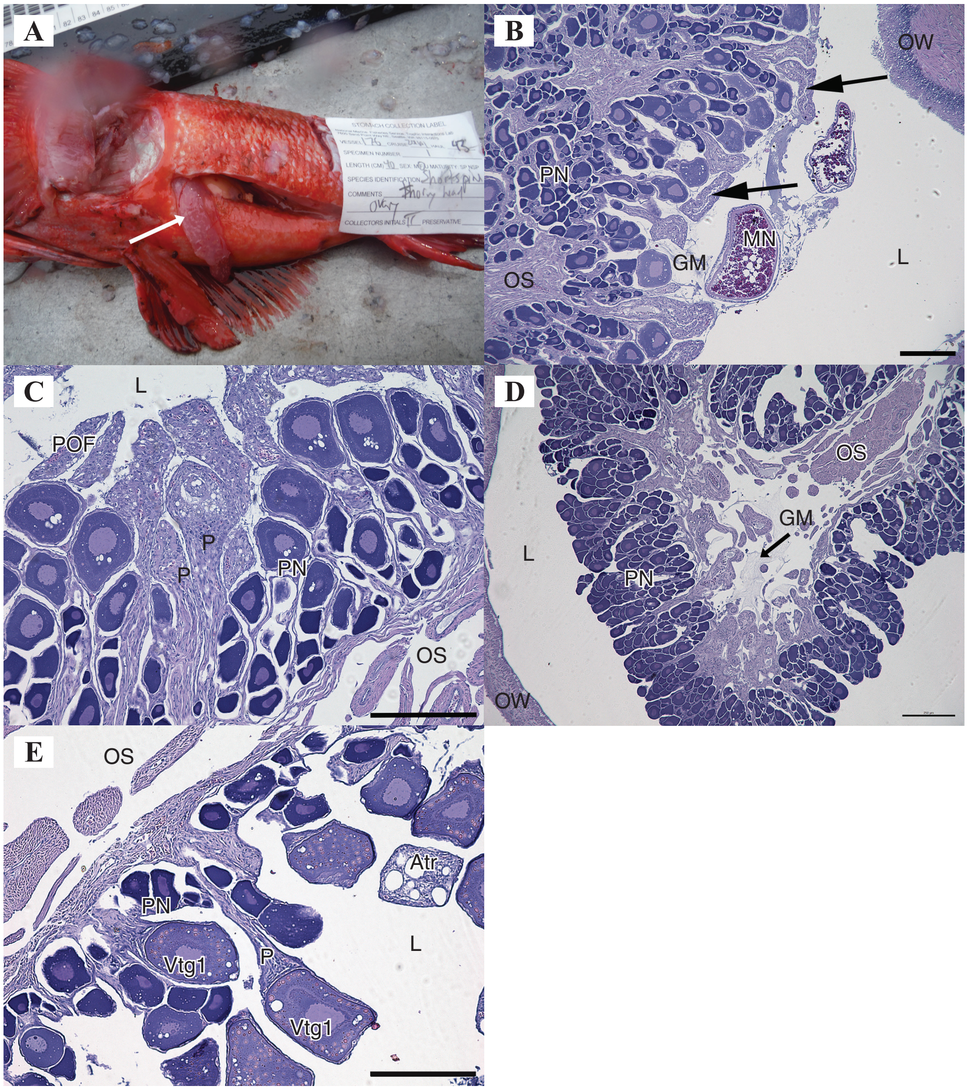

Figure 5

Histological images of ovarian tissue from shortspine thornyhead (*Sebastolobus alascanus*) collected in Alaska in 2014 and 2016, illustrating regressing, regenerating, and early developing phases of reproduction. (**A**) This female, with a fork length of 40 cm, was collected in June 2016; the white arrow indicates the ovary from this specimen. (**B**) In tissue from this 40-cm-FL female, the presence of remnant or atretic migratory nucleus (MN) oocytes and postovulatory follicles (POFs, indicated by the black arrows) signifies that this specimen was in the regressing phase; also labeled are ovarian stroma (OS), the ovarian wall (OW), and a lumen cavity (L) (scale bar: 0.25 mm). (**C**) Given the presence of atretic peduncles (P) surrounded by perinuclear (PN) oocytes in this sample, this 53-cm-FL female, collected in June 2016, was in the regenerating phase (scale bar: 0.25 mm). (**D**) The ovary in this image is from a 36-cm-FL female, collected in June 2016, that was in the regenerating phase, with remnant gelatinous material (GM) from previous spawning (scale bar: 0.25 mm). (**E**) This sample is from a 48-cm-FL mature female, collected in October 2014, in an early developing phase with late-stage atresia (Atr), early P formation, and the onset of primary vitellogenesis (Vtg1) (scale bar: 0.25 mm).

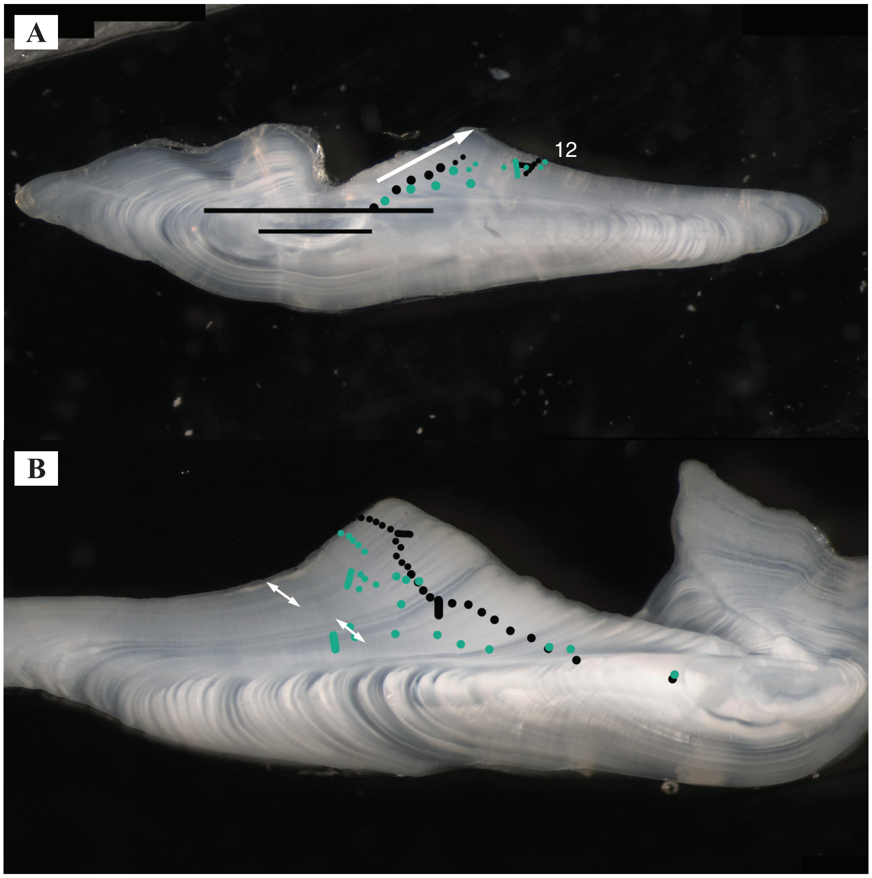

Figure 6

Images of transverse thin sections of otoliths of shortspine thornyhead (*Sebastolobus alascanus*) captured in the Aleutian Islands in Alaska. Each reader made annotations of annual marks independently, with black and green dots differentiating the marks of the 2 readers. (**A**) For this otolith section, from a specimen collected in July 2016, an age of 12 years was assigned. The preferred reading axis was near the sulcus ridge (indicated by the white arrow). (**B**) This otolith section, from a specimen collected in July 2015, is an example of one with ambiguous areas (indicated by the white arrows) that made annuli interpretation difficult. The scales of the bars in panel A are 1 and 2 mm and apply to both panels.

has provided some of this needed information. The main objectives of this study were to provide maturity ogives from histological examination for potential use in future stock assessments and to record oocyte development of shortspine thornyhead collected during different seasons. The results of this study, combined with existing data, contribute to our knowledge of the reproductive biology and maturity of this species. Also provided herein is a description of preliminary work on aging specimens of shortspine thornyhead that could provide the basis for future research on a larger scale.

The shortcomings of the age and maturity analysis are in part due to data limitations that prevent intrepretation of increment growth and annuli patterns at the edge across different months and timing of sampling. Determination of annulus formation would be improved with sampling over a broader temporal scale. In studies dedicated to determining length and age at maturity, samples collected immediately prior to or during spawning are ideal (e.g., Hunter et al., 1992). Because of the small number of spawning females observed in this study, identifying a core or peak spawning season was not possible. Although seasonal collections across the calendar year were not available, spawning periodicity could be reasonably determined. Length composition data indicate that longline fisheries capture shortspine thornyhead that are larger than those caught during bottom-trawl research surveys. The mean length of specimens in this study was

Table 3

Statistics used to compare precision in age estimates between readers for otoliths from specimens of shortspine thornyhead (*Sebastolobus alascanus*) collected in the Gulf of Alaska and the Aleutian Islands from 2014 through 2016 to assess maturity (number of samples [*n*]=85). Average age for all samples are noted for each reader. Relative bias or deviation from exact agreement is represented by the number of samples for which the age assigned by Reader 1 deviated from the age of Reader 2: underaging (−bias) or overaging (+bias). Precision of aging was assessed by using percent agreement (PA), average percent error (APE), and coefficient of variance (CV). For comparison, historical (2001–2022) evaluations of the precision of age estimates for difficult-to-age blackspotted rockfish (*Sebastes melanostictus*) (*n*=1279) and rougheye rockfish (*S. aleutianus*) (*n*=2716), used in age-structured assessment models, are provided from the Age and Growth Program of the NOAA Alaska Fisheries Science Center.

	Average age						
Species	Reader 1	Reader 2	−bias	+bias	PA	APE	CV
Shortspine thornyhead	12.35	12.16	30	33	25.9	6.69	9.45
Blackspotted rockfish					21.3	6.64	9.39
Rougheye rockfish					19.4	6.64	8.97

28.2 cm FL, compared to a mean length of 39.6 cm FL observed in longline fisheries (Rodgveller[4]). Obtaining larger shortspine thornyhead and specimens in an overall broader size range would result in a better understanding of spawning seasonality, ovarian development, and maturity schedules.

Histological analysis of samples may require some empirical understanding of the reproductive biology of the species being examined when identifying mature and immature fish. For many species, mature fish may have histological features similar to those of immature fish during periods of inactivity (e.g., Brown-Peterson et al., 2011). However, as in many teleosts, some characteristics (e.g., postovulatory follicles or tertiary vitellogenesis) can be used to distinguish between mature and immature shortspine thornyhead. Although the reproductive biology of shortspine thornyhead has rarely been studied, ovaries from females have histological features similar to those of more broadly studied rockfishes (*Sebastes* spp.).

Estimates of size and age at maturity for shortspine thornyhead are extremely limited. Pearson and Gunderson (2003) studied shortspine thornyhead off Alaska and the West Coast and found regional differences in female length at 50% maturity: 21.5 cm FL and 18.2 cm FL off Alaska and the West Coast, respectively. The maturity curve for this species off the West Coast was approaching being regarded as knife-edged, with most females maturing at sizes between 17 and 19 cm FL. The estimate from Pearson and Gunderson (2003) for specimens in Alaska covered a broad area of the eastern Bering Sea, Aleutian Islands, and Gulf of Alaska. Results from the more recent study described herein indicate that the lower bound length at 50% maturity (21 cm FL) for unidentified mature specimens is similar to estimates from Pearson and Gunderson (2003). Data from a recent preliminary study also indicate that latitude and depth may have a considerable affect on the variability of length at maturity of shortspine thornyhead, with longer lengths at maturity found at lower latitudes and deeper waters along the West Coast (Head[5]; see also Zahner et al., 2023). Regional differences in length or age at maturity of shortspine thornyhead would not be unexpected in Alaska, as ecological boundaries exist across its longitudinal range, in the Gulf of Alaska at 147°W (e.g., Coffin and Mueter, 2016) and in the Aleutian Islands, east and west of Samalga Pass (e.g., Hunt and Stabeno, 2005), and may be sources of variation. Therefore, samples covering broader spatial and temporal scales would be needed.

Reports on an age at maturity for this species have come from only 2 studies. Miller (1985) found that shortspine thornyhead reached 50% maturity at the age of 12 years in southeastern Alaska; however, this estimate, calculated by using the von Bertalanffy (1938) growth function, was based on data for a combined population of males and females. The aging method and reliability of the ages from that study are also unknown. Butler et al.[1] reported an estimated age at maturity of 13 years for specimens from the West Coast, sexes combined, but this estimate was based on visual inspections of maturity status in the field, a method considered less reliable than histological analysis. Still, the age at 50% maturity estimated in the study described herein is similar to those from these 2 previous studies.

The reliability of the ages used in creating a maturity ogive is of critical importance to stock assessment. Estimating ages of shortspine thornyhead has historically been difficult. Very little age composition data exists for this species. Previous aging studies for populations on the West Coast in which the thin-section method was used have had mixed results with precision of age assignments, as evaluated through between-reader comparisions (Butler et al.[1]; Kline, 1996). Butler et al.[1] reported a CV value of 8.65 for age estimates. Values for precision metrics from a more recent age-validation study with fish sampled in

---

[4] Rodgveller, C. 2016. Personal commun. Auke Bay Lab., Alaska Fish. Sci. Cent., Natl. Mar. Fish. Serv., 17109 Pt. Lena Loop Rd., Juneau, AK 99801.

[5] Head, M. 2024. Unpubl. data. Fish. Resour. Anal. Monit. Div., Northwest Fish. Sci. Cent., Natl. Mar. Fish. Serv., 2725 Montlake Blvd. E, Bldg. South, Seattle, WA.

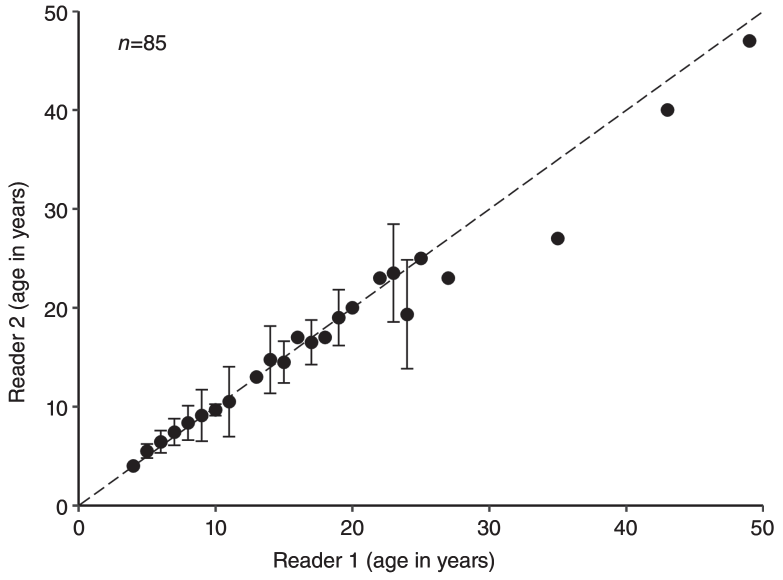

Figure 7

Age-bias plot for comparison of the precision of age estimates between 2 readers of otoliths from shortspine thornyhead (*Sebastolobus alascanus*) collected in the Aleutian Islands in Alaska for this study from 2014 through 2016 (number of samples [*n*]=85). The 1:1 line represents agreement (±0 years) between readers. Error bars indicate standard deviations.

Alaska (Kastelle et al., 2020) are similar to results from Butler et al.[1] and from this study (APE=6.16; CV=8.72). Kline (1996) reported large differences in age estimates between readers with APE and CV values as high as 14.80 and 20.90, respectively. The historical precision of aging of rougheye and blackspotted rockfish, in which ages are incorporated into age-structured models (Spencer et al., 2024), is comparable to that in this study.

In general, aging shortspine thornyhead becomes more difficult with older fish. In the study described herein ages from the maturity investigation were documented within a narrower age range than what is typical when confirming the full age range of a species. For example, the maximum age range would need to be addressed if determining whether a species is short-lived or long-lived. It is possible that the annual increments in the otoliths from the oldest individuals may be too unclear to obtain an age. The shortspine thornyhead is considered a long-lived species, but the maximum age for this species is uncertain because of the difficulty in age determination. Butler et al.[1] suggested that its longevity is greater than 100 years, and Kline (1996) reported a maximum age of at least 80 years. The need for thorough examination of the age range and age reading techniques used for this species is ongoing. However, given the similarity in precision numbers with those for species currently modeled in stock assessments (i.e., rougheye rockfish and blackspotted rockfish), results reported herein may provide a foundation for continued work on age determination.

The reliability and reproducibility of age estimation can be assessed by using measures of precision. Age validation goes further. It is used to measure the accuracy of age estimation and to describe how well ages determined from counting annuli compare with known ages (i.e., to measure statistical bias). Age validation with the bomb radiocarbon (^{14}C) technique, considered the gold standard of age validation methods (Campana, 2001), has been inconclusive for shortspine thornyhead (Kastelle et al., 2020). The levels of bomb-produced ^{14}C measured in otolith cores from shortspine thornyhead in the aforementioned study did not have the expected form of a pulse curve, in contrast to the curve for redstripe rockfish (*S. proriger*) in that study; the values were scattered below and to the right of the reference chronology based on that for Pacific halibut (*Hippoglossus stenolepis*) (Kastelle et al. (2020). According to Kastelle et al. (2020), the observed low and delayed concentration of ^{14}C could have resulted from the use of juvenile Pacific halibut as the reference chronology. Depth-related differences in ocean mixing of ^{14}C exist (Nydal, 1993). Shortspine thornyhead occupy deeper depths than Pacific halibut, below the mixed surface layer, where the rate of ^{14}C is reduced. Juvenile Pacific halibut usually become benthic at depths less than 120 m (IPHC, 1998), and juvenile shortspine thornyhead inhabit depths greater than 400 m (e.g., Jacobson and Vetter, 1996). In the study described herein, all juvenile shortspine thornyhead ≤20 cm FL were caught at depths greater than 400 m. Aside from experimenting with an

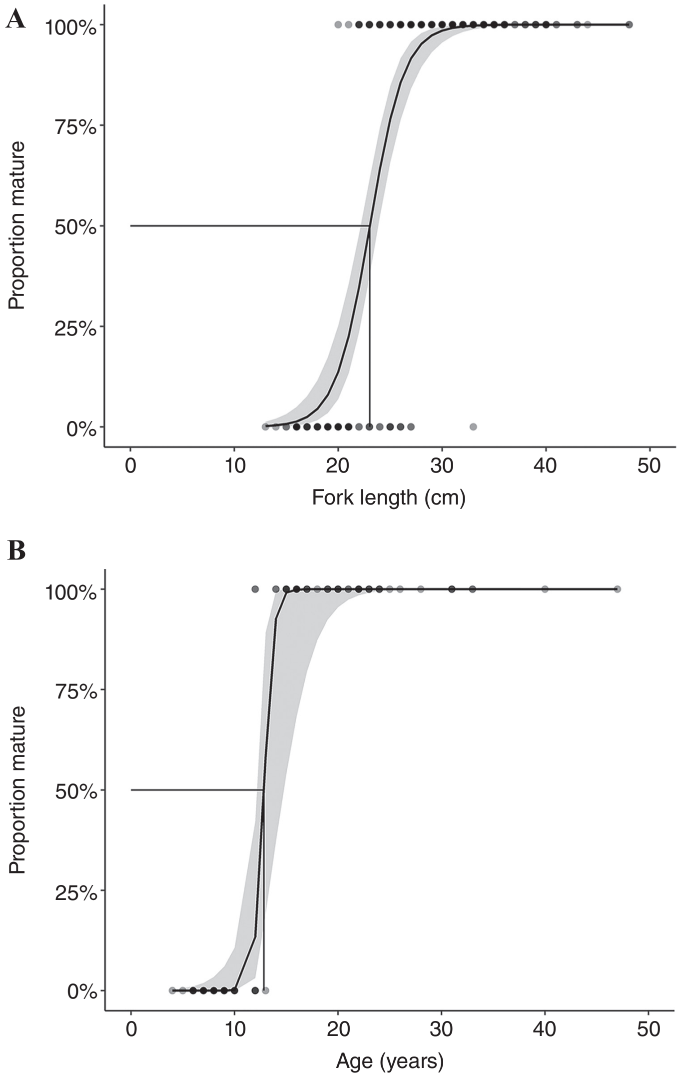

Figure 8

Ogives of (**A**) length at maturity (sample size [*n*]=273) and (**B**) age at maturity (*n*=107) for female shortspine thornyhead (*Sebastolobus alascanus*) collected in Alaska from 2014 through 2016. The shaded areas denote the 95% confidence intervals (CIs), and the horizontal and vertical black lines represent the intersections at the 50% estimate. For estimation of length at maturity, specimens from both the Aleutian Islands and Gulf of Alaska were included. For estimation of age at maturity, only specimens from the Aleutian Islands were included.

ecologically similar reference species for age validation, future research should include a larger, more representative sample of shortspine thornyhead across Alaska. Such an effort would include aging of females sampled from different areas. Aging of shortspine thornyhead remains a priority for the assessment of the stock in the Gulf of Alaska (Siwicke et al., 2024).

Observations of the reproductive development of shortspine thornyhead in this study differed little from what has been known previously about this species, but whether determinate batch spawning exists for this species remains a question. Wakefield (1990) found that the longspine thornyhead off the West Coast is a multiple spawner with determinate fecundity that releases 2–4 annual batches. Furthermore, Koya et al. (1995) noted that the broadfin thornyhead (*Sebastolobus macrochir*) appears to spawn twice during the spawning season in waters off Hokkaido, Japan. This strategy has not been clearly defined in shortspine thornyhead. Secondary ooctye development (i.e., vitellogenesis) in the study described herein was observed to occur at the end of vascularized peduncles that protrude from the ovarian stroma, similar to results from previous studies. Pearson and Gunderson (2003) did not find any hydrated oocytes or postovulatory follicles co-occurring with vitellogenic oocytes in their analysis of histological sections, but in this study some evidence of females with these batch-spawning characteristics was found for specimens from the Gulf of Alaska (e.g., Fig. 4D). Although some females had these characteristics in this study, a relatively high percentage (>50%) of hydrated oocytes from these females were atretic, possibly indicating some form of downregulation of fecundity in shortspine thornyhead.

It is common for fish species with determinate fecundity to recruit more oocytes than will ultimately be spawned (Kjesbu, 2009). This possibility will need to be examined more thoroughly for the shortspine thornyhead. Pearson and Gunderson (2003) concluded that batch spawning did not occur off coasts from Northern California to Alaska for shortspine thornyhead. Cooper et al. (2005) corroborated this finding of Pearson and Gunderson (2003), reporting that fecundity did not decrease during the spawning season, although some samples within their fecundity-length regression did not meet the criteria for this conclusion. The production of multiple batches could enable species, such as the shortspine thornyhead, to spread the risk among its offspring and mitigate consequences of deleterious environmental effects (Hočevar et al., 2021). It should be noted that updated histological information from specimens of shortspine thornyhead caught off the West Coast indicates that batch spawning is a possibility (Zahner et al., 2023). The collection of larger sample sizes, also noted in Cooper et al. (2005), over multiple years would be needed to evaluate the question of whether the shortspine thornyhead is truly a batch-spawning species.

One of the priorities in management of shortspine thornyhead is an upward movement within the management tier structure. Groundfish stocks in Alaska waters are managed according to 6 tiers that are based on the quality and amount of data available for stock assessment

Table 4

Estimates of length and age at 50% maturity (L_{50} and A_{50}) for shortspine thornyhead (*Sebastolobus alascanus*) and summary of statistics from binary logistic regression with generalized linear models. In addition to those from the base models for length and age, results are provided from models fitted with datasets in which all samples classified as *unidentified mature* (length: number of samples [*n*]=47; age: *n*=5) were treated as either mature or immature. Also included are standard errors of the mean (SEs) and 95% confidence intervals (95% CIs) for the lengths and ages at 50% maturity. The 95% CIs are from bootstrapping after 10,000 replications. Models were fitted to data from specimens collected in the Aleutian Islands and Gulf of Alaska from 2014 through 2016. Specimens were classified as unidentified mature if they had moderate overlapping of features used to determine maturity. Lengths are fork lengths given in centimeters, and ages are given in years.

		Coefficient				
Trait	Model	α	β	L_{50} or A_{50}	SE	95% CI
Length	Base	−13.9183	0.6040	23.04	1.9386	22.28–23.80
	Mature	−19.4075	0.9238	21.00	0.1651	20.32–21.69
	Immature	−10.7836	0.4239	25.43	0.0507	24.59–26.29
Age	Base	−28.2598	2.1995	12.84	0.8406	12.00–13.51
	Mature	−15.1892	1.3293	11.43	0.2528	10.02–12.55
	Immature	−34.0250	2.6070	13.05	1.0510	12.10–13.94

and harvest specification (NPFMC, 2024). Stocks with the most available data are in Tier 1 and are assessed with complex age-structured population models to support assessment and fishery management; in contrast, harvest recommendations for stocks in Tier 6 are based on historical catches because no other reliable data are available. Stocks without age-specific information on size and proportion mature are typically managed in Tier 5, for which a harvest rate is computed by multiplying an exploitation rate (based on an estimate of natural mortality) by a biomass estimate (typically from a trawl survey).

Information on size and maturity at age would allow target rates of fishing mortality to be based on the conservation of reproductive potential (as it would be for stocks in Tier 4). Moving the shortspine thornyhead to a Tier 4 designation from a Tier 5 classification would result in species-specific fishing reference points that would allow managers to calculate the overfishing level and acceptable biological catch for stocks of this species on the basis of a rate that reduces spawning biomass per recruit to 35% or 40% of the unfished value. These values would be reported separately from those for other species in the complex, offering an improved level of management scrutiny. A new designation to Tier 4 management would require the use of the following information: von Bertalanffy growth curves; weight–length relationships; fishery selectivity age, or the age at which fish are vulnerable to fishery gear; and reliable estimates of natural mortality and age at 50% maturity with proportions (ogives). Fully evaluating age and growth characteristics is one of the most important components of research that could improve the management of this species (Siwicke et al., 2024).

Conclusions

The acquisition of updated life history information for shortspine thornyhead, such as maturity at age, improves the level of data quality necessary for more effective management. The estimate of maturity at age from this study is the first based on histological examination for this species. A value for this reproductive characterisitic is needed for calculating spawning stock biomass per recruit, which in turn is used to evaluate the effects of fishing mortality and age at first capture on the spawning biomass of a stock. The results of this study underscore the need to improve aging methods with greater spatiotemporal coverage. The thin-section method is often used for difficult-to-age species, and future work with shortspine thornyhead should continue to use this method. Refining age-validation methods with more applicable reference species would be invaluable in the aging process. Reproductive development observed in this study appears to be similar to that in previous studies, but obtaining larger specimens during spawning within a sampling design would be needed to further evaluate maturity and whether shortspine thornyhead are batch spawners.

Resumen

Se utilizaron ovarios de hembras de chancharro alacrán (*Sebastolobus alascanus*) capturadas en las islas Aleutianas y el golfo de Alaska entre 2014 y 2016 para investigar aspectos de la biología reproductiva de esta especie. Aunque la especie es abundante en ambas áreas geográficas, los datos publicados sobre su reproducción siguen siendo limitados. Se examinaron histológicamente los ovarios para determinar su desarrollo, así como la longitud y edad de madurez. La estacionalidad del desarrollo ovárico fue similar entre las distintas zonas geográficas con hembras desovando en mayo y junio. En octubre se observaron ovarios maduros en fases tempranas de desarrollo. En las hembras, la longitud al 50% de madurez fue de 23.0 cm de longitud furcal (LF) (intervalo de confianza [IC] al 95 %: 22.3–23.8 cm LF), y la edad al 50% de madurez fue de 12.8 años (IC 95%: 12.00–13.51 años), todas madurando a edades entre 11 y 14 años. La precisión en las estimaciones de edad entre los lectores fue aceptable (coeficiente de variación=9.45; error porcentual medio=6.69; porcentaje de concordancia=25.9 %), en comparación con la de las estimaciones para especies de pez roca difíciles de datar (*Sebastes* spp.). Este estudio proporciona conocimientos adicionales sobre la biología reproductiva del chancharro alacrán y mayor comprensión de su ciclo biológico para el manejo pesquero. Para identificar mejor la madurez de esta especie y las diferencias entre zonas geográficas, se necesita mayor tamaño de muestra y cobertura espaciotemporal para el muestreo de especímenes que son colectados para estudios de edad.

Acknowledgments

The author thanks C. Conrath and K. Echave for thoughtful reviews that improved this manuscript. Additionally, the author thanks personnel of the Age and Growth Program of the AFSC Resource Ecology and Fisheries Management Division for assistance with age criteria, age reading, and methods.

Literature cited

Beamish, R. J., and D. A. Fournier.
1981. A method for comparing the precision of a set of age determinations. Can. J. Fish. Aquat. Sci. 38:982–983. Crossref

Begg, G. A., K. D. Friedland, and J. B. Pearce.
1999. Stock identification and its role in stock assessment and fisheries management: an overview. Fish. Res. 43:1–8.

Bowker, A. H.
1948. A test for symmetry in contingency tables. J. Am. Stat. Assoc. 43:572–574. Crossref

Brown-Peterson, N. J., D. M. Wyanski, F. Saborido-Rey, B. J. Macewicz, and S. K. Lowerre-Barbieri.
2011. A standardized terminology for describing reproductive development in fishes. Mar. Coast. Fish. 3:52–70. Crossref

Campana, S. E.
2001. Accuracy, precision and quality control in age determination, including a review of the use and abuse of age validation methods. J. Fish Biol. 59:197–242. Crossref

Campana, S. E., M. C. Annand, and J. I. McMillan.
1995. Graphical and statistical methods for determining the consistency of age determinations. Trans. Am. Fish. Soc. 124:131–138. Crossref

Coffin, B., and F. Mueter.
2016. Environmental covariates of sablefish (*Anoplopoma fimbria*) and Pacific ocean perch (*Sebastes alutus*) recruitment in the Gulf of Alaska. Deep-Sea Res., II 132:194–209. Crossref

Cooper, D. W., K. E. Pearson, and D. R. Gunderson.
2005. Fecundity of shortspine thornyhead (*Sebastolobus alascanus*) and longspine thornyhead (*S. altivelis*) (Scorpaenidae) from the northeastern Pacific Ocean, determined by stereological and gravimetric techniques. Fish. Bull. 103:15–22.

Echave, K. B., K. A. Siwicke, J. Sullivan, B. Ferris, and P-J. F. Hulson.
2022. Assessment of the Thornyhead stock complex in the Gulf of Alaska, 57 p. *In* Stock assessment and fishery evaluation report for the groundfish resources of the Gulf of Alaska. North Pac. Fish. Manag. Council, Anchorage, AK. [Available from website.]

Erickson, D. L., and E. K. Pikitch.
1993. A histological description of shortspine thornyhead, *Sebastolobus alascanus*, ovaries: structures associated with the production of gelatinous egg masses. Environ. Biol. Fishes 36:273–282. Crossref

Evans, G. T., and J. M. Hoenig.
1998. Testing and viewing symmetry in contingency tables, with application to readers of fish ages. Biometrics 54:620–629.

Feldman, A. T., and D. Wolfe.
2014. Tissue processing and hematoxylin and eosin staining. *In* Histopathology: methods and protocols (C. Day, ed.), p. 31–43. Humana Press, New York.

Fruh, E. L., A. Keller, J. Trantham, and V. Simon.
2010. Accuracy of sex determination for northeastern Pacific Ocean thornyheads (*Sebastolobus altivelis* and *S. alascanus*). Fish. Bull. 108:226–232.

Hočevar, S., J. A. Hutchings, and A. Kuparinen.
2021. Multiple-batch spawning as a bet-hedging strategy in highly stochastic environments: an exploratory analysis of Atlantic cod. Evol. Appl. 14:1980–1992. Crossref

Hunt, G. L., Jr., and P. J. Stabeno.
2005. Oceanography and ecology of the Aleutian Archipelago: spatial and temporal variation. Fish. Oceanogr. 14(s1):292–306.

Hunter, J. R., B. J. Macewicz, N. C.-H. Lo, and C. A. Kimbrell.
1992. Fecundity, spawning, and maturity of female Dover sole, *Microstomus pacificus*, with an evaluation of assumptions and precision. Fish. Bull. 90:101–128.

IPHC (International Pacific Halibut Commission).
1998. The Pacific halibut: biology, fishery, and management. Int. Pac. Halibut Comm., Tech. Rep. 40, 63 p. [Available from website.]

Jacobson, L. D.
1990. Thornyheads—stock assessment for 1990, 78 p. Appendix D. *In* Status of the Pacific coast groundfish fishery through 1990 and recommended acceptable biological catches for 1991. Stock assessment and fishery evaluation. Pac. Fish. Manag. Council, Portland, OR.

Jacobson, L. D., and R. D. Vetter.
1996. Bathymetric demography and niche separation of thornyhead rockfish: *Sebastolobus alascanus* and *Sebastolobus altivelis*. Can. J. Fish. Aquat. Sci. 53:600–609. Crossref

Kastelle, C., T. Helser, T. TenBrink, C. Hutchinson, B. Goetz, C. Gburski, and I. Benson.
2020. Age validation of four rockfishes (genera *Sebastes* and *Sebastolobus*) with bomb-produced radiocarbon. Mar. Freshw. Res. 71:1355–1366. Crossref

Kjesbu, O. S.
2009. Applied fish reproductive biology: contribution of individual reproductive potential to recruitment and fisheries management. *In* Fish reproductive biology: implications for assessment and management (T. Jakobsen, M. J. Fogarty, B. A. Megrey, and E. Moksness (eds.), p. 293–332. Wiley-Blackwell, Chichester, UK.

Kline, D. E.
1996. Radiochemical age verification for two deep-sea rockfishes: *Sebastolobus altivelis* and *S. alascanus*. M.S. thesis, 124 p. San José State University, San Jose, CA. [Available from website.]

Koya, Y., T. Hamatsu, and T. Matsubara.
1995. Annual reproductive cycle and spawning characteristics of the female Kichiji rockfish *Sebastolobus macrochir*. Fish. Sci. 61:203–208. Crossref

Love, M. S., M. Yoklavich, and L. Thorsteinson.
2002. The rockfishes of the northeast Pacific, 405 p. Univ. Calif. Press, Berkeley, CA.

Lowerre-Barbieri, S. K., N. J. Brown-Peterson, D. M. Wyanski, H. E. Moncrief-Cox, K. J. Kolmos, H. S. Menendez, B. K. Barnett, and C. Friess.
2023. A unified framework and terminology for reproductive traits integral to understanding fish population productivity. Mar. Coast. Fish. 15:e10276. Crossref

Matta, M. E, and D. K. Kimura (eds.).
2012. Age determination manual of the Alaska Fisheries Science Center Age and Growth Program. NOAA Professional Paper NMFS 13, 97 p. [Available from website.]

McFadden, D.
1974. Conditional logit analysis of qualitative choice behavior. *In* Frontiers in econometrics (P. Zarembka, ed.), p. 105–142. Academic Press, New York.

Miller, P. P.
1985. Life history study of the shortspine thornyhead, *Sebastolobus alascanus*, at Cape Ommaney, southeastern Alaska. M.S. thesis, 76 p. Univ. Alaska, Juneau, AK.

Morgan, M. J.
2008. Integrating reproductive biology into scientific advice for fisheries management. J. Northwest Atl. Fish. Sci. 41:37–51. Crossref

Morgan, M. J., and J. M. Hoenig.
1997. Estimating maturity-at-age from length stratified sampling. J. Northwest Atl. Fish. Sci. 21:51–63. Crossref

NPFMC (North Pacific Fishery Management Council).
2024. Fishery management plan for the groundfish fisheries of the Gulf of Alaska, 145 p. North Pac. Fish. Manag. Council, Anchorage, AK. [Available from website.]

Nydal, R.
1993. Application of bomb ^{14}C as a tracer in the global carbon cycle. Trends Geophys. Res. 2:355–364.

Ogle, D. H., J. C. Doll, A. P. Wheeler, and A. Dinno.
2023. FSA: fisheries stock analysis. R package, vers. 0.9.5. [Available from website.]

Omori, K. L., C. A. Tribuzio, and B. Ferris.
2023. Assessment of the Other Rockfish stock complex in the Gulf of Alaska, 72 p. *In* Stock assessment and fishery evaluation report for the groundfish resources of the Gulf of Alaska. North Pac. Fish. Manag. Council, Anchorage, AK. [Available from website.]

Pearson, K. E., and D. R. Gunderson.
2003. Reproductive biology and ecology of shortspine thornyhead rockfish, *Sebastolobus alascanus*, and longspine thornyhead, *S. altivelis*, from the northeastern Pacific Ocean. Environ. Biol. Fishes 67:117–136. Crossref

R Core Team.
2024. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. [Available from website, accessed June 2024].

Siwicke, K. A., K. B. Echave, and B. Ferriss.
2024. Assessment of the Thornyhead stock complex in the Gulf of Alaska, 58 p. *In* Stock assessment and fishery evaluation report for the groundfish resources of the Gulf of Alaska. North Pac. Fish. Manag. Council, Anchorage, AK. [Available from website.]

Smith, D. C., S. G. Roberston, G. E. Fenton, and S. A. Short.
1995. Age determination and growth of orange roughy (*Hoplostethus atlanticus*): a comparison of annulus counts with radiometric ageing. Can. J. Fish. Aquat. Sci. 52:391–401. Crossref

Spencer, P. D, J. N. Ianelli, and N. Laman.
2024. Assessment of blackspotted and rougheye rockfish stock complex in the Bering Sea/Aleutian Islands, 101 p. *In* Stock assessment and fishery evaluation report for the groundfish resources of the Bering Sea/Aleutian Islands regions. North Pac. Fish. Manag. Council, Anchorage, AK. [Available from website.]

Starr, P. J., and R. Haigh.
2017. Stock assessment of the coastwide population of shortspine thornyhead (*Sebastolobus alascanus*) in 2015 off the British Columbia coast. DFO Can. Sci. Advis. Secr. Res. Doc. 2017/015, 174 p. [Available from website.]

Sullivan, J., M. Callahan, A. Kingham, T. TenBrink, I. Ortiz, E. Siddon, and P. Spencer.
2022a. Assessment of the Other Rockfish stock complex in the Bering Sea/Aleutian Islands, 39 p. *In* Stock assessment and fishery evaluation report for the groundfish resources of the Bering Sea/Aleutian Islands regions. North Pac. Fish. Manag. Council, Anchorage, AK. [Available from website.]

Sullivan, J. Y., C. A. Tribuzio, and K. B. Echave.
2022b. A review of available life history data and updated estimates of natural mortality for several rockfish species in Alaska. NOAA Tech. Memo. NMFS-AFSC-443, 45 p. [Available from website.]

von Bertalanffy, L.
1938. A quantitative theory of organic growth (inquiries on growth laws. II). Hum. Biol. 10:181–213.

von Szalay, P. G., and N. W. Raring.
2020. Data report: 2018 Aleutian Islands bottom trawl survey. NOAA Tech. Memo. NMFS-AFSC-409, 175 p. [Available from website.]

Wakefield, W. W.
1990. Patterns in the distribution of demersal fishes on the upper continental slope off central California with studies on the role of ontogenetic vertical migration in particle flux. Ph.D. diss., 281 p. Univ. Calif. San Diego, San Diego CA.

Zahner, J. A., M. Heller-Shipley, H. A. Oleynik, S. G. Beyer, P-Y. Hernvann, M. Véron., A. N. Odell, J. Y. Sullivan, A. L. Hayes, K. L. Oken, et al.
2023. Status of shortspine thornyhead (*Sebastolobus alascanus*) along the U.S. West Coast in 2023, 135 p. Pac. Fish. Manag. Council, Portland, OR. [Available from website.]