




Reproductive biology and ecology of Pacific hagfish (*Eptatretus stoutii*) and black hagfish (*Eptatretus deani*)

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Abstract

The reproductive biology of Pacific hagfish *Eptatretus stoutii* (Lockington, 1878) and black hagfish *Eptatretus deani* (Evermann & Goldsborough, 1907) was assessed using current and historical data. Our results found that the reproductive characteristics of both hagfish species reflect those of *K*-selected species, which tend to live long and exhibit slow growth rates, low fecundity (approximately 20 eggs per female) and late maturity. Additionally, females of both species commence maturation prior to males. This study provides a population profile for both species of hagfish, but further assessments are needed to effectively manage a sustainable hagfish fishery.

KEYWORDS

development curves, fecundity, growth parameters, hagfish reproduction, length–weight relationships, sustainable fisheries

1 | INTRODUCTION

Understanding the life history of a fish population is as important as knowing the biomass when managing a sustainable fishery (Berkeley *et al.*, 2004; Hutchings, 2002). Selective pressures due to fishing can reduce genotypic variation and disrupt the spatial distribution within a population, preventing the full recovery of a depleted population (Berkeley *et al.*, 2004; Heino & Godo, 2002; Hutchings, 2000; Juanes *et al.*, 2007). It is especially important to understand basic reproductive characteristics such as fecundity, age-at-maturity and size-at-maturity in order to optimize fishing mortality of late-maturing species (Brander, 1981; Walker & Hislop, 1998). Benthic ecosystems, in particular, often consist of these late-maturing species that are highly vulnerable to overfishing (DFO, 2000; Hutchings, 1999). This study explores the life histories of two hagfish species with the goal of providing information that can help limit overfishing of future hagfish fisheries.

Prior to the 1960s, inshore hagfish *Eptatretus burgeri* (Girard, 1855) were primarily fished in the Sado Strait of the Japan Sea as a food source for both Korea and Japan with limited manufacturing of “eelskin” from the hagfish skin (Gorbman *et al.*, 1990; Strahan &

Honma, 1960). After 1960 an increase in demand for “eelskin” resulted in an increase in hagfish fishing in both countries. Because of a lack of studies on reproductive traits of hagfish species the stock biomass slowly declined as a result of overfishing through the 1980s (Gorbman *et al.*, 1990). By 1988 overfishing of Asian stocks and the demand for “eelskin” resulted in the expansion of new hagfish fisheries in the north-east Pacific Ocean, including Baja California, California, Oregon, and British Columbia and the Atlantic Ocean (Ellis *et al.*, 2015; Gorbman *et al.*, 1990; Kato, 1990). The new fisheries in the Pacific Ocean targeted the two species of hagfish for which stock assessments are not available due to limited data, Pacific hagfish *Eptatretus stoutii* (Lockington, 1878) and black hagfish *Eptatretus deani* (Evermann & Goldsborough, 1907).

E. stoutii and *E. deani* are two of 83 species of hagfish that make up the most primitive class of vertebrates, Myxini (Knapp *et al.*, 2011; Martini & Beulig, 2013). Both of these hagfish species span extensive ranges along the continental shelf and slope of the north-west coast of North America. *E. stoutii* range from Pt San Pablo, Baja California to south-eastern Alaska at depths of 16–966 m (Gotshall & Dyer, 1987; Wisner & McMillan, 1990). *E. deani* range from Cedros Island, Baja California to south-eastern Alaska at depths of 107–2743 m

(Wisner & McMillan, 1990). In British Columbia, the new hagfish fisheries constantly fluctuated, open through intermittent periods from 1988–1992 and 1999–2001, due to changes in demand and the reluctance to overfish given the dearth of reproductive and length/weight data available for both species (Benson *et al.*, 2001). However, even with the new fisheries efforts, only limited reproductive data have been collected for a few species of hagfish, dominated by *E. burgeri* (Ichikawa *et al.*, 2000; Kobayashi *et al.*, 1972; Nozaki *et al.*, 2000) and secondarily by *E. stoutii* (Barss, 1993; Benson *et al.*, 2001; Gorbman, 1990; Johnson, 1994).

An issue which impacts hagfish fisheries is the differentiation of sexes in both *E. stoutii* and *E. deani*. Previous research suggested that these hagfish were protandrous hermaphrodites, juvenile hermaphrodites or dioecious (Gorbman, 1990). After extensive histological examination Gorbman (1990) determined that *E. stoutii* may be juvenile protogynous hermaphrodites becoming sexually differentiated males and females after maturity with the incidence of adult hermaphroditism in only 0.3% of the population. The only other author to study this species appears to be in agreement with the results of the histological examination (Johnson, 1994). However, the historical definition of hermaphrodites used in Gorbman (1990) and Johnson (1994) is inaccurate as the terms “juvenile hermaphroditism” and “adult hermaphroditism” indicate that the individual is capable of producing both male and female gametes, which was not the stated definition in either study. Furthermore, Johnson (1994) had shown the female to male sex ratio as effectively 1:1 at mature lengths with females developing earlier than males. Therefore, based on the analyses in both Gorbman (1990) and Johnson (1994) the historical use of “juvenile hermaphroditism” was used to describe females developing earlier than males. However, it was not meant to convey that the juvenile hagfish were capable of producing both female and male gametes. Furthermore, “adult hermaphroditism” may be inferred as intersex individuals (individuals with both developed ovarian and testicular tissues, functionality unknown), which are extraordinarily rare within the hagfish population. Thus far, no histological examination has been performed on *E. deani*. In both species mature females have a low fecundity of 1–30 eggs with no seasonal or annual cycles identified and a mean sex ratio of approximately 1.8:1 (female to male) and 2.58:1 for *E. stoutii* and *E. deani*, respectively, for all specimens collected, but the sex ratio at mature lengths is effectively 1:1 (Gorbman, 1990; Johnson, 1994; Leask & Beamish, 1999). Size differences also occur between species and sexes. Based on historical data, *E. deani* are larger in both mean weight and length compared to *E. stoutii* (Barss, 1993; Johnson, 1994; Leask & Beamish, 1999). In terms of mean weight and length, *E. stoutii* females are smaller than the males whereas *E. deani* females are larger than the males (Barss, 1993; Johnson, 1994; Leask & Beamish, 1999). The differences in size between species has been attributed to food availability at different depths (Johnson, 1994).

An experimental fishery opened off the west coast of Vancouver Island in 2013 and was created in part to enhance our understanding of *E. stoutii* and *E. deani* reproductive traits. The objective of this study was to quantify hagfish reproductive characteristics to determine fecundity, length-at-maturity, length–size frequencies and length–weight relationships. Additionally, this study examines the similarities and differences

between this experimental fishery and the few previous *E. stoutii* and *E. deani* fisheries. Better knowledge of the reproductive and ecological traits of *E. stoutii* and *E. deani* will inform the scientific advice used to guide management and lead to a sustainable exploitation of hagfish fisheries on the west coast of North America and could potentially be expanded to other species of hagfish around the world.

2 | MATERIALS AND METHODS

2.1 | Study area

In 2012 Lenico Holdings Inc. received the only permit to fish for *E. stoutii* and *E. deani* off the west coast of Vancouver Island in an experimental fishery. The experimental fishery was set to run from 2013 to 2016 with possible extensions based on survey results. Under the permit three survey types were required: depth-stratified, depletion and a biological index site at Kirby Point (PFMA 23–7). Two fishing vessels, F.V. *Ocean Marauder* and F.V. *Viking Sunrise*, collected samples from multiple Pacific Fishing Management Areas (PFMA), specifically targeting PFMA 23/123, 25/125 and 08/108–09/109, which represent high, medium and low effort areas, respectively. Dependent on the survey different traps were utilized. For depth-stratified and depletion surveys, 25,227 l barrels with 16 mm escape holes were spaced 25 fathoms apart for one set. For consistency with the earlier fisheries, Korean traps, thin, long traps with 16 mm holes, were used to survey Kirby Point and gather biological data. Each set of traps was filled with commercial bait and ranged in soak time from 4 to 48 h. After the specified soak times the traps were hauled on board and the observer randomly selected approximately 100 hagfish per set to freeze for dissection. In the case of F.V. *Ocean Marauder* samples, the hagfish removed for biological data were frozen on board in ~25 kg bags. The F.V. *Viking Sunrise* did not have an onboard freezer, so hagfish were kept cool in tanks and then frozen after offloading in the harbour. The frozen bags of hagfish from the early years of the experimental fishery remained frozen for 1–2 years until July 2014, when we began dissections.

2.2 | Ethics statement

The hagfish used for this study were immediately placed from their traps into the onboard fishing vessel's freezer used for storing commercial fish product or kept in cool tanks and frozen at a commercial fishing freezer facility. The ethics statement is not applicable to our research as no experiments were performed on live hagfish and all collected hagfish were frozen using commercial fishing facilities.

2.3 | Dissection and reproductive stages

The 25 kg frozen bags of hagfish were removed individually from industrial freezers for dissection. The hagfish were removed and

submerged in a flooded sink of cold water to thaw for 2–3 h. After thawing, individual hagfish were pulled off the large block of fish to remove excess frozen slime and waste. The hagfish were individually weighed (wet weight ± 0.01 g), measured (total length ± 0.1 cm) and dissected to determine sex and reproductive stage. Gonadal tissue was removed and weighed (± 0.01 g); however, in select cases, due to extended freezing, the intestine often burst preventing clean removal of gonadal tissue. Reproductive stages were determined after a brief histological examination based on two methods outlined by Martini and Beulig (2013) and Gorbman (1990) (see Table 1).

Histological observations were made macroscopically (Table 1). It should be noted that under a microscope Stage 0 hagfish could have been classified into one of three categories: undifferentiated juvenile hagfish (*i.e.*, no detectable gonadal tissues), immature female, or sterile adults (*i.e.*, adults without identifiable gonadal tissue), but in macroscopic inspection all were combined as a Stage 0 hagfish (Gorbman, 1990; Martini & Beulig, 2013). Male reproductive stages are thought to be linear (*e.g.*, with increasing size/age males move from Stage –1 to Stage –4, possibly maintaining Stage 4 reproductive status for their lifespan) while female reproductive stages (Stages 1 to 8) are representative of a cyclical

reproductive cycle. Thus, the stages cannot be used to describe age-at-maturity in female hagfish, but instead can be used to identify the size of the first developmental cycle, the size at which half of the females have undergone reproduction and the smallest size females are capable of spawning. Intersex hagfish (Stage 9) are adult hagfish with both mature ovaries and testicular follicles present simultaneously. As no genetic analyses were performed to determine gonad functionality, intersex is the preferred terminology for what was historically termed “adult hermaphroditic” hagfish.

Each hagfish was dissected along the left side of the body. A ventral incision in the left gill pore was used to cut posteriorly for the length of the hagfish. The mesentery connecting the intestine and muscle wall was then carefully examined to identify reproductive stages. If present, the lengths of the three most average-sized eggs were measured with a calliper to calculate an estimated egg length with which to identify the reproductive female stage (Table 1). The total number of eggs was then counted to estimate fecundity in Stage 7 hagfish. Flaccid postovulatory follicles (POFs), which are capsules of recently spawned mature eggs left in the body cavity, were counted to estimate fecundity postspawning.

TABLE 1 Stages of sexual differentiation for both *E. stoutii* and *E. deani*

Reproductive stage	Description
Unknown sex (Stage 0s)	
Stage 0	No identifiable gonads; undifferentiated
Females	
Stage 1	Egg length < 1 mm
Stage 2	Egg length 1.01–3 mm
Stage 3	Egg length 3.01–7 mm
Stage 4	Egg length 7.01–15 mm
Stage 5	Egg length 15.01–23 mm
Stage 6	Egg length 23.01–31 mm
Stage 7	Egg length 31.01+ mm
Stage 8	Large, flaccid postovulatory follicles indicating recent spawning activity
Intersex	
Stage 9	Developed testes and ovaries simultaneously present
Males	
Stage –1	Testicular band present
Stage –2	Small testicular follicles containing fluid
Stage –3	Enlarged testicular follicles, cloacal gland <12 mm in length
Stage –4	Distended testicular follicles, cloacal gland 12+ mm in length

Note. Methodology adapted from Gorbman (1990) and Martini and Beulig (2013). The descriptions are based on macroscopic observations. The female stages are cyclical whereas the male stages are presumed linear over their lifetime.

2.4 | Statistical analysis

Length–weight relationships were calculated using the equation:

$$W = aL^b$$

where W is the wet weight, L is the total length, a is a scaling coefficient for the weight at length of the fish and b is a shape parameter for the body form of the fish species for both *E. stoutii* and *E. deani* to assess and compare condition (Brodziak, 2012; Ricker, 1973, 1975). The parameters a and b were estimated using linear regression analysis on log-transformed data. A three-parameter polynomial equation was used, with the y axis normalized as a percentage and 100 defined as the maximum, to estimate the percentage of Stage 0 hagfish as a function of total length (*i.e.*, TL_{50}) (Martini & Beulig, 2013). Separate female and male curves indicating size-at-gonadal development were generated using the same polynomial equation under the assumption that the genetic sex ratio is 1:1 (Martini & Beulig, 2013). ANOVA was used to identify the interaction of logarithmic length and sex on the length–weight model between sexes for each species. *Post hoc* analysis was performed using the Holm and Tukey HSD methods to determine which factors were significant. All statistical analyses were performed using RStudio with R 3.6.1 and the FSA package (Ogle, 2019).

3 | RESULTS

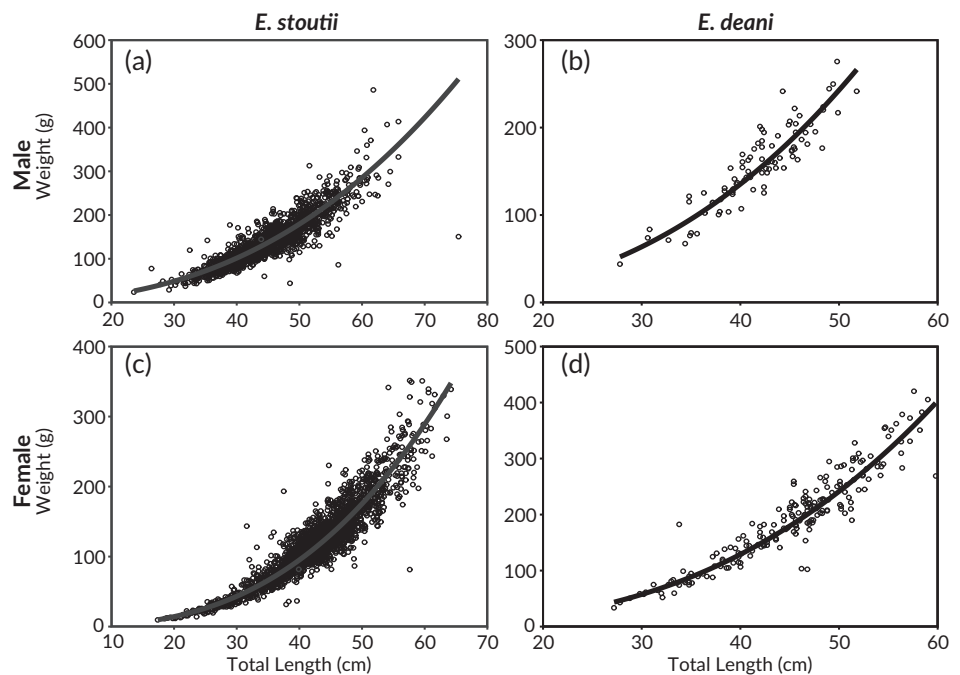
3.1 | Length–weight relationship

Frozen specimens, such as those used for the present study, have been found to weigh slightly less at a given total length (Martini and

TABLE 2 Mean total length (mm), standard deviation (s.d.) and range for both *E. stoutii* and *E. deani* (no intersex individuals were found in *E. deani* samples)

<i>E. stoutii</i>				<i>E. deani</i>			
Mean (mm)	s.d. (mm)	Range (mm)	n	Mean (mm)	s.d. (mm)	Range (mm)	n
Total				Total			
428	76.7	107–754	3904	432	70.7	256–598	303
Males				Males			
452	62.8	236–754	1495	417	46.1	278–518	88
Females				Females			
423	72.3	174–642	2204	451	70.6	272–598	194
Stage 0 s				Stage 0 s			
288	59.3	107–460	196	323	34.8	256–398	21
Intersex							
535	78.8	388–634	9				

FIGURE 1 A scatterplot of weight (g) versus total length (cm) with a nonlinear regression curve of $W = aL^b$. (a) *E. stoutii* male weight-length regression curve: $W = 8.34e^{-03}L^{2.55}$, $R^2 = 0.83$, $P < 0.001$, $n = 1495$, $F_{1,1493} = 7270$. (b) *E. deani* male weight-length regression curve: $W = 8.59e^{-03}L^{2.62}$, $R^2 = 0.83$, $P < 0.001$, $n = 88$, $F_{1,86} = 435.5$. (c) *E. stoutii* female weight-length regression curve: $W = 3.88e^{-03}L^{2.74}$, $R^2 = 0.91$, $P < 0.001$, $n = 2204$, $F_{1,2202} = 22,180$. (d) *E. deani* female weight-length regression curve: $W = 4.06e^{-03}L^{2.81}$, $R^2 = 0.91$, $P < 0.001$, $n = 194$, $F_{1,192} = 1828$



Beulig, 2013), so the data presented herein may underestimate the weight at a given length.

A total of 2204 females, 1495 males, nine intersex individuals and 196 Stage 0s were sampled for *E. stoutii* (Table 2). The male *E. stoutii* mean weight was 142.74 g (23.41–485.83 g) and mean length was 452 mm (236–754 mm) whereas the female *E. stoutii* mean weight was 120.51 g (9.56–351.51 g) and mean length was 423 mm (174–642 mm). Significant differences in the slopes of the length-weight relationships (Figure 1a,c) were observed for male and female *E. stoutii* (ANOVA, $F_{3, 3896} = 18.8$, $P < 0.001$). A *post hoc* analysis showed that the male *E. stoutii* slope was significantly lower than the female slope, indicating lower weight at length compared to females. The Stage 0 *E. stoutii* slope was significantly lower than for both the male and female hagfish (Table 3).

A total of 194 females, 88 males and 21 Stage 0s were sampled for *E. deani*. No intersex individuals were identified in the *E. deani*

samples (Table 2). The male *E. deani* mean weight was 156.63 g (43.86–275.60 g) and the mean length was 417 mm (278–518 mm), and in contrast to *E. stoutii*, *E. deani* females were larger than males with a mean weight of 195.38 g (33.56–420.24 g) and a mean length of 451 mm (272–598 mm). Significant differences in the slope of the length-weight relationships (Figure 1b,d) were observed for male and female *E. deani* (ANOVA, $F_{2,297} = 2.6$, $P = 0.07$). However, there were significant differences in the y intercept of the length-weight relationship (ANOVA, $F_{2,297} = 6.09$, $P = 0.003$). A *post hoc* analysis showed that only the y intercept for *E. deani* Stage 0s was significantly lower than for both male and female hagfish. There was no significant difference between male and female y intercepts (Table 4).

All hagfish longer than the maximum length of Stage 0s were found to be male, female, or intersex individuals. However, some Stage 0s were larger than the mean length for both species and

TABLE 3 Post hoc analysis of *E. stoutii* weight–length relationships using the Holm method to determine significant interaction effects amongst sexes

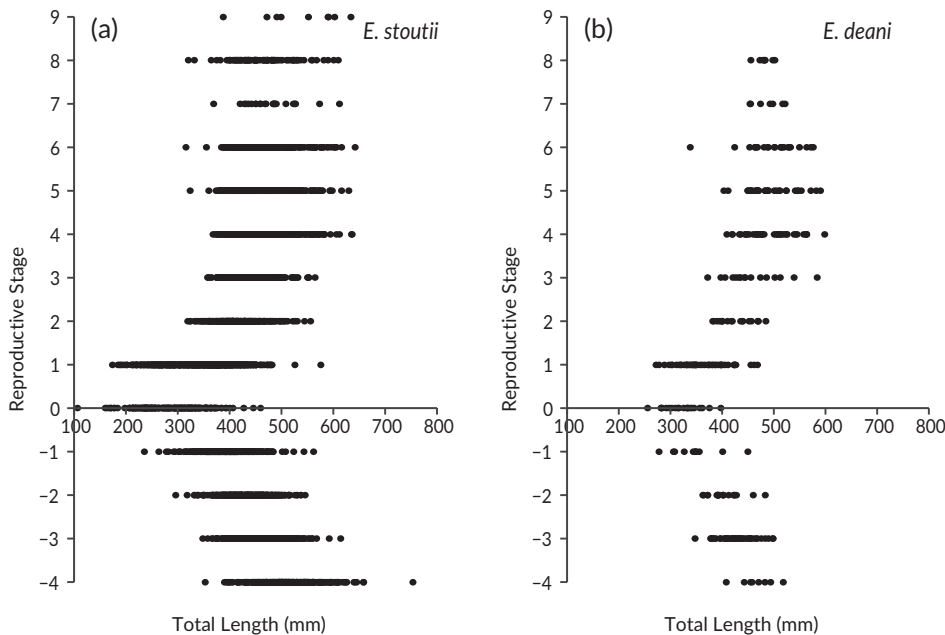
Sex comparison	Difference in slope	95% LCI	95% UCI	Unadjusted P-value	Adjusted P -value
I-F	−0.470	−1.20	0.257	0.205	0.615
M-F	−0.196	−0.265	−0.126	<0.001	<0.001
O-F	−0.334	−0.445	−0.222	<0.001	<0.001
M-I	0.274	−0.454	1.00	0.460	0.921
O-I	0.136	−0.597	0.869	0.716	0.921
O-M	−0.138	−0.258	−0.0175	0.0248	0.0992

Note. The sex on the left has a slope that is either smaller or larger (based on the differences in slope column) than the sex on the right. F, female; I, intersex; LCI, lower confidence interval; M, male; O, Stage 0; UCI, upper confidence interval.

Sex comparison	Difference in intercept	95% LCI	95% UCI	Adjusted P value
M-F	0.0354	−0.00942	0.0803	0.152
O-F	−0.0936	−0.174	−0.0134	0.0174
O-M	−0.129	−0.214	−0.0443	0.00114

TABLE 4 Post hoc analysis of *E. deani* weight–length relationships using the Tukey HSD method to determine significant differences amongst sexes

Note. The sex on the left has a y intercept that is either smaller or larger (based on the differences in intercepts column) than the sex on the right. F, female; LCI, lower confidence interval; M, male; O, Stage 0s; UCI, upper confidence interval.

**FIGURE 2** Total length (mm) for each reproductive stage for *E. stoutii* and *E. deani*. Reproductive Stages −4 to −1 represent males, Stages 1 to 8 represent females, Stage 0 represents Stage 0s and Stage 9 represents intersex

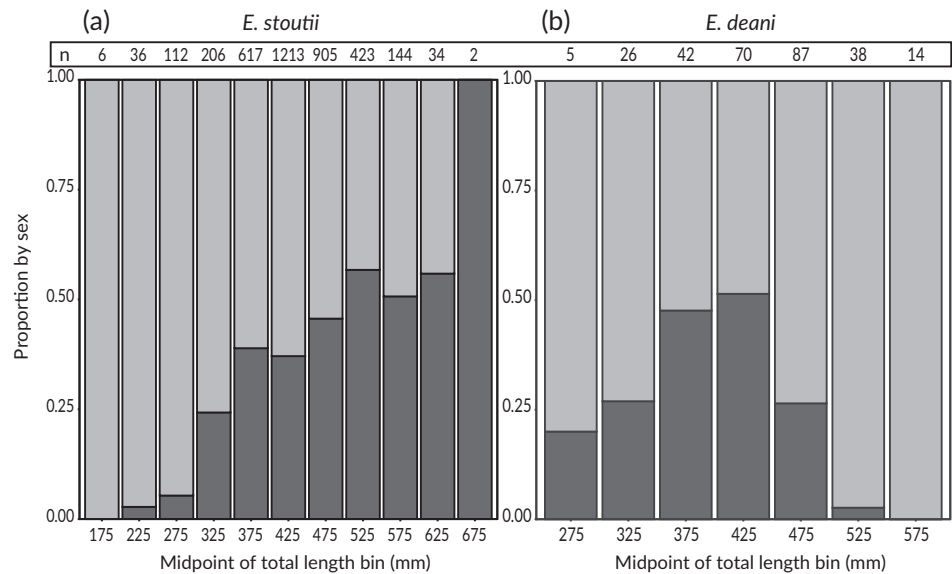
genders. Thus, all hagfish commenced gonadal maturation after the Stage 0s maximum length of 460 mm for *E. stoutii* and 398 mm for *E. deani*, but there was variability in length in reproductive stages for both species (Figure 2a,b). The length variability in the females of both species is representative of the cyclical nature of the female reproductive cycle, which occurs in all sizes of mature females (i.e., recycling through Stages 1–8). In contrast, the length variability in males suggests potential differences in male gonadal maturation or possibly a cyclical nature similar to the females. The stages of male

maturation significantly increased with length for both *E. stoutii* (LM, $F_{3,1491} = 463.7$, $P < 0.001$, $r^2 = 0.48$) and *E. deani* (LM, $F_{3,84} = 23.51$, $P < 0.001$, $r^2 = 0.44$).

3.2 | Sex ratio

Fish were separated into four distinct sex categories: female, male, intersex and Stage 0 (see Table 1). The majority of our samples were

FIGURE 3 (a) *E. stoutii* proportion by sex (male and female) broken into 50 mm total length intervals with the midpoint shown. The sample size of each interval is shown above each column. The average sex ratio was 1.47 with a range of 50:1 at 250–274 mm to 0.7:1 at 500–524 mm. One male was 754 mm and is not shown. (b) *E. deani* proportion by sex (male and female) broken into 50 mm total length intervals with the midpoint shown. The sample size of each interval is shown above each column. The mean sex ratio was 2.20 with a range of 0.9:1 at 400–424 mm to 23:1 at 500–524 mm. Gender: ■ M; □ F



female. Approximately 60% of the *E. stoutii* total population was female or a mean sex ratio of 1.47:1 excluding intersex individuals and Stage 0s. The *E. deani* population was 69% female or a mean sex ratio of 2.20:1 excluding Stage 0s. However, the mean is not representative of the mature population and as size increased both species approached an effective 1:1 sex ratio.

The data were subdivided into 50 mm length bins to assess ontogenetic changes in sex ratios (Figure 3). The sampled *E. stoutii* population was dominated by females at lengths less than 300 mm, but became slightly male dominated above 500 mm, with an effective sex ratio of 1:1 (Figure 3). All *E. stoutii* males were greater than 200 mm whereas six females were found between 175 and 200 mm. Similarly, no females were found greater than 650 mm, while two males were found between 650 and 700 mm, and one male was 754 mm. The *E. deani* population maintained a 3:1 female to male ratio in sizes less than 350 mm and declined to an effectively 1:1 ratio around 400 mm, but then increased to 23:1 at lengths greater than 500 mm. No males were found greater than 550 mm whereas 14 females were found between 550 and 600 mm. The large variability in ratios at longer lengths is likely due to the limited *E. deani* sample size in this study and is most likely not representative of the population's sex ratio.

3.3 | Fecundity

Fecundity was estimated for Stage 7 (stage prior to spawning) based on the number of eggs present and Stage 8 (postspawning) based on the number of postovulatory follicles. The mean fecundity based on the presence of eggs in Stage 7 *E. stoutii* was 18.0 ± 5.84 s.d. ($n = 23$) and in Stage 7 *E. deani* was 19.9 ± 3.85 s.d. ($n = 7$). The mean fecundity based on the presence of postovulatory follicles in Stage 8 *E. stoutii* was 19.5 ± 3.97 s.d. ($n = 17$) and in Stage 8 *E. deani* was 14.0 ± 5.66 s.d. ($n = 2$). The time for postovulatory follicles to

degenerate in hagfish is unknown, thus there is substantial uncertainty when using postovulatory follicle counts for species fecundity. Results of a two-sample *t*-test comparing mean fecundity between species and reproductive stages was not significant ($P > 0.05$) for both Stage 7 and Stage 8. The smallest Stage 7 or Stage 8 *E. stoutii* (i.e., first spawner) was 320 mm whereas the smallest Stage 7 or Stage 8 *E. stoutii* was 454 mm.

3.4 | Development curves

Results of estimating TL_{50} , the total length at which 50% of the population exhibits development of ovaries or testes, suggests that males of both *E. stoutii* and *E. deani* (308.48 and 312.35 mm, respectively) mature at larger sizes than females (190.71 and 276.16 mm, respectively) (Figure 4a,b). Figure 4c suggests that half the population of Stage 0s of *E. stoutii* and *E. deani* commence development of either ovaries or testes at 222.61 and 288.79 mm, respectively.

4 | DISCUSSION

The reproductive and biological traits found in this study largely corroborate the results from previous studies of *E. stoutii* and *E. deani* fisheries (Barss, 1993; Benson *et al.*, 2001; Gorbman, 1990; Johnson, 1994; Leask & Beamish, 1999). The length–weight relationships show sexual dimorphism in both *E. stoutii* and *E. deani* across all known sampled populations (this study; Barss, 1993; Johnson, 1994). Females in both species commence maturation at significantly smaller sizes than the males. Furthermore, our results showed that the sex ratio of *E. stoutii* shifts from female dominated to effectively 1:1 with increasing length, corroborating that females mature at smaller sizes than males (Gorbman, 1990; Johnson, 1994). Similarly, *E. deani* also had an effective 1:1 sex ratio, however, due to a limited *E. deani* sample size more females were observed at longer lengths. Both

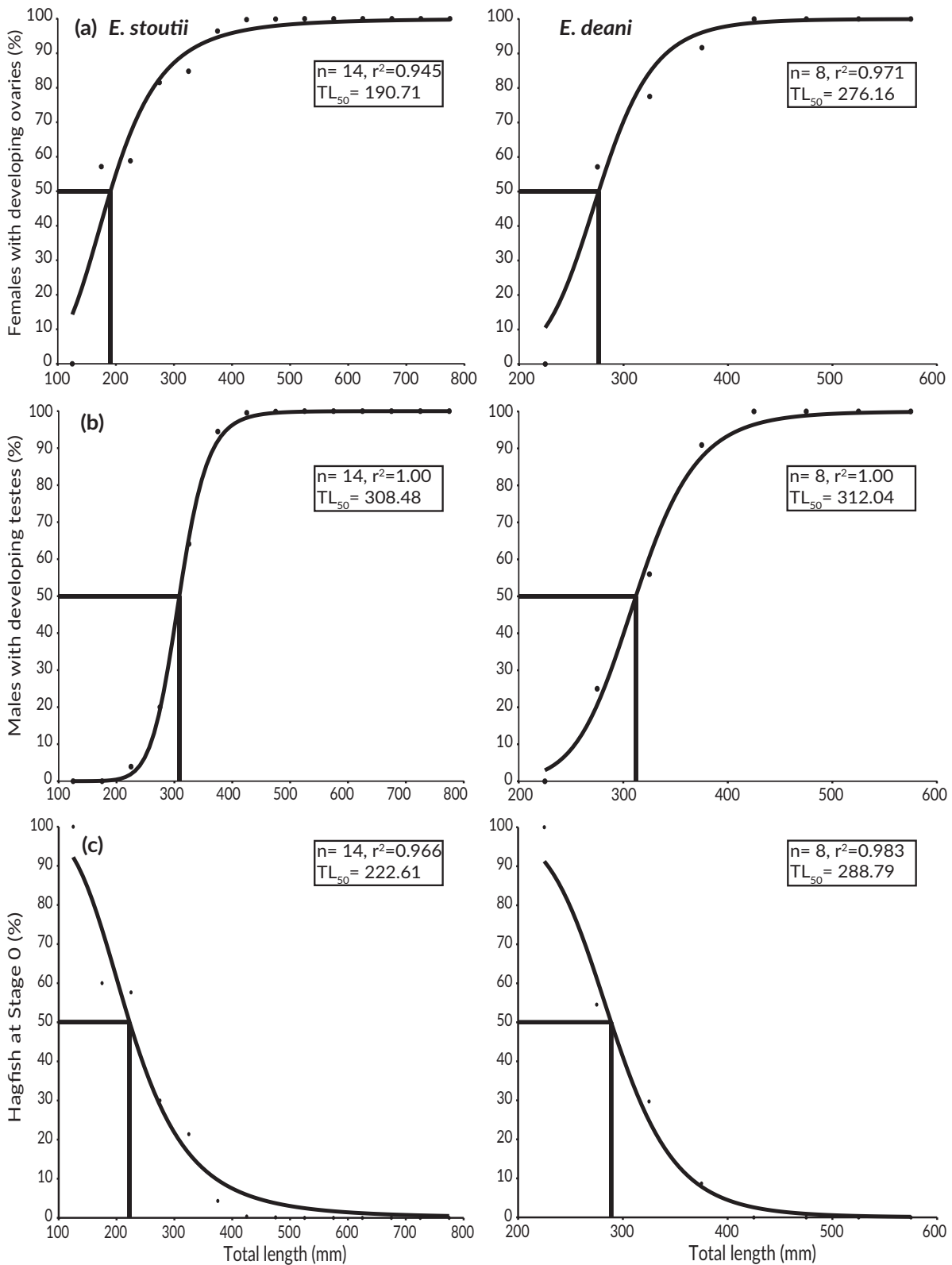


FIGURE 4 Sexual development curves for *E. stoutii* (left) and *E. deani* (right). The data were sorted into 50 mm intervals. For males and females it is assumed the genetic sex ratio is 1:1. Each curve used a variation of the three-parameter logistic equation: percent = $100 / (1 + (TL_{50}/X)^b)$.

(a) Female development curve. Percentage for females was determined as $(Female / (Female + (Stage0s/2)))$. *E. stoutii*: $TL_{50} = 190.71, b = 4.24$; *E. deani*: $TL_{50} = 276.16, b = 10.45$.

(b) Male development curve. Percentage for males was determined as $(Male / (Male + (Stage0s/2)))$. *E. stoutii*: $TL_{50} = 308.48, b = 12.49$; *E. deani*: $TL_{50} = 312.04, b = 10.67$.

(c) Stage 0s development curve. Percentage for Stage 0s was determined as $(Stage\ 0\ s / (Female + Male + Stage\ 0\ s))$. *E. stoutii*: $TL_{50} = 222.61, b = -4.29$; *E. deani*: $TL_{50} = 288.79, b = -9.41$.

TABLE 5 Review of total length statistics for all existing *E. stoutii* and *E. deani* fisheries data

Reference	Year	Location	Sublocation	Sample size	Average (mm)	Minimum (mm)	Maximum (mm)
<i>E. stoutii</i>							
Current study	2013–2016	British Columbia, CA	All locations	3904	428	107	754
Benson <i>et al.</i> , 2001	1999–2001	British Columbia, CA	Kirby Point, BC (PFMA 23–7)	552	387	208	597
Leask & Beamish, 1999	1988–1992	British Columbia, CA	Amphitrite Point, BC (PFMA 123–5)	407	431	174	594
			Kirby Point, BC (PFMA 23–7)	9631	401	186	631
			All locations	Not available	426	160	730
			Kirby Point, BC (PFMA 23–7)		415	160	720
			Amphitrite Point, BC (PFMA 123–5)		438	170	730
Johnson, 1994	1990–1991	California, USA	Monterey Submarine Canyon	6699	349	107	508
Barss, 1993	1988–1992	Oregon, USA		788	402	200	670
<i>E. deani</i>							
Current study	2013–2016	British Columbia, CA	All locations	303	432	256	598
Johnson, 1994	1990–1991	California, USA	Monterey Submarine Canyon	3311	349	213	543
Barss, 1993	1988–1992	Oregon, USA		635	345	200	520

species have a very low mean fecundity ranging from 14 to 20 based on eggs or postovulatory follicles per female.

4.1 | Review of reproductive terminology and sex determination in *E. stoutii* and *E. deani*

Previous hagfish reproductive studies lacked detailed reproductive terminology, therefore a short summary is provided here with up-to-date reproductive fisheries terminology (following Lowerre-Barbieri *et al.*, 2011). Reproductive studies suggest that *E. stoutii* and *E. deani* are iteroparous, *K*-selected species with an asynchronous spawning cycle (Barss, 1993; Benson *et al.*, 2001; Gorbman, 1990; Johnson, 1994; Leask & Beamish, 1999). Moreover, the maintained standing stock of oocytes through ovulation and recrudescence observed in our study and others suggests that both species are batch spawners with indeterminate lifetime fecundity (Barss, 1993; Gorbman, 1990; Johnson, 1994). Previous histology suggests that *E. stoutii* are dioecious, with females developing at smaller sizes than males (Gorbman, 1990; Johnson, 1994). Additionally, a low incidence (0.03%–0.23% of the population) of intersex individuals exists in mature *E. stoutii*, similar to previous studies (Barss, 1993; Johnson, 1994). Comparatively, a lack of histological data for *E. deani* prevents any determination of sex prior to maturity, however, based on macroscopic observations and sex ratios in this study and in Johnson (1994), *E. deani* are also dioecious. Johnson (1994) observed intersex *E. deani* in 0.24% of the population in California, while none were observed for this study in British Columbia.

4.2 | Length–weight relationships across fisheries

Despite increased interest in hagfish fisheries, there is a dearth of length and weight data for both *E. stoutii* and *E. deani*. Table 5 provides a review of all available total length data from current and previous *E. stoutii* and *E. deani* fisheries. Our study targeted areas that have been surveyed in earlier hagfish fisheries, such as Kirby Point (PFMA 23–7) and Amphitrite Point (PFMA 123–5). The mean length for the Kirby Point 1989–1992 *E. stoutii* fishery was larger ($415 \text{ mm} \pm 10.1 \text{ s.e.}$) than both the 2000–2001 fishery ($401 \text{ mm} \pm 2.24 \text{ s.e.}$) and the 2013–2016 fishery ($387 \text{ mm} \pm 3.19 \text{ s.e.}$) (Benson *et al.*, 2001; Leask & Beamish, 1999). Furthermore, the length range at Kirby Point has decreased since the 1989–1992 fishery from 160–720 to 208–597 mm in the current fishery (Benson *et al.*, 2001; Leask & Beamish, 1999). Similar traps were used across fisheries at Kirby Point, suggesting that selectivity should be similar, but perhaps both larger and smaller fish have migrated to a different location. However, we would not expect fishing to cause such narrowing given the lack of fishing for 10–15 year periods between fisheries. At Amphitrite Point the mean length for *E. stoutii* has decreased slightly from $438 \text{ mm} \pm 5.39 \text{ s.e.}$ in 1989–1992 to $431 \text{ mm} \pm 2.56 \text{ s.e.}$ in the 2013–2016 fishery (Leask & Beamish, 1999). However, it should be noted that the mean length for the total population of *E. stoutii* in the

current fishery ($428 \text{ mm} \pm 1.23 \text{ s.e.}$) is only slightly larger than location-specific means from the 1989–1992 and 2000–2001 fisheries, suggesting consistency in sizes across the subpopulations and perhaps movement between them.

In comparison to other fisheries, *E. stoutii* mean length in British Columbia was larger than that found in California ($336 \text{ mm} \pm 19.4 \text{ s.e.}$) and Oregon ($396 \text{ mm} \pm 3.52 \text{ s.e.}$) (Barss, 1993; Johnson, 1994). Although the minimum size captured was identical between British Columbia and California at 107 mm, the minimum found in Oregon was larger at 200 mm. Moreover, the maxima for Oregon (670 mm) and California (508 mm) were much smaller than that found in the British Columbia fisheries (754 mm). The differences in minima are likely the result of variable sized escape holes in each trap across fisheries (Barss, 1993; Johnson, 1994). The differences in maxima may be the result of a multitude of variables such as food resources, location, trap soak time and depth.

The mean length for *E. deani* ($432 \text{ mm} \pm 4.06 \text{ s.e.}$, range: 256–598 mm) in the British Columbia fishery was much larger than that of the Oregon fishery ($345 \text{ mm} \pm 4.19 \text{ s.e.}$, range: 200–520 mm) or the California fishery ($349 \text{ mm} \pm 20.6 \text{ s.e.}$, range: 213–543 mm) (Barss, 1993; Johnson, 1994). The differences in mean length can be explained by differing size-selective gear between studies. For instance Johnson (1994) used traps with 7 mm holes and Barss (1993) used traps with 8 mm holes, while most of the traps in our study had 16 mm holes. Therefore, our study may have missed a substantial portion of smaller hagfish due to the larger escape holes or perhaps we missed smaller *E. deani* habitats. *E. deani* were only caught as bycatch in the previous two British Columbia fisheries, resulting in no substantial data, therefore we are unable to make any direct comparisons to the current fishery.

Overall, the mean length for *E. stoutii* ($428 \text{ mm} \pm 1.23 \text{ s.e.}$) was slightly smaller than the mean length for *E. deani* ($432 \text{ mm} \pm 4.06 \text{ s.e.}$), but intraspecific differences were variable. Male *E. stoutii* were lighter-at-length than female *E. stoutii* (Table 3), and on average males were smaller than females (Table 2). This intraspecific variation could be the result of differing energy usage, with females gathering more food to maintain a standing stock of oocytes, or perhaps it is a consequence of protogynous hermaphroditism in *E. stoutii*. In contrast, female *E. deani* were significantly heavier-at-length than male *E. deani* (Table 4) and on average females were longer than males (Table 2). Sexual dimorphism of species length was observed to be more extreme in longer adult *E. deani* compared to *E. stoutii* (Figure 3). This extreme size difference in longer *E. deani* may be the result of an evolutionary shift in deep-sea fish towards larger females, which may provide males with a better chance to locate and fertilize a female via random encounter, therefore increasing the reproductive success of the population (Stein & Percy, 1982; Warner, 1984). Interspecific variation can be attributed to differing weight at length between species or differing metabolic rates between a shallower and deeper species (*E. stoutii* 16–966 m, *E. deani* 107–2743 m). Furthermore, interspecific variation in weight-at-length between *E. stoutii* and *E. deani* appears to be consistent across North American populations, therefore it is likely the result of habitat or metabolic differences (Barss, 1993; Johnson, 1994).

There is uncertainty in our size-based conclusions due to a variety of factors. The traps used in this study utilized 16 mm holes that may have allowed smaller hagfish to escape, thus the study may overestimate the minimum size of the first spawning female for *E. stoutii* and *E. deani* (320 and 454 mm, respectively). The samples acquired for this study were taken at random times throughout the year due to unforeseen problems during the sampling process, resulting in a dataset that could not be analysed for seasonal trends. Given the limited depth range of captured *E. deani* compared to the known depth range, there is uncertainty as to whether the collected samples fully captured a representation of the *E. deani* populations off the coast of Vancouver Island.

4.3 | Sex ratio and development curves

Both hagfish species had strongly female-dominated sex ratios at smaller lengths. However, in both species sex ratios were effectively 1:1 at mature sizes. *E. stoutii* exhibited a large female-to-male ratio at the smallest sizes (250 mm), but as size increased the sex ratio normalized to approximately 1:1. A similar progression in sex ratio in *E. stoutii* was noted in California (Johnson, 1994). Our results showed that the TL_{50} , or lengths at which sexual development began, for males and females were significantly different, with males starting development at larger lengths. Additionally, the progression towards an effective 1:1 sex ratio at larger sizes indicates an asynchronous growth rate between the two sexes. In conclusion, our results strongly corroborate those of Martini and Beulig (2013), suggesting that hagfish sexes have asynchronous growth rates.

In contrast, *E. deani* were female-dominated at both size extremes with a high ratio of 23:1 (female-to-male) at 500+ mm, but reached an effective 1:1 ratio around 400 mm. This pattern is similar to *E. stoutii*, but the extreme increase in sex ratio at larger sizes is likely the result of a low sample size ($n = 303$) and location-specific fishing pressure during the study (Gorbman & Dickhoff, 1978; Johnson, 1994). The development curves also showed a significant difference in TL_{50} between males and females, suggesting asynchronous growth rates between the sexes similar to *E. stoutii*. Further studies should be performed to better capture the trends observed in this study.

Limited numbers of intersex *E. stoutii* were identified at larger lengths. Overall, we found nine intersex adults, or a total incidence of 0.23% ranging in size from 388 to 634 mm. A similar low incidence (0.20%) of intersex adults was found in the Oregon fishery while a much lower (0.03%) incidence was found in California (Barss, 1993; Johnson, 1994). The reported incidence of intersex individuals in larger hagfish is also low in other species such as the broadgilled hagfish *Eptatretus cirrhatus* (Forster, 1801) (0.25%) (Martini & Beulig, 2013), *E. burgeri* (<0.1%) (Patzner, 1977) and *E. deani* (0.24%) (Johnson, 1994).

The Stage 0 development curves suggest that undifferentiated *E. deani* are significantly larger than *E. stoutii*. The lack of Stage 0 hagfish greater than 460 mm in *E. stoutii* and 398 mm in *E. deani* suggests

that hagfish larger than those sizes have likely all undergone sexual differentiation. The lack of larger Stage 0s corroborates the similar findings for *E. cirrhatus* made by Martini and Beulig (2013).

4.4 | Comparing fecundity between species and fisheries

Fecundity of *E. stoutii* and *E. deani* is represented by Stage 7 and 8 females based on egg counts or postovulatory follicle counts, respectively. The low fecundity of *E. stoutii* and *E. deani* found in British Columbia populations is consistent with that of other populations (Barss, 1993; Gorbman, 1990; Johnson, 1994). Furthermore, low fecundity is common amongst deep-sea species, which tend to be on the far *K*-selected end of the life history spectrum (Koslow *et al.*, 2000).

For both species, the number of eggs decreased from ~200 in Stage 1 to means of 18 and 20 in Stage 7 for *E. stoutii* and *E. deani*, respectively. The atresia of eggs with increasing egg length is likely due to the energetic cost to maintain yolk production in larger eggs (Gorbman, 1990; Johnson, 1994). In both species we found that the trade-off between egg size and egg number in larger females is not substantial.

4.5 | Conclusion

The reproductive characteristics of *E. stoutii* and *E. deani* create a variety of concerns for the implementation of a sustainable hagfish fishery. The total lengths at which 50% of the population exhibited development of ovaries, TL_{50} , were 190.71 and 276.16 mm for *E. stoutii* and *E. deani* females, respectively. Additionally, the sizes of first spawning *E. stoutii* and *E. deani* females were 320 and 454 mm, respectively. A low fecundity of approximately 20 eggs per spawning cycle for both *E. stoutii* and *E. deani*, and the possibility that asynchronous spawning hagfish may take up to 2–3 years per cycle is particularly a cause for concern when managing these fisheries (Patzner, 1978). *E. burgeri* in the north-west Pacific was found to require a minimum of 7 months between spawning cycles (Ota *et al.*, 2007). Our study provides a population profile that may be used to assist with trap characteristics, but for the fishery to be managed effectively a full stock assessment and data on lifespan and recruitment are necessary.

Other reproductive features such as skipped spawning, fisheries-induced evolution and the trade-off between survival, reproduction and growth should be accounted for when estimating the spawning stock biomass in fisheries (Lowerre-Barbieri *et al.*, 2011). Each of these can impact fecundity and spawning seasons, onset of sexual maturity, and reproductive lifespan (Lowerre-Barbieri *et al.*, 2011).

Hagfish fisheries continue to be of interest around the world, but without proper population and life history assessments historical fisheries have collapsed (Ellis *et al.*, 2015). This study collates the current and historical *E. stoutii* and *E. deani* reproductive data in an effort to provide decision makers with the necessary population information

to maintain a sustainable hagfish fishery. However, more data is needed to identify seasonal migrations and spawning cycles for both species of hagfish. We recommend that future research examines immunoreactive gonadotropic releasing hormone cycles in *E. stoutii* and *E. deani* alongside reproductive stages to identify these two data gaps (Powell *et al.* 2005). Furthermore, a methodology to age hagfish is still required; previous attempts at using micro-statoconia to age hagfish failed (Lee *et al.*, 2007). Instead, we recommend using mark-and-recapture methods similar to those of Nakamura (1994) to age and estimate growth rates or, if possible, raise hagfish in captivity. To continue to grow and prevent depletion of the British Columbia hagfish fishery and future fisheries, further research into both species' life histories and stock assessments is recommended.

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CONTRIBUTIONS

A.G.F. contributed to the idea, data generation, data analysis, manuscript preparation and funding. E.M.M. contributed to the data generation, data analysis and manuscript preparation. R.J.C. contributed to the data generation, data analysis and manuscript preparation. F.J. contributed to the idea, data generation, manuscript preparation and funding.

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