Maturity and fecundity of arrowtooth flounder, *Atheresthes stomias*, from the Gulf of Alaska

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Abstract.—Maturity and total fecundity are reported for arrowtooth flounder, *Atheresthes stomias*, from the Gulf of Alaska. Histological examination of both ovarian and testicular tissues revealed that the maturity state of both sexes could not be determined reliably by macroscopic assessment. Maturity for females ranged from the early perinucleus to the migratory nucleus stage; none of the fish had postovulatory follicles or hydrated oocytes, indicating all samples were collected prior to the spawning season. Condition factor (CF), gonadosomatic index (GSI), and hepatosomatic index (HSI) increased significantly in the later stages of female development. Eyed-side ovarian lobes were significantly heavier than blind-side lobes, but oocyte size and density (oocytes/gram) did not vary between lobes of the ovary or within the individual ovarian lobes. Total fecundity increased exponentially with length ($F=0.0429 \times L^{4.020}$) and linearly with somatic weight ($F=350.4 \times W - 138{,}482$), with estimates ranging from 250,000 to 2,340,000 oocytes. Histological analysis of tissues indicated that females reach 50% maturity (L_{50}) at 47 cm, males at 42 cm. This estimate of male L_{50} is probably high because no males in this study were ready to spawn, whereas a decrease in CF and an increase in GSI indicate body changes at a size of 30–35 cm.

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Arrowtooth flounder, *Atheresthes stomias*, is a large piscivorous flatfish with a range in U.S. waters from California (Allen and Smith, 1988) through the Gulf of Alaska, the Aleutian Islands, and the eastern Bering Sea. Although it is the most abundant groundfish in the Gulf of Alaska and is concentrated in relatively shallow waters (101–200 m, Martin and Clausen, 1995), arrowtooth flounder has experienced only limited commercial harvesting. Arrowtooth flounder flesh softens soon after capture, possibly owing to an enzyme released from a myxosporean parasite (Greene and Babbitt, 1990), greatly reducing its commercial value. Recent advances in food processing, however, have allowed production of marketable quality arrowtooth flounder fillets (Greene and Babbitt, 1990) and surimi (Wasson et al., 1992; Porter et al., 1993; Reppond et al., 1993), which may stimulate further development of a fishery.

Hunter and Macewicz (1985, a and b), Hunter et al. (1992), Morrison (1990), and others have carefully examined many of the assumptions of maturity and fecundity work and have provided histological details that made this project possible. Rickey's (1995) research off the Washington coast has shown that arrowtooth flounders are group-synchronous batch spawners, and researchers generally agree on a fall or winter spawning period (Pertseva-Ostroumova, 1961; Shuntov, 1970; Fargo et al., 1981; Rickey, 1995; Hosie and Barss[1]). Studies on arrowtooth flounder have calculated length at 50% maturity (L_{50}) for both males and females from different areas, but only by using macroscopic maturity assessment (Hosie and Barss[1] for Oregon; Fargo et al., 1981, for British Columbia, Canada; Rickey, 1995, for Washington). Rickey (1995) included histological analysis and descriptions of different maturity stages of ovarian tissues but did not use histological analysis for calculating L_{50} and did not examine males histologically.

No study has ever reported weight-based or length-based estimates of total fecundity (as defined in Hunter et al., 1992), nor have researchers examined possible differences in oocyte density or oocyte size between or within ovarian lobes, which could bias total fecundity estimation. Researchers also have not reported changes in condition factor, gonadosomatic index, and hepatosomatic index with maturity stage; such information could provide useful information on development.

In this study, I report on the maturity and total fecundity of arrowtooth flounder in the Gulf of Alaska.

[1] Hosie, M. J., and W. H. Barss. 1977. Age and length at maturity of arrowtooth flounder, *Atheresthes stomias*, in Oregon waters. Marine Field Laboratory, Oregon Dep. Fish and Wildlife, P.O. Box 5430, Charleston, OR 97420. Unpubl. manuscr., 9 p.

Histology is used to determine maturity, and detailed descriptions of maturity stages (adapted from Rickey, 1995) are provided for both males and females. Changes in condition factor, gonadosomatic index, and hepatosomatic index are reported for the different maturity stages. Another objective of this study is to assess methods for describing arrowtooth flounder maturity (macroscopic vs. histologic) and for determining total fecundity. The accuracy of macroscopic maturity staging is assessed by comparing histological staging with macroscopic staging for all fish sampled, since Rickey (1995) noted the possibility of misassigning maturity stages by macroscopic means. Comparisons are made between this study and results from arrowtooth flounder maturity studies conducted from the eastern Bering Sea to Oregon.

Materials and methods

Maturity

Arrowtooth flounder were collected from bottom trawl hauls aboard the NOAA vessel *Miller Freeman* (cruise 93-10) on Portlock Bank near the eastern end of Kodiak Island, Alaska. The hauls were made during daylight hours from 6 to 16 September 1993 in depths ranging from 66 to 165 m. Fork lengths (cm) were recorded, and somatic fish weights (less stomach contents) were measured to ±2 g on an electronic scale. The gonadal tissues were removed from the fish within a few hours of capture and preserved in a 10% formalin solution neutrally buffered with sodium acetate. Eyed-side and blind-side lobes of the ovary were dissected apart and stored separately. Livers were removed and weighed on the vessel (±2 gm). Specimens less than 20 cm in length were weighed on the vessel and preserved whole in a 10% formalin solution. Preserved fish were later dissected in the laboratory, and liver weights were measured to ±0.001 gm.

The author assigned a macroscopic maturity stage to males and females (Table 1) based on external appearance of gonads, according to descriptions adapted from Rickey (1995). (The author is an experienced groundfish biologist and prior to this project had examined the appearance of arrowtooth flounder gonadal tissue, through sex determination work, on thousands of arrowtooth flounders). Collections were initially limited to two fish per centimeter for each sex; additional females were collected over the length range where macroscopic maturity stages overlapped.

The accuracy of macroscopic stages assigned to whole ovaries was assessed by histological analysis of the ovarian sections. After being preserved in formalin, gonadal tissues were blotted dry and weighed on an electronic scale (±0.001 g) in the laboratory. Sections for histology were approximately 3 mm thick. For females, the sections were cut perpendicularly through the eyed-side ovarian lobe as near to the posterior end of the lobe in order for the section to fit on a slide. For males, the section was cut perpendicularly through a distal lobe of the testis, or through the entire organ, if small. Histological samples were dehydrated, infiltrated with paraffin, and embedded in blocks of paraffin. Sections were cut from the frozen blocks on a microtome at a thickness of 5 μ, heat-fixed to a glass slide, and stained with hematoxylin and eosin. Under a compound microscope, the ovary samples were assigned one of 11 maturity stages on the basis of the most advanced oocyte seen (Table 2). Atresia of large, yolked oocytes was noted, but not quantified.

The gonadosomatic index (GSI) was calculated to show differences in development of the gonads with respect to body weight:

$$GSI = (\textit{gonad weight} \times 100)/\textit{somatic weight}.$$

Condition factor (CF) was calculated as an overall measure of robustness of the fish:

$$CF = (\textit{somatic weight} \times 100)/\textit{length}^3.$$

A hepatosomatic index (HSI) was also calculated to estimate the relative size of the liver to body weight:

$$HSI = (\textit{liver weight} \times 100)/(\textit{liver} - \textit{free somatic weight}).$$

Although HSI is generally not included in maturity studies, the liver plays an important role in sexual maturity of both sexes. Oocyte yolk comes from the manufacture of vitellogenin in the liver (Wallace, 1985), and HSI may be a good predictor of male gonadal development, as was shown for Pacific cod (*Gadus macrocephalus*; Smith et al., 1990).

Significant differences between mean values of length, weight, GSI, CF, and HSI at the different maturity stages were tested with a one-way analysis of variance (ANOVA, α=0.05). The mean values were further tested with a Tukey test to reveal which means were significantly different. For purposes of these tests, fish in the late perinucleus stage (stage 4) were combined with those that had atresia of previously vitellogenic oocytes but that did not yet have mature oocytes beyond the late perinucleus stage (stage 11) in the current season.

Females were classified as mature if their oocytes had entered the cortical alveoli stage (stage 5; Rickey,

1995) or showed atresia of vitellogenic oocytes. Males whose testes contained either spermatids or spermatogonia were classified as mature. The proportion mature at each length was calculated by

$$P_x = 1/(1+e^{ax+b}),$$

where P_x is the proportion mature at a given length x, and a and b are constants. Size at fifty percent

Table 1

Macroscopic and histological descriptions of developmental stages used to classify male and female arrowtooth flounder, *Atheresthes stomias* (adapted from Rickey, 1995). Mean oocyte diameter in parentheses.

Macroscopic stage and description	Histological stage and description
Females	
A Immature Ovaries small and pink with no oocytes visible.	**1 Oogonia** Very small (2.5 μ) and staining dark purple.
	2 Chromatin nucleolus Nucleus large, one nucleolus, cytoplasm layer thin, both staining dark purple (25–75 μ).
	3 Early perinucleus Nuclear material granular, several nucleoli around perimeter of dark-purple-staining nucleus, lighter purple vacuoles (cortical alveoli) forming around nucleus and moving outward in dark-purple-staining cytoplasm. Cytoplasm growing in thickness (37.5–75 μ).
	4 Late perinucleus Material in nucleus often moving to one side leaving much of nucleus clear, becoming fibrous with lampbrush chromosomes. Many nucleoli evenly spaced around perimeter of nucleus, cytoplasm staining less purple, ring of light purple vacuoles (cortical alveoli) still moving outward, sometimes dividing cytoplasm into two zones (150–162.5 μ).
B Developing Ovaries white to yellow, firm, oocytes visible.	**5 Cortical alveoli** Some lampbrush chromosomes still present, but nuclear material dispersing and nucleus turning light purple, collapsing inward. Vacuoles in cytoplasm (cortical alveoli) near cell wall, clear, one to three layers thick, cytoplasm much lighter purple (325–375 μ).
	6 Early vitellogenesis Nucleus light purple to pink in color, collapsing inward. Cortical alveoli increasing in diameter, on the outer margin of the cell wall. First yolk globules (pink) in cytoplasm, generally closer to the center of the oocyte than the cortical alveoli, sometimes in spokelike configuration. Cytoplasm less than 50% filled with yolk (375–425 μ). Yolk globules 7.5 μ.
	7 Late vitellogenesis Pink-staining yolk globules occupy 50–100% of the cytoplasm. Oocyte diameter 500 μ and yolk globules expanding to 12.5 μ.
	8 Migratory nucleus Yolk globules coalescing and increasing in diameter (25–37.5 μ), nucleus sometimes visible as a crescent shape, cortical alveoli no longer visible near edge of cytoplasm, oocyte large (625–725 μ).
C Gravid Hydrated oocytes present.	**9 Hydrated** Nucleus no longer visible, yolk coalescing and filling cytoplasm as continuous material.
D Ripe and running Oocytes extruded with light pressure.	**10 Spawning** Postovulatory follicles present.
E Spent or resting Ovaries bloodshot, flaccid, and dark red to purple.	**11 Atretic** Atresia of large, previously yolked oocytes, no stages beyond late perinucleus present.
Males	
Immature Testes small and threadlike, pink.	Spermatogonia, primary or secondary. Spermatocytes present.
Mature Testes enlarged, folded, brown or white in color.	Spermatids or spermatogonia present.

maturity was estimated by substituting 0.5 for P_x. The constants a and b were estimated through iterative, nonlinear regression by the StatGraphics Plus (version 6.1 for DOS) program.

Total fecundity

Weighed samples (±0.0001 g) of whole oocytes from the most mature females (stage 8, Table 1) were counted and measured under a dissecting scope with Optimas image analysis software, and numbers were expanded to the whole ovary by using the gravimetric method. Only yolked oocytes, which were opaque, appeared as dark images on the computer monitor with back lighting. Immature oocytes, which were without yolk, were translucent and not discernible on the screen. The Optimas software automatically measured the area of the oocytes by delimiting the circumference, from which the diameters were derived. Individual measurements of oocyte diameters were normalized with a cubic transform (diameter^3) because the distributions were skewed to the left (negatively) (Zar, 1984). Possible differences of oocyte density (oocytes/gram) and mean oocyte diameters between ovary lobes were tested with paired t-tests. Two-way ANOVA's were used in testing for differences in oocyte density and diameter among anterior, medial, and posterior positions within the same ovarian lobe.

Possible differences between the weights of the eyed-side and blind-side ovarian lobes were tested with a paired t-test, and the relation between the lobe weights was described with a linear regression.

Results

Maturity

Gonadal tissue samples were collected from a total of 176 female and 58 male arrowtooth flounder. Damage to the ovarian lobes, or other tissues, and loss of ovarian tissue during dissection and storage were common in the larger, more mature females. This damage or loss of tissue resulted in a lower sample size (n=158) for measurements such as GSI and HSI. In addition, the ovarian lobes of three fish were so small that the lobes were not separated during dis-

Table 2

Histological analysis of macroscopic maturity stages.

Macroscopic maturity stage		Microscopic maturity stage	Count	Percent	Number with atresia	Percent per stage with atresia
Stage A (Immature)		3	11	14.5	0	0.0
		4	51	67.1	0	0.0
		5	6	7.9	5	83.3
		11	8	10.5	8	100.0
	Subtotal		76		13	17.1
Stage B (Developing)		5	1	2.0	1	100.0
		6	3	6.0	1	33.3
		7	31	62.0	6	19.4
		8	15	30.0	0	0.0
	Subtotal		50		8	16.0
Stage E (Spent or resting)		4	2	4.4	0	0.0
		5	13	28.9	6	46.2
		6	11	24.4	2	18.2
		7	11	24.4	1	9.1
		8	4	8.9	0	0.0
		11	4	8.9	4	100.0
	Subtotal		45		13	28.9
Stage A or E (Developing, or spent or resting)		7	3	100.0	1	33.3
Unidentified		4	1	50.0	0	0.0
		6	1	50.0	0	0.0
	Total		176			

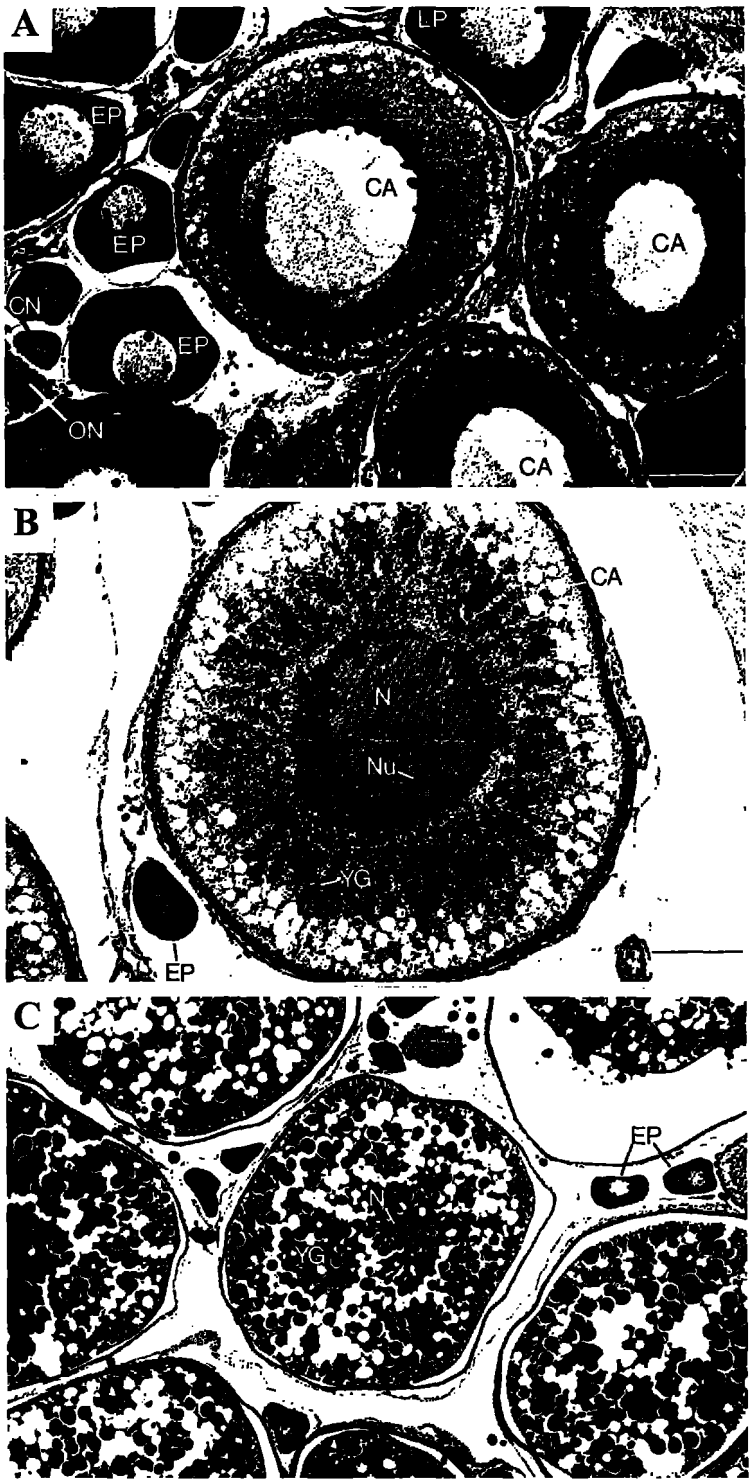

Figure 1

Oocytes in arrowtooth flounder, *Atheresthes stomias*, at different stages of development. (**A**) Oocytes of a 57-cm-FL female at the cortical alveoli stage as well as less mature oocytes. (**B**) Oocyte of a 66-cm-FL female at the early vitellogenesis stage. (**C**) Oocytes of a 82- cm- FL female at the migratory nucleus stage. Bar = 0.1 mm; ON = oogonial nest; CN = chromatin nucleolus; EP = early perinucleus; LP = late perinucleus; CA = either cortical alveoli stage oocytes or cortical alveoli structures (with arrow); N = nucleus; Nu = nucleolus; YG = yolk globule.

section, making them unavailable for the lobe-weight comparison.

In the five-tier macroscopic staging scale for females (Table 1), fish were classified only as "immature" (stage A), "developing" (stage B), or "spent or resting" (stage E). No females were found with hydrated oocytes ("gravid," stage C) or that were "ripe and running" (stage D). The two-tier macroscopic maturity scale for males was abandoned early in the study because of lack of confidence in assigning stages—nearly all males appeared to be "immature."

Histological analysis revealed that all females were in stages 3–8 and stage 11 of oocyte development (from early perinucleus to the migratory nucleus stage, and the atretic stage, Table 2). The lack of hydrated oocytes or postovulatory follicles in any of the ovaries indicated that these samples were collected prior to the spawning season. None of the males were ready to spawn but in some specimens, spermatids and spermatozoa were present, indicating that the males were preparing to spawn.

Figure 1 shows photographs of histological sections taken from females at three different stages of maturity. The progression of size increase of oocytes from the oogonial nest stage through the cortical alveoli stage can be seen in Figure 1A. Some specimens in early vitellogenesis, such as shown in Figure 1B, had yolk globules arranged in a spokelike configuration in the cytoplasm. The increase in oocyte size in the migratory nucleus stage, in comparison with oocyte size in the early perinucleus stage, and the increase in size of yolk globules are shown in Figure 1C.

The categories of maturity stages, based on macroscopic examination, are shown in Table 2. Most of the females classified macroscopically as "immature" (stage A, n=76, length range 14–64 cm) were in the early or late perinucleus stage (n=62, 81.6%). A total of 18.4% (14 of 76) of these females classified macroscopically as "immature" were either in the process of maturing (cortical alveoli stage) or showed evidence that they had been mature the previous season (atresia of previously yolked oocytes).

Table 3

Tukey test results showing significant differences (<) and equalities (___) between arrowtooth flounder (*Atheresthes stomias*) females in different stages of development, as determined by histology (EP = early perinucleus, LP = late perinucleus, CA = cortical alveoli, EV = early vitellogenesis, LV = late vitellogenesis, and MN = migratory nucleus).

Variable	Histological stage											
Length	EP	<	LP	<	CA		EV		LV			MN
Weight	EP		LP	<	CA		EV		LV			MN
Condition factor	EP		EV		CA		LP	<	LV	<		MN
Gonadosomatic index	EP		LP	<	CA	<	EV	<	LV	<		MN
Hepatosomatic index	EP		LP		CA		EV	<	LV	<		MN

Histological examination of females classified macroscopically as "developing" (stage B, n=50, length range 47– 83 cm) revealed that they were in vitellogenesis and thus correctly classified. Most of the females had oocytes that were in some phase of yolk acquisition (early vitellogenesis to migratory nucleus stages), and only 2.0% were in the cortical alveoli stage. Sixteen percent of these fish had atretic oocytes.

Most of the females categorized as "spent or resting" (stage E, n=45, length range 49–83 cm) were in some stage of vitellogenesis (n=39, 86.7%) and should have been classified as "developing." The percentage of fish with atresia declined with increasing maturity stage, from 46.2% in the cortical alveoli stage to 0.0% in the migratory nucleus stage. Overall, 28.9% of these "spent or resting" fish had atresia, the highest rate of all three macroscopic stages. Only 4 fish out of 45 were correctly determined to be "spent or resting" (late perinucleus with atresia).

Three females were assigned a combined macroscopic classification of "developing" or "spent or resting." In two of the fish the anterior portion of the ovarian lobes appeared to be "developing" whereas the posterior ends appeared to be "spent or resting." In the third fish the blind-side ovarian lobe appeared to be "developing" whereas the eyed-side appeared to be "spent or resting." Histological examination demonstrated that all three of these fish were in late vitellogenesis; even samples taken from the portions of the ovary that were macroscopically classified as "spent or resting" demonstrated that the fish were in late vitellogenesis.

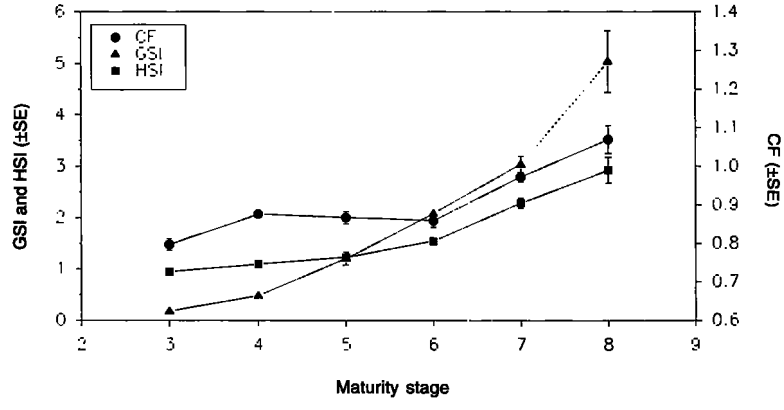

Figure 2

Mean values (±SE) of condition factor (CF), gonadosomatic index (GSI), and hepatosomatic index (HSI) for the stages of female arrowtooth flounder maturity, as determined by histology.

I failed to classify two females macroscopically because of size-based bias. A large fish (66 cm), in which the ovary appeared to be "immature," was actually in the early vitellogenesis stage. A small fish (20 cm), in which the ovary appeared to be "developing," was in the late perinucleus stage.

Mean values of CF, HSI, and GSI of the histological stages for females are presented in Figure 2, with significant differences shown in Table 3. Condition factors of the first four stages were not significantly different, but CF was higher in the late vitellogenesis stage and highest in the migratory nucleus stage (Single-factor ANOVA; df=5, F=25.9, P<0.001; Tukey tests). The small decline in mean CF values between

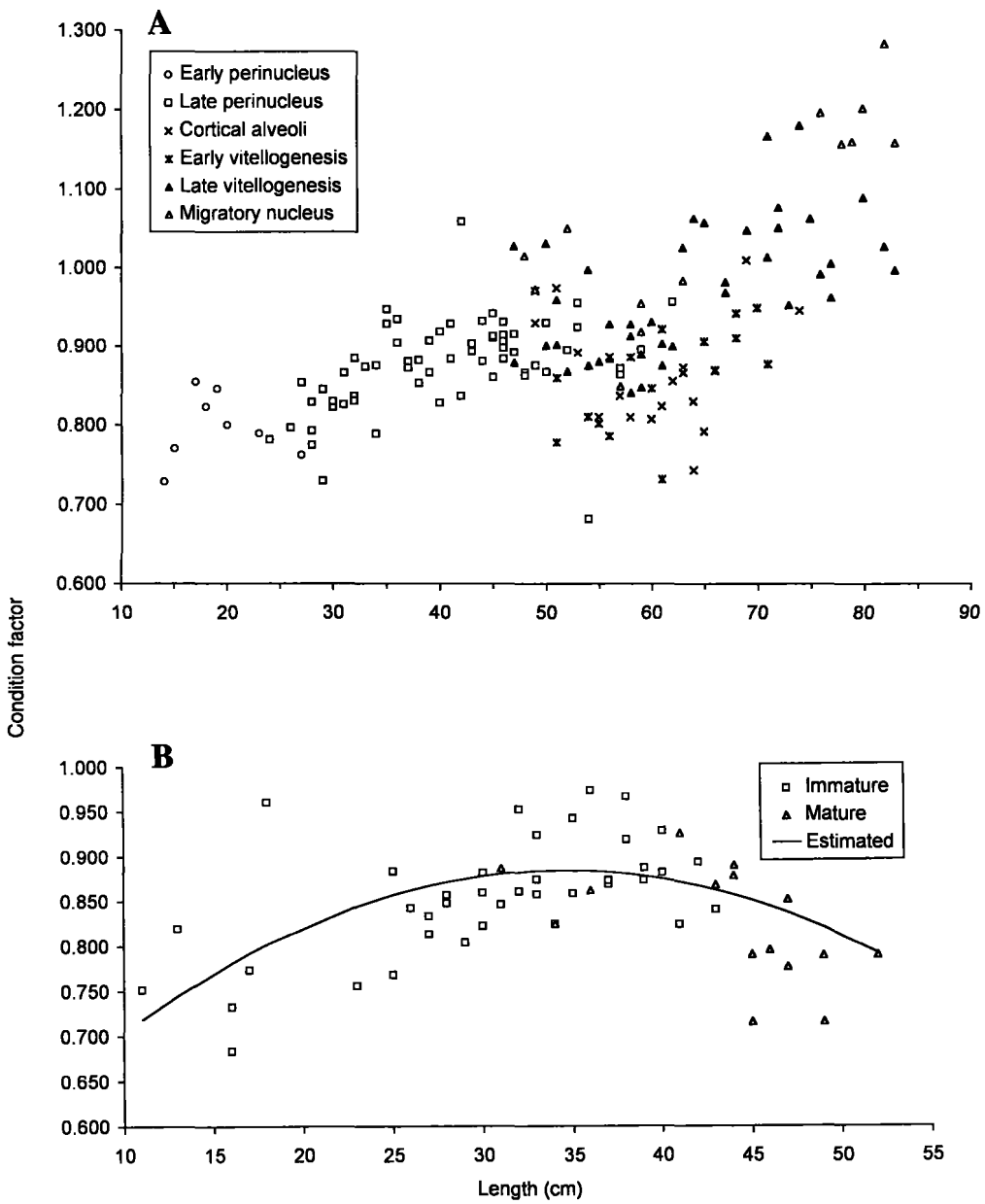

Figure 3

Condition factor by length and maturity stage for female arrowtooth flounder (**A**) and for male arrowtooth flounder (**B**).

stages 4, 5, and 6 was not significant (Fig. 2), but there was a similar decline in CF in fish between 50 and 60 cm in length (Fig. 3A). Condition factor of immature males (0.854) was not significantly different (t-test; df=56, $P>0.05$) from that for mature males (0.822); however, the regression fit of the relationship (df=55, F=4680, P=<0.001, r^2=0.31) shows that CF increased with length for small fish, reached a peak at 34.5 cm, and declined in larger fish (Fig. 3B).

Hepatosomatic index varied significantly among female maturity groups (single-factor ANOVA; df=5, F=59.0, $P<0.001$) and was significantly greater in both the late vitellogenesis stage (2.281) and migratory nucleus stage (2.921). In general, HSI increased

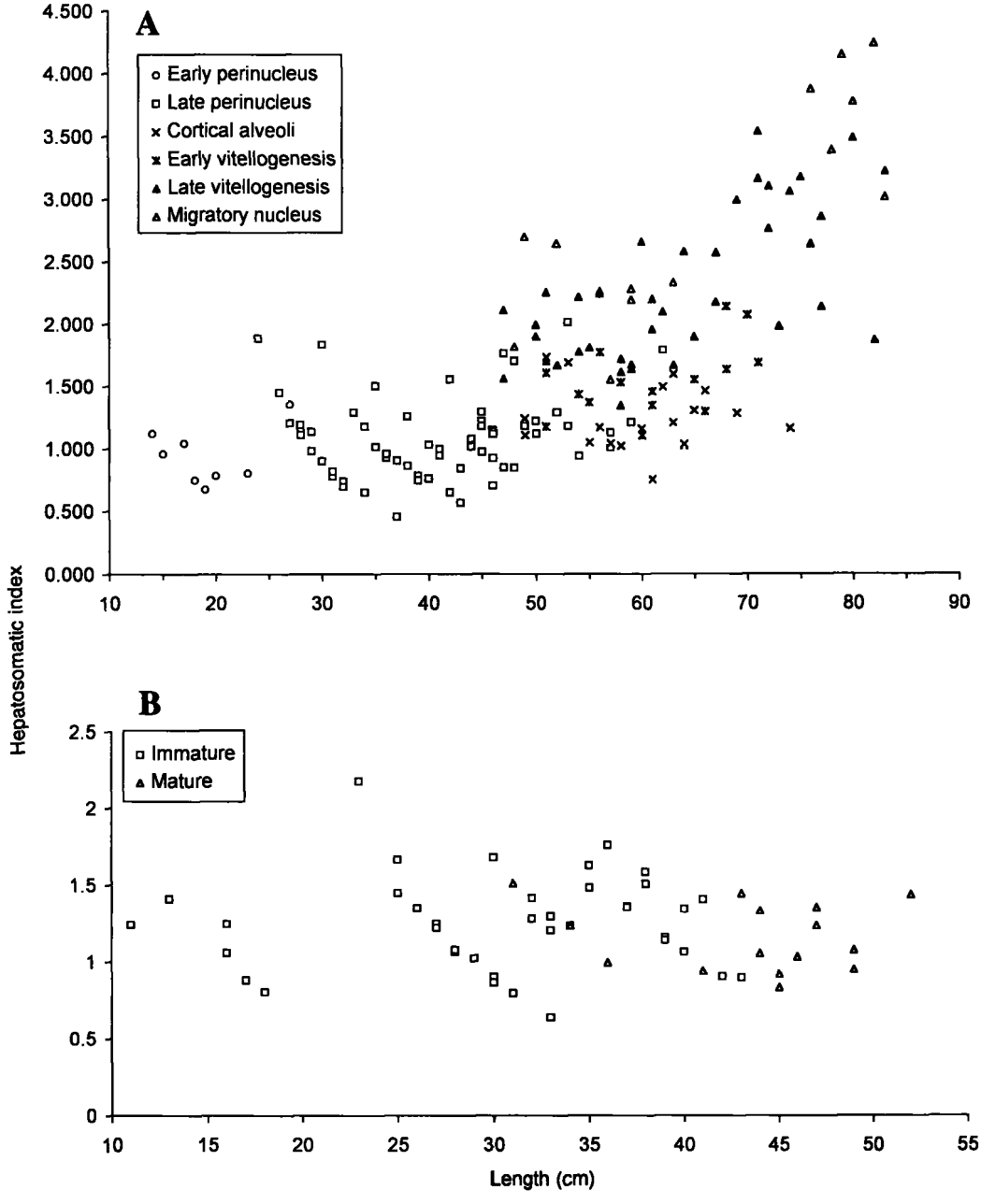

Figure 4

Hepatosomatic index by length and maturity stage for female arrowtooth flounder (**A**) and for male arrowtooth flounder (**B**).

with increasing female length (Fig. 4A). There was no difference in HSI between mature and immature males (unpaired *t*-test; df=27, $P>0.05$), and no trends in the data (Fig. 4B).

Gonadosomatic index varied significantly among female maturity groups (single-factor ANOVA; df=5, $F=91.9$, $P<0.001$). The Tukey test revealed that despite more than doubling, the GSI did not change significantly between the early and late perinucleus stages (Table 3). After that, the GSI was significantly greater in each succeeding stage of maturity (Table 3). Figure 5A shows that GSI remained low until fish reached lengths over 45 cm. GSI was significantly greater in mature males than in immature males

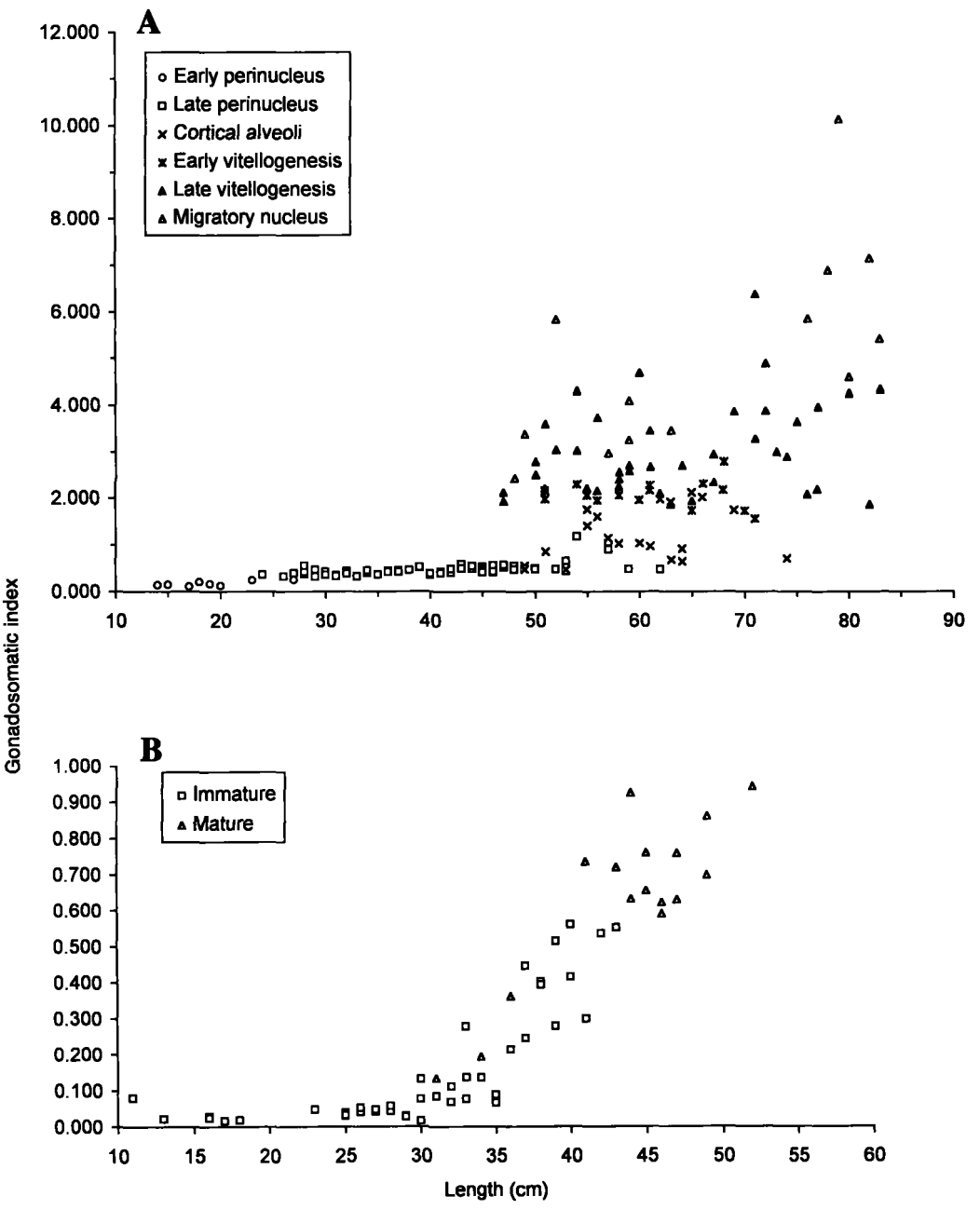

Figure 5

Gonadosomatic index by length and maturity stage for female arrowtooth flounder (**A**) and for male arrowtooth flounder (**B**).

(unpaired t-test; df=27, $P<0.001$); the increase began between 30 and 35 cm in length (Fig. 5B).

According to histological analysis, L_{50} for females occurred at 46.9 cm (df=174, F=897, r^2=0.76, Fig. 6A) and at 42.2 cm (df=56, F=69, r^2=0.60, Fig. 6B) for males. According to macroscopic staging, L_{50} for females occurred at 49.9 cm (df=172, F=748, r^2=0.76, Fig. 6A).

Total fecundity

In general, the eyed-side ovary lobes were heavier than the blind-side lobes (paired t-test; df=154, t=2.663, P=0.009). Linear regression analysis (df=153, F=2365, $P<0.001$, r^2=0.94) described the relation between the weight of ovarian lobes as

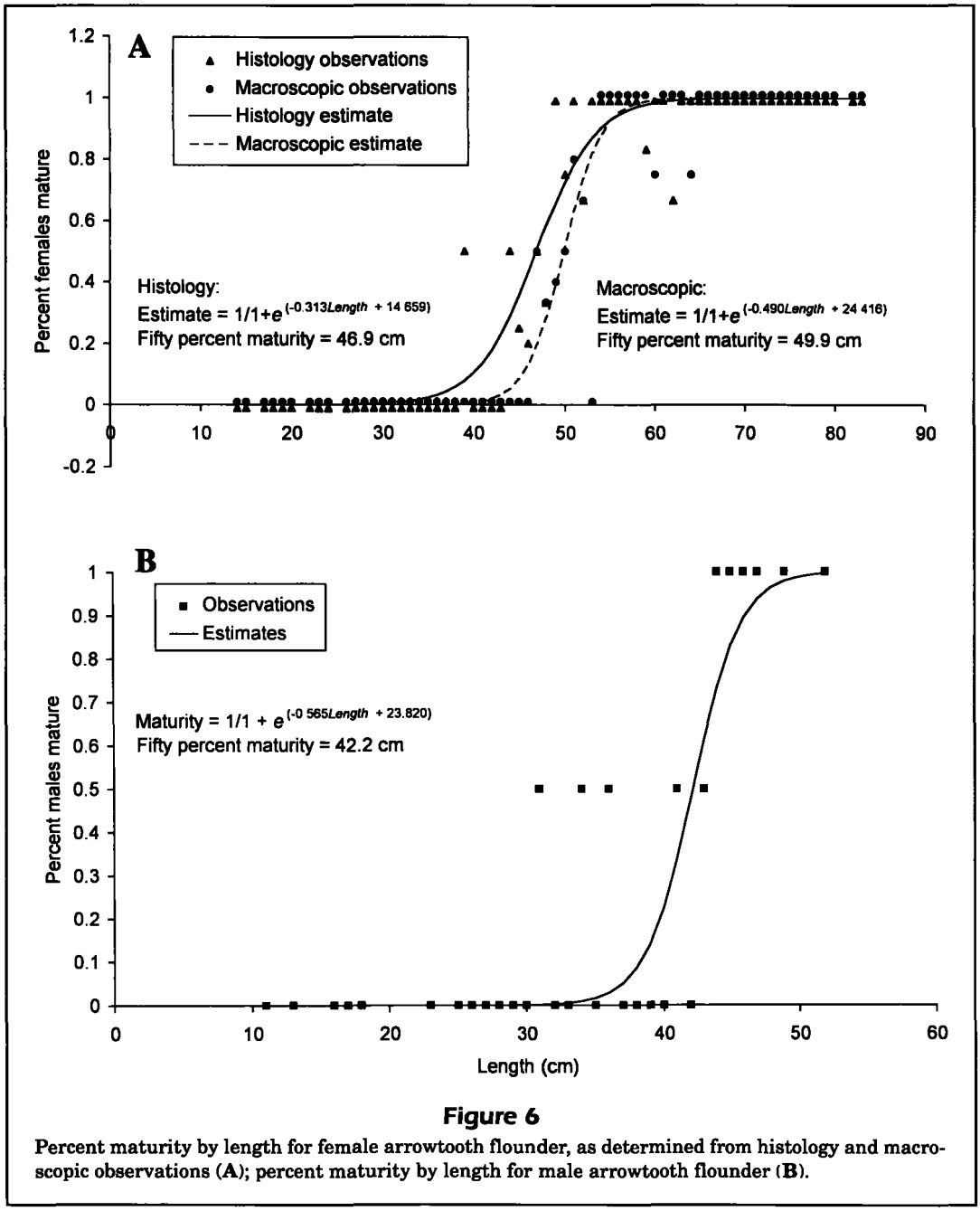

Figure 6

Percent maturity by length for female arrowtooth flounder, as determined from histology and macroscopic observations (**A**); percent maturity by length for male arrowtooth flounder (**B**).

$$W_B = 0.843(W_E) + 1.398,$$

where W_B = the weight of the blind-side lobe; and
W_E = the weight of the eyed-side ovary lobe.

All the frequency distributions of the diameter of maturing oocytes were unimodal and had a long tail on the left. A cubic transform (diameter^3) normalized the distributions. The transformed values of the mean diameter of oocytes did not vary significantly among positions (anterior, medial, posterior) within the same ovarian lobe (two-factor ANOVA, df=2, $P>0.05$) or between lobes (paired t-test, df=9, $P>0.05$). Density of oocytes (count of oocytes per gram of ovarian tissue) also did not vary significantly between positions within ovarian lobes (two-factor ANOVA, df=2, $P>0.05$) or among ovarian lobes (paired t-test, df=9, $P>0.05$). Thus samples for total fecundity were combined from the different positions and ovarian lobes.

Total fecundity was significantly related to fish length (df=11, $F=125.7$, $P<0.001$, $r^2=0.92$) by the equation

$$\ln(F) = 4.020 \ln(L) - 3.149,$$

from which was derived

$$F = 0.0429 (L)^{4.020},$$

where F = total fecundity; and
L = fork length in centimeters (Fig. 7A).

Length-based total fecundity estimates ranged from 246,000 (48 cm) to 2,224,000 (83 cm) oocytes. Total fecundity was also significantly related to somatic fish weight (df=11, F=264.7, P<0.001, r^2=0.96):

$$F = 350.4(W) - 138{,}482,$$

where F = total fecundity; and
W = somatic weight in grams (Fig. 7B).

Weight-based total fecundity estimates ranged from 255,000 (1,122 g) to 2,339,000 (7,070 g) oocytes.

Discussion

Maturity

Histological analyses demonstrated that the assignment of macroscopic maturity stages was not always reliable. Although it was confirmed through histol-

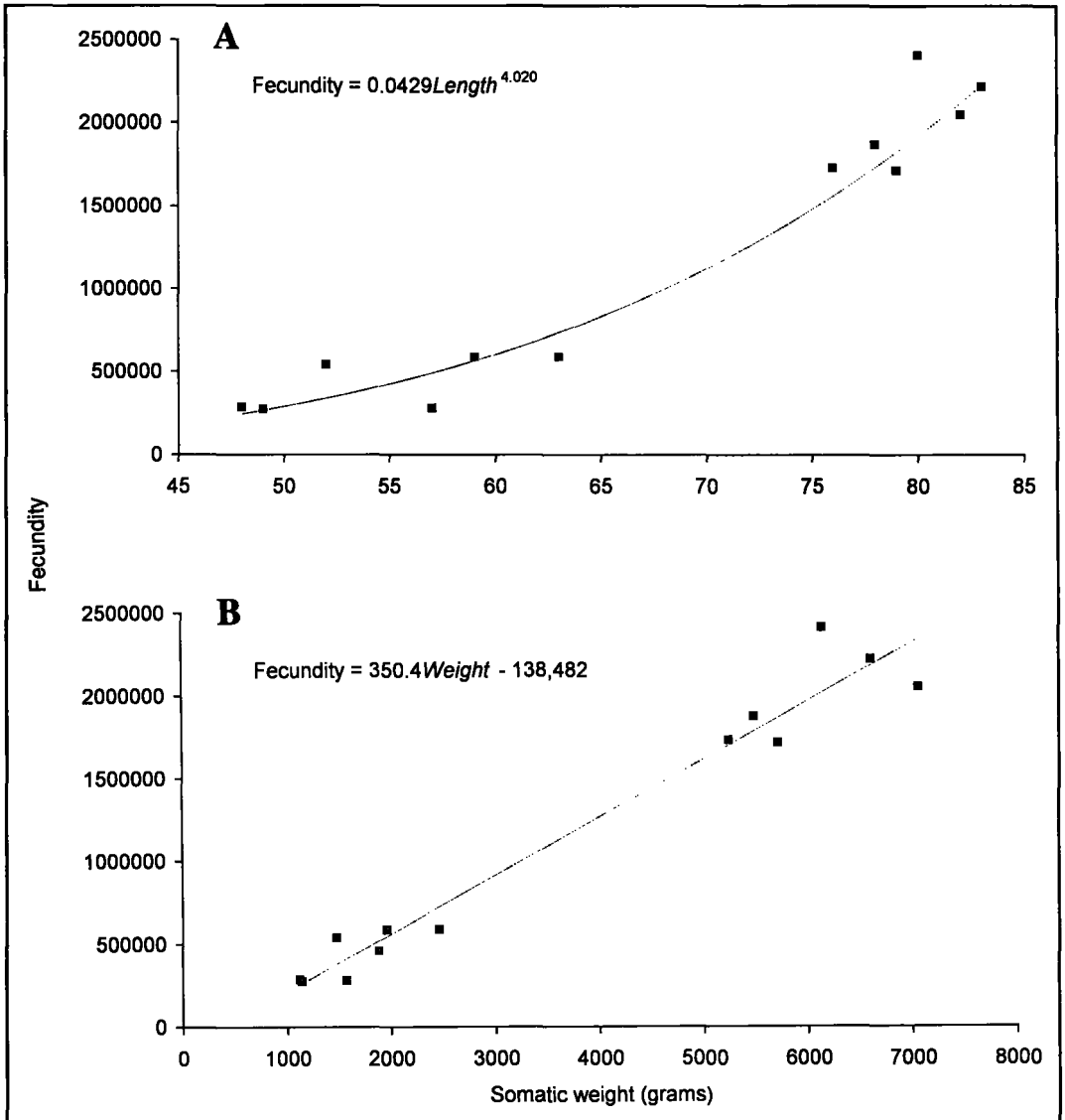

Figure 7

Total fecundity by length for female arrowtooth flounder (**A**); total fecundity by weight for female arrowtooth flounder (**B**).

ogy that none of the "immature" females had begun acquiring yolk, some had begun the process of maturing oocytes, and several had atresia of large, previously yolked oocytes, indicating that these females had probably spawned during the previous year. All females classified macroscopically as "developing" had maturing oocytes to spawn, most of them in the later stages of vitellogenesis. Few of the fish classified as "spent or resting" were actually resting: most were in vitellogenesis and should have been classified as "developing." In addition, the author was unable to assign a single maturity stage to ovaries with a mixed appearance and to assign a stage for ovaries from some females.

The several females correctly classified as "spent or resting" deserve some discussion. These fish had oocytes only as advanced as the late perinucleus stage and had degenerating oocytes present, which had previously been yolked. These fish were classified as mature because they had previously contained yolked oocytes, but they were unable to spawn soon, despite the upcoming spawning season, and they did not show signs of recent spawning. Hunter and Macewicz (1985, a and b) have reported histological details on creation and resorption of atretic oocytes and postovulatory follicles in the northern anchovy, *Engraulis mordax*. Their results have shown that the relatively rapid resorption of yolked oocytes (after 23 days of starvation; Hunter and Macewicz, 1985a) and postovulatory follicles (after 3–4 days; Hunter and Macewicz, 1985b) seems to contradict my assertion that atretic vitellogenic oocytes from the previous spawning season were still being resorbed in arrowtooth flounder just prior to the spawning season. A comparison of the reproductive cycle of arrowtooth flounder (which is a determinate-spawning benthic flatfish, dwelling in relatively cold northern waters) with that of the northern anchovy (an indeterminate-spawning pelagic roundfish, occupying much warmer southern waters) is not without merit. It is important to note, however, that significant differences could occur in the rate in which these species cycle between reproductive stages. Hunter and Macewicz (1985b, p. 87) caution that "the duration of postovulatory stages must be newly estimated for each species, and an assumption that the duration of these stages in a new species is similar to the northern anchovy is highly speculative." Perhaps further sampling of this arrowtooth population closer to or during the spawning season could have provided more information on the further development of these "spent or resting" fish.

Macroscopic classification was not successfully applied to the males. Only by histologic work was male maturity confidently assessed. Rickey (1995, p. 130), in her nearly year-round sampling of arrowtooth flounder, also had difficulty with assigning macroscopic maturity stages to males, stating that males ". . . did not show grossly apparent developmental changes over time . . . no spawning males were seen."

In the present study, females were classified as mature if they had oocytes as advanced as the cortical alveoli stage (Rickey, 1995), or showed atresia of previously vitellogenic oocytes. Significant differences in GSI and HSI occurred between the late perinucleus and cortical alveoli stages, and fish at the cortical alveoli stage were also longer and heavier. The insignificant but noticeable decline in condition factor in the cortical alveoli and early vitellogenic stages also indicates an emphasis in gonad growth over somatic growth. Rickey (1995), in examining Washington coast arrowtooth flounder collected during the spawning season, found that all of the fish had either matured beyond the cortical alveoli stage or had not yet matured that far. This finding supports the idea that fish in the cortical alveoli stage prior to the spawning season will mature during the same spawning season. Histology is regarded as the best method available to assess maturity (Hunter et al., 1992; West, 1990), but Hunter et al. (1992) concluded that even with the broadest criteria defining maturity, some spent fish are not identifiable as postspawners when sampling is done after spawning has commenced.

Hosie and Barss[1] determined that Oregon arrowtooth flounder males reach L_{50} at 29 cm and females reach L_{50} at 44 cm. Rickey (1995) determined that Washington males reach L_{50} at 28.0 cm and females reach L_{50} at 36.8 cm. Fargo et al. (1981) determined that British Columbia males reach L_{50} at 31 cm and females reach L_{50} at 37 cm. All the above studies determined maturity by using macroscopic classification of arrowtooth flounder gonads.

It was thought that macroscopic observations of maturity would result in a lower L_{50}, as all the other arrowtooth flounder maturity studies showed, but instead the L_{50} based on macroscopic observations was 3 cm higher. This finding is the opposite of that found in a study by Walsh and Bowering (1981) who compared macroscopic and histological staging of Greenland halibut (*Reinhardtius hippoglossoides*) ovaries and demonstrated that L_{50} was 3 cm higher in the maturity ogive derived from histological work.

Time of sampling in relation to the spawning season may have been a factor in determining female L_{50}. Hunter et al. (1992) showed that estimates of L_{50} for female Dover sole (*Microstomus pacificus*) taken during the spawning season were higher than estimates of L_{50} for female Dover sole taken just prior to the spawning season, whereas Rickey (1995) found

the opposite for arrowtooth flounder; her highest L_{50} values were derived from fish taken prior to spawning and her lowest value was derived from fish taken during the spawning season. The Oregon study occurred from September through June (Hosie and Barss[1]), the Washington study occurred nearly year-round (Rickey, 1995), and the British Columbia study occurred only in June (Fargo et al., 1981).

Histological examination revealed that most mature males in this study had only a small portion of their testes filled with spermatozoa; and thus they were not yet ready to spawn. It is likely that, as these large males continued to develop sexually during the season, other smaller males would have become sexually mature, thus lowering the male L_{50}. The male L_{50} value of 42.2 cm determined in this study should be viewed as a high estimate. Male GSI values started increasing at around 30 cm in length, and CF values began declining at 34.5 cm; both trends indicate a transition from somatic growth to gonad maturation at a much smaller size than that for the L_{50} reported here.

In general, the largest females were the most mature in this study, indicating that they might spawn the earliest. The high values of CF, GSI, and HSI for these largest, most mature females also show that these fish are best able to support the burden of spawning. The noticeable but insignificant drop in CF for females in the cortical alveoli and early vitellogenesis stages (Fig. 2), at around 50–60 cm in length (Fig. 3A), if real, can be explained by two possibilities. Either these mid-size fish are affected more by vitellogenesis than are the larger fish, or all females suffer losses in CF in the early stages of vitellogenesis and recover during later maturity stages. Gonadosomatic index was also highest in the largest males; thus they appear to mature earlier in the season than smaller males. The largest, most mature males had decreasing CF values that indicated an impact of maturing testes on body composition.

The spawning habits of arrowtooth flounder are not well known. Shuntov (1970) was unable to determine accurate spawning times for arrowtooth flounder in the eastern Bering Sea but nonetheless stated that they were close to those of Kamchatka flounder (*Atheresthes evermanni*), which were found in spawning condition in January and March. Fargo et al. (1981), using macroscopic observations of gonads collected in June from Hecate Strait, concluded that spawning takes place prior to June, probably in spring months. Rickey (1995) showed that spawning occurred off the Washington coast from September through December, and possibly as late as February. Hosie and Barss[1] reported a December–March spawning period for arrowtooth flounder off the Oregon coast. Pertseva-Ostroumova (1961) reported arrowtooth flounder spawning in the Bering Sea from January through March. The results presented here, that a spawning season begins after September, are supported by all of the studies mentioned above.

Total fecundity

Both macroscopic and microscopic observations showed that this study was made prior to the spawning season: none of the females were "ripe and running," had hydrated oocytes, or had postovulatory follicles, and none of the males were ready to spawn. Thus no bias due to loss of oocytes was expected.

Total fecundity estimates for arrowtooth flounder had not been previously reported in the literature. The only other member of the genus, Kamchatka flounder, has an estimated fecundity range of 130,000–500,000 oocytes (Pertseva-Ostroumova, 1961), which is much lower than what is reported here for arrowtooth flounder. As with many other flatfish species, arrowtooth flounder total fecundity increases linearly with fish weight and in a curvilinear fashion with length (Hempel, 1979). The largest arrowtooth flounder in this study had about 10 times as many oocytes as the smallest fish for which total fecundity was estimated. The unimodal frequency distribution of maturing oocyte diameters is supported by Rickey's (1995) determination that arrowtooth flounder is a group-synchronous spawner.

The significant difference in weight between the eyed-side and blind-side lobes has not been previously reported for arrowtooth flounder but has been reported for sole (*Solea solea*, Witthames and Walker, 1995). Nichol[2] found that blind-side lobes were significantly larger than eyed-side lobes in yellowfin sole (*Pleuronectes asper*). This finding suggests that in flatfish species both ovarian lobes should be considered when calculating GSI or total fecundity. Because there were no significant differences in mean oocyte diameter or mean oocyte density within or between ovarian lobes, total fecundity samples may be taken from any portion of the ovary. In his review paper, West (1990) mentioned that typically there is no difference in oocyte size or diameter frequency distribution between ovarian lobes, but differences along the length of the ovary and in cross sections do occur in some species. Hunter et al. (1992) found no differences in oocyte density between ovarian lobes, along the length of a lobe, or by cross section of a lobe in Dover sole.

[2] Nichol, D. G. 1995. Resource Assessment and Conservation Engineering Div., Alaska Fish. Sci. Center, 7600 Sand Point Way NE, Seattle, WA 98115. Personal commun.

Although this study provides the first information on total fecundity of arrowtooth flounders, subsampling of ovarian tissue for total fecundity, histology of males, comparison of macroscopic and histological methods, and relation of ancillary body measures such as CF, GSI, and HSI, there is still much that is unknown about this species. The lag of male maturity in comparison to that of females in this study, and the lack of spawning males in Rickey's (1995) study are parts of an interesting riddle. Possible seasonal migrations proposed by Shuntov (1970) and Rickey (1995) need to be thoroughly documented, as well as possible spawning migrations. Differences in size at maturity found in this study, compared with those found in studies conducted in southern waters, need to be explored. A study, in which collections are made at preselected depths and in which age and histological data are collected at regular intervals throughout a year, would answer many questions.

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