Annual fecundity, batch fecundity, and oocyte atresia of Atka mackerel (*Pleurogrammus monopterygius*) in Alaskan waters

Susanne F. McDermott (contact author)[1]
Katherine P. Maslenikov[2]
Donald R. Gunderson[2]

Email address for S F. McDermott: Susanne.McDermott@noaa.gov

[1] National Marine Fisheries Service
Alaska Fisheries Science Center
7600 Sand Point Way NE
Seattle, Washington 98115

[2] University of Washington
School of Aquatic and Fisheries Sciences
Box 355020
Seattle, Washington 98195

Abstract—Annual potential fecundity, batch fecundity, and oocyte atresia were estimated for Atka mackerel (*Pleurogrammus monopterygius*) collected in Alaskan waters during 1993–94. Atka mackerel were assumed to be determinate spawners on the basis of decreasing fecundity after batch spawning events. Histological examination of the ovaries indicated that oocytes in the vitellogenic stage and higher had been spawned in the current spawning season. For an average female of 40 cm, potential annual fecundity was estimated to be 41,994 eggs, average batch size (i.e., batch fecundity) was estimated to be 6689 eggs, and there were 6.13 batches per spawning season. Atresia was estimated by examining postspawning specimens and was found to be substantial. The average amount of atresia for a 40-cm fish was estimated to be 11,329 eggs, resulting in an estimated realized fecundity of only 30,664 eggs and 4.64 batches of eggs per spawning season.

Manuscript submitted 22 April 2004 to the Scientific Editor's Office.

Manuscript approved for publication 15 March 2006 by the Scientific Editor.

Fish. Bull. 105:19–29 (2007).

The reproductive biology of Atka mackerel (*Pleurogrammus monopterygius*) is characterized by batch spawning by females and nest-guarding by males. This member of the greenling family (Hexagrammidae) is distributed in Russian and Alaskan waters where it is usually found in dense aggregations and associated with areas of fast currents, such as the passes between the Aleutian Islands (Lowe et al., 2002). Peak spawning occurs from July through October in Alaskan waters (McDermott and Lowe, 1997) and from June through September off Kamchatka (Zolotov, 1993). Batches of adhesive eggs are spawned in rock crevices and are guarded by males until they hatch (Gorbunova, 1962; Zolotov, 1993). Studies with archival tags have indicated that males guard nests for 3–4 months (Nichol and Somerton, 2002). Batches of eggs in different phases of development were found within one nest, indicating a promiscuous mating system (Zolotov and Tokranov, 1989; Zolotov, 1993; Lowe et al., 2003).

Atka mackerel females spawn their annual complement of eggs in several batches over the course of the spawning season. Zolotov (1993) reported that females spawn an average of three batches of eggs per season and that there is at least a two-week hiatus between spawnings in Kamchatkan waters. To estimate the number of batches spawned by a female, it is necessary to estimate annual fecundity and batch fecundity. Annual fecundity is defined as the total number of eggs spawned by a female in a single year and batch fecundity is defined as the numbers of eggs released at one time (Nichol and Acuna, 2001). Direct estimation of annual fecundity is possible if the number of eggs to be spawned that season is fixed or determinate (Hunter et al., 1985). Fish with determinate fecundity are described as showing a well-defined hiatus (or gap) in oocyte-size distribution between the advanced oocytes that will be spawned that year and the immature oocytes that will not develop until the following spawning seasons (Hunter et al., 1985). Species that are characterized by continuous oocyte development and oocyte-size distributions have often been described as indeterminate spawners (Hunter et al., 1985) that have the ability to develop unyolked oocytes continually and add them to the standing stock of advanced-yolked oocytes even after spawning begins. Hunter and Macewicz (2001) stated that potential fecundity can be estimated if three key requirements are met: 1) one can identify a certain standing stock or size range of

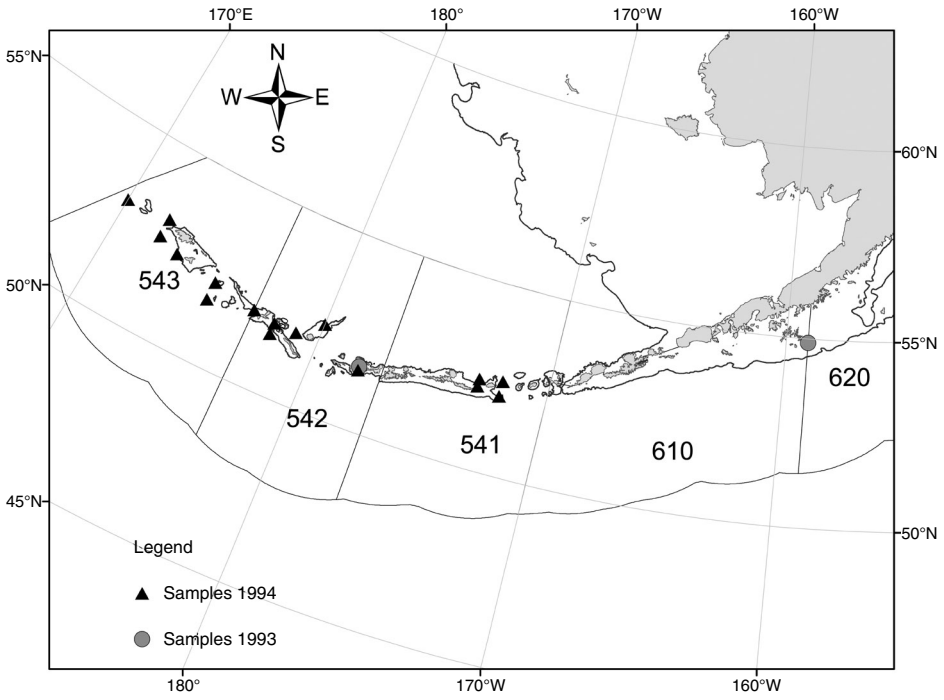

Figure 1

Sampling locations for Atka mackerel (*Pleurogrammus monopterygius)* collected for estimates of annual fecundity and batch fecundity in 1993–94 in the Aleutian Islands, Alaska.

oocytes into which no new oocytes are recruited once spawning begins; 2) females used to estimate potential fecundity have not spawned; and 3) atretic losses are negligible or can be estimated. Recent studies have shown that many fish species reabsorb a substantial number of their oocytes before spawning or at the end of the spawning season—a process known as atresia (Hunter and Macewicz, 1985; Kjesbu et al., 1991; Ma et al., 1998) Atretic losses in Icelandic cod (*Gadus morhua*) and Atlantic herring (*Clupea harengus*) occur mainly during the earlier phase of vitellogenic development, decrease as oocytes mature, and are negligible near the time of spawning (Harðardóttir et al., 2001, Kurita et al., 2003). Scombroid fishes (mackerels and tunas) have been described as having extensive atresia at the end of their spawning season (Hunter and Macewicz, 2001).

Previous studies (Zolotov, 1993) have described Atka mackerel as determinate spawners. However, no study to date has examined the oocyte-size distribution or shown that fecundity decreases after spawning. We examined the oocyte-size distribution for mature oocytes over time. Additionally, all ovaries were examined histologically to identify advanced oocyte stages, presence of postovulatory follicles, and oocyte atresia. We estimated potential annual fecundity and batch fecundity. The number of batches to be spawned was calculated by dividing total fecundity by batch fecundity. Potential fecundity was studied by comparing prespawning individuals with those that had spawned at least one batch of eggs in order to determine if advanced oocytes are added throughout the spawning season. Atresia of mature oocytes was estimated from ovaries of postspawning females to calculate realized fecundity as a measure of oocytes actually spawned per year.

Materials and methods

Data collection

All Atka mackerel examined in this study were either collected by the National Marine Fisheries Service (NMFS) fisheries observers aboard commercial fishing vessels during the commercial Atka mackerel fishery in 1993 or by Alaska Fisheries Science Center (AFSC) scientists during the 1994 NMFS bottom trawl survey of the Aleutian Islands (Table 1, Fig. 1).

During both years, Atka mackerel were subsampled from individual trawl tows. Collections were stratified by fish size; no more than five fish per size group were collected in each NMFS statistical area during a sampling year. The fork length of each fish was measured to the nearest centimeter, and each fish was weighed to the nearest 0.1 kg. In most cases, the stomach was emptied before weighing the fish. The ovaries were excised and placed in labeled cloth bags in 10% formalin solution buffered with sodium acetate (20 g per liter solution). In order to determine maturity stage, and presence of atresia, all ovaries were processed histologically. Four ovarian sections (4-μm thick) were stained

Table 1

Number of fish collected by year, month, and National Marine Fisheries Service (NMFS) statistical area. The number of samples with postovulatory follicles, i.e., in spawning or postspawning condition are shown in parentheses.

		NMFS statistical areas				
Year	Month	541	542	543	620	Total
1993	October		4 (4)		5 (5)	9
1994	June	57				57
	July		49	34 (11)		83
	August			10 (9)		10
Total		57	53	44	5	159

with hematoxilin (Sigma Aldrich, St. Louis, MI) and eosin counterstain (Sigma Aldrich, St. Louis, MI) (H&E). Maturity stages were determined by using categories developed by McDermott and Lowe (1997). Ovaries of prespawning females were defined by the lack of hydrated oocytes in June and the absence of postovulatory follicles once hydrated oocytes were present in July. Presence of atresia was determined according to classifications developed by Hunter and Macewitz (1985).

For the estimation of annual fecundity, only females whose ovaries had not shown any signs of releasing oocytes (i.e., all hydrated oocytes were within their follicles and ovaries contained no postovulatory follicles) were used. Different stages of postovulatory follicles can be distinguished in fish that have spawned multiple batches (McDermott and Lowe, 1997). These different stages indicate that postovulatory follicles persist in ovaries longer than the time period between batch spawning events, minimizing the possibility of incorrectly classifying a partly spent fish as a prespawning fish. Prespawning and partly spent specimens were compared to examine determinate spawning.

Gravimetric method

The gravimetric method was used to count and measure oocytes in weighed samples of Atka mackerel ovarian tissue (Hunter et al., 1985). In our fecundity analysis, small cross-sections were excised from preserved Atka mackerel ovaries. The amount of tissue removed was dependent on the size of eggs present, typically ranging from 0.3 g to 2.5 g. The target sample size was approximately 1000 eggs. The cross-section was divided into wedges in order to ensure a representative sample of ovarian wall tissue in relation to the tissue containing eggs. Ovarian wall tissue weight represents a substantial part of total ovary weight and needed to be represented proportionally in the subsamples. The samples were weighed to the nearest 0.001 g and allowed to sit in water for several hours before handling to reduce exposure to formalin. Ovary tissue was teased apart manually under a dissecting microscope and spread evenly in a 50% solution of glycerol in a dish over a grid partitioned by 1-cm squares. The dissecting microscope was equipped with a Javelin Ultrachip CCTV video camera (model JE-7442, Javelin Electronics, Los Angeles, CA), connected to a computer equipped with BioScan Optimas 4.0 scanning software (Bioscan Inc., Edmonds, WA).

All oocyte stages used in our study were previously described by McDermott and Lowe (1997). It was possible to distinguish the cortical alveoli oocyte stage (stage 3) from the more advanced oocyte stages (stage 4 [oil droplet stage] and stage 5 [vitellogenic stage]) when using the dissecting microscope and camera image to examine whole eggs. Oocytes in stage 4 and above showed a distinct ring around the nucleus, which was attributed to the oil and yolk droplets accumulating in the oocyte. Stage-3 oocytes did not show a distinct ring around the nucleus. However, it was not possible to distinguish oil-droplet oocytes (stage 4) from vitellogenic oocytes or more advanced stages (stage 5+) when examining whole eggs. Because oocyte development is usually attributed to oil-droplet and yolk accumulation, it was initially assumed that oocytes below stage 4 would not be spawned in the current spawning event and therefore would serve as reserve oocytes to be spawned in later spawning seasons. To determine oocyte-size composition, all oocytes stage 4 and above were measured along a vertical axis in each 1-cm square of a grid until 250 eggs had been measured. All eggs in the sample determined to be oocyte stage 4 or above were then counted manually under the dissecting microscope to arrive at an estimate of the number of eggs present per gram of tissue that were oocyte stage 4 and greater.

Location of tissue samples within the ovary

We examined six specimens to determine if location of tissue samples within the ovary affected estimates of fecundity. Two specimens had ovaries in the vitellogenic stage, two had ovaries in the early hydration stage, and two had ovaries in the spawning stage. We took three tissue samples per ovary lobe (six per specimen). The samples were taken from the anterior, center, and posterior location within each lobe of the ovary.

All eggs within the tissue sample that were oocyte stage 4 and above were counted and the first 100 oocytes were measured. Analysis of variance (ANOVA) (S-plus, 7.0 for Windows, Insightful Corp., Seattle, WA) (Venables and Ripley, 2002) was used for this examination with ovary lobe (left or right), position within the ovary, and maturity stage as factors. This analysis was carried out for the mean number of eggs per gram of tissue and mean egg size as response variables. The ANOVA indicated that the tissue sample could be taken from either lobe of the ovaries at any location. All further samples were therefore taken from a central location within either one of the ovary lobes.

Determinate versus indeterminate spawning

Direct estimation of annual fecundity is possible if the number of eggs to be spawned that season is fixed (determinate) and there is a well-defined gap in the oocyte-size distribution between advanced oocytes that will be spawned that year and the immature oocytes. In contrast, indeterminate spawners have the ability to develop unyolked oocytes continually and add them to the standing stock of advanced-yolk oocytes even after spawning begins.

To examine whether Atka mackerel are determinate spawners as previously described (Zolotov, 1993), we measured their oocytes to obtain a size distribution for oocytes over time. Additionally, we compared the potential fecundity of prespawning fish with the potential fecundity of fish that had spawned at least one batch. When all oocytes stage 4 and greater were summed, the tally exceeded the expected number of oocytes to be spawned per year, given the number of eggs in the first batch and the previous estimate of an average of three batches per female (Zolotov, 1993). This total number of oocytes led to the hypothesis that stage-4 oocytes may be developed, but not spawned, in a given year and are part of the standing stock of oocytes to be spawned in the following year. This hypothesis was supported when we found both oil droplet oocytes and atretic advanced-stage oocytes in the spent ovaries of nine specimens collected in 1993 (Fig. 2A).

The specimens from 1994 were consequently divided into two ovary stages:

1 Prespawning-stage ovaries: ovaries with the most advanced oocyte stage of vitellogenic or hydrated oocytes that showed no evidence of having been spawned, i.e., did not have postovulatory follicles (POFs).
2 Spawning-stage ovaries: ovaries that had spawned at least one batch of eggs and therefore contained POFs.

Potential annual fecundity was estimated with the gravimetric method and the total number of oocytes were further divided into stage-4 and stage-5+ oocytes by using the methods described below. The data were log-transformed and linear regressions were fitted by using S-plus. Ovaries of prespawning and spawning fish were compared by testing for differences in intercepts and slopes with S-Plus (Venables and Ripley, 2002).

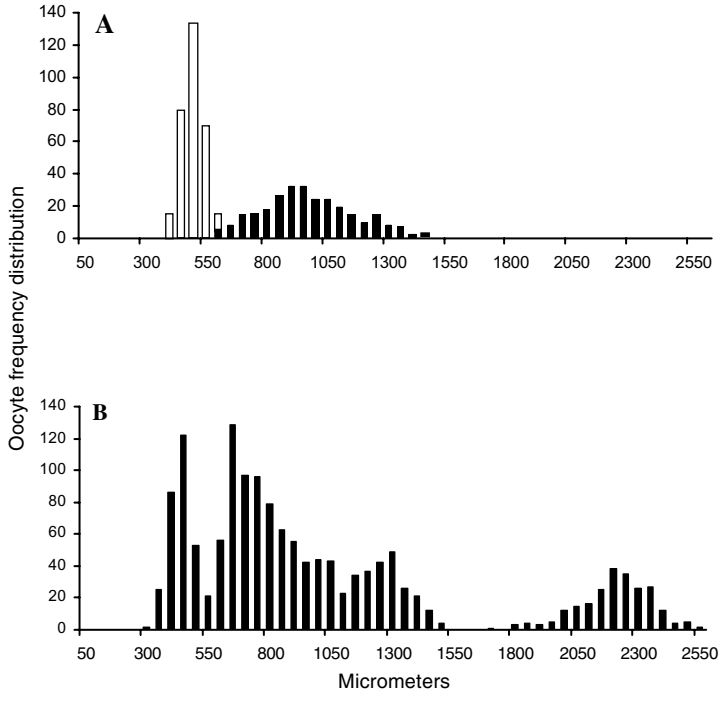

Figure 2

Atka mackerel (*Pleurogrammus monopterygius)* oocyte-size frequency distribution of (**A**) stage-4 (clear bars) and advanced atretic eggs (black bars) typical of a recently spent ovary, measured from whole oocytes (October 1993); (**B**) an ovary collected on 2 August 1994, with a hydrated batch of oocytes ready to be spawned (oocytes larger than 1800 μm are hydrated).

Separation of stage-4 oocytes from more advanced oocytes

To test whether Atka mackerel retain all of their stage-4 oocytes as a standing stock for the next year's fecundity, it became necessary to separate the stage-4 oocytes from the rest of the more developed oocyte stages and then subtract the stage-4 oocytes from the total oocyte count. It was not possible to distinguish the oil-droplet–stage oocytes from oocytes in the vitellogenic stage or migratory nucleus stage when examining whole oocytes with the dissecting microscope image and the Optimas software. Therefore, we examined nine ovaries that were recently spent, which contained only healthy stage-4 oocytes and atretic hydrated oocytes that could be easily distinguished (Fig. 2A). The average size distribution of stage-4 oocytes was estimated by measuring approximately 250 stage-4 oocytes per ovary. This size distribution could then be applied to the prespawning-stage ovaries, assuming that stage-4 oocyte-size distributions in spent ovaries were the same as those in prespawning-stage ovaries. To test this assumption, the size distribution from prespawning-stage ovaries in histological preparations was compared to the size distribution in postspawning fish by using ANOVA.

In order to deduct the population of stage-4 oocytes from the whole population of stage 5+ oocytes in prespawning-stage ovaries, we determined the size overlap between stage-4 and stage-5 oocytes by examining histological sections from six prespawning-stage ovaries. All oocytes that had been sectioned through the nucleus were measured with a compound microscope and camera system with Optimas software. We determined that all oocytes smaller than 525 μm were stage-4 oocytes and did not overlap in size with stage-5 oocytes in the prespawning-stage ovaries (Fig. 3A). We used the postspawning-stage ovaries that had only stage-4 oocytes and atretic hydrated oocytes to estimate the proportion of stage-4 oocytes that was less then 525 μm. This proportion was then applied to the prespawning-stage ovaries to estimate the number of stage-4 oocytes present.

The total number of stage-4 oocytes in the tissue sample for each prespawning-stage ovary was estimated from

$$\hat{n}_{4i} = \frac{c_i}{\hat{p}} \quad (1)$$

and

$$\hat{p} = \frac{g_i}{m_i}\,, \quad (2)$$

where $\hat{n}_{4i}$ = estimated total number of stage-4 oocytes in a tissue sample of a prespawning specimen i;

c_i = total number of stage-4 oocytes <525 μm in a tissue sample for a prespawning specimen i;

$\hat{p}$ = the estimated proportion of total stage-4 oocytes <525 μm, estimated from ovaries of a postspawning female;

g_i = total number of stage-4 oocytes <525 μm in postspawning-stage ovaries; and

m_i = total number of all stage-4 oocytes in postspawning-stage ovaries.

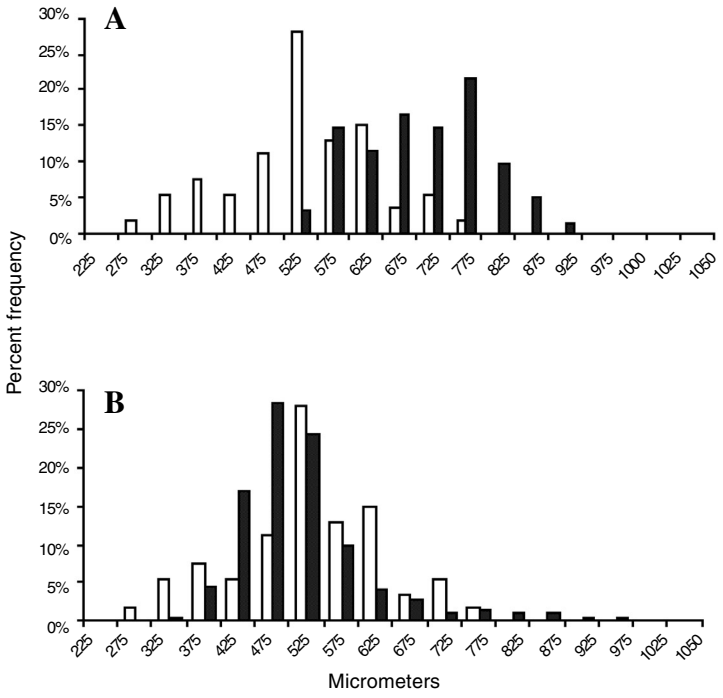

Figure 3

Combined size distributions of (**A**) stage 4 (clear bars) and stage 5 (black bars) oocytes from histological slides of six prespawning Atka mackerel (*Pleurogrammus monopterygius)* specimens (1994); (**B**) stage-4 oocytes from prespawning (clear bars) and postspawning (black bars) fish, measured from histological slides of 1993 and 1994 Atka mackerel specimen.

Estimation of potential annual fecundity and batch fecundity

Potential annual fecundity and batch fecundity were calculated by using prespawning specimens. Two scenarios were examined for potential fecundity:

Scenario 1: potential fecundity$_{\text{total}}$ (counting oocytes stage 4 and greater); and

Scenario 2: potential fecundity$_{\text{stage5+}}$ (counting only oocytes stage 5+).

The following equation was used:

$$\hat{F}_i = \frac{n_i O_i}{W_i}\,, \quad (3)$$

where $\hat{F}_i$ = estimated potential fecundity or batch fecundity for a prespawning specimen i;

n_i = number of oocytes in the tissue sample of a prespawning specimen (for potential fecundity$_{\text{total}}$: oocytes of stage 4 and greater; for potential fecundity$_{\text{stage5+,}}$ oocytes of stage 5+, for batch fecundity, number of hydrated oocytes);

O_i = total ovary weight (g) for a prespawning specimen i; and

W_i = weight of tissue sample (g) for a prespawning specimen i.

Prespawning-stage ovaries that contained oocytes in the early hydration stage (stage 7) or greater were examined to estimate batch fecundity. Atka mackerel appear to hydrate one batch of oocytes at a time and the hydrated oocytes can be clearly separated from less developed oocytes by a gap in oocyte-size distribution (Fig. 2B).

Length-fecundity relationships

Length-fecundity relationships and their 95% confidence intervals were computed for potential annual fecundity ($\hat{F}_i$), batch fecundity ($\hat{B}_l$), and the number of atretic oocytes ($\hat{E}_l$) by using nonlinear regression in S-plus (Venables and Ripley, 2002) with the following model:

$$Y = aL^b \quad (4)$$

where y = $\hat{F}_i$, $\hat{B}_i$, $\hat{E}_i$;
a and b = fecundity parameters to be estimated; and
L = fork length.

Oocyte atresia

Occurrence of atresia was divided into high occurrence (more than 10% of oocytes are atretic) and low occurrence (less than 10% of oocytes are atretric) by examining visually all histological slides. Because incidence of atresia was low in prespawning- and spawning-stage ovaries, it was not quantified further.

The occurrence of oocyte atresia in spent oocytes or oocytes that had been spawned was determined by counting the number of atretic oocytes present in the tissue sample of whole oocytes. Atretic eggs were easily distinguished from nonatretic eggs by their shriveled appearance, dark to almost black coloration, and dense texture. In postspawning fish, it appeared that all oocytes in an advanced stage were atretic and that stage-4 or smaller oocytes were healthy (Fig. 2A). When the histological slides of the same specimen were examined for verification of the oocyte stages, it appeared that all atretic oocytes that were counted corresponded to alpha and beta atresia stages (Hunter and Macewicz, 1985). The total number of atretic oocytes for each specimen (E_i) was calculated by multiplying atretic oocytes per gram of tissue by total weight of both ovaries.

Realized annual fecundity

Realized annual fecundity is defined as the number of oocytes actually spawned per fish in a given year. In order to take the occurrence of atresia into account, a predicted realized fecundity-at-length was calculated by subtracting predicted atresia-at-length from the predicted potential fecundity-at-length, by using

$$\hat{R}_l = \hat{F}_l - \hat{E}_l, \quad (5)$$

where $\hat{R}_l$ = estimated realized annual fecundity at length l;
$\hat{F}_l$ = estimated potential annual fecundity at length l; and
$\hat{E}_l$ = estimated number of atretic oocytes at length l.

Variance (Var) of the predictions at length was calculated as the sum of the variances (estimated with S-plus) of the predicted values for potential fecundity-at-length and atresia-at-length:

$$Var(\hat{R}_l) = Var(\hat{F}_l) + Var(\hat{E}_l). \quad (6)$$

Annual number of batches spawned

The potential number of batches spawned for each specimen i was estimated from

$$\hat{D}_i^{pot} = \frac{\hat{F}_i}{\hat{B}_i}, \quad (7)$$

where ($\hat{D}_i^{pot}$) = the potential number of batches spawned for each specimen i;
$\hat{F}_i$ = potential fecundity for specimen i, and
$\hat{B}_i$ = batch fecundity for specimen i.

Batch number for realized fecundity for specimen i was calculated by using the predicted proportion of atretic eggs per length category and applying it to each specimen:

$$\hat{D}_{il}^{real} = \frac{\hat{F}_i(1 - p_l^{atr})}{\hat{B}_i}, \quad (8)$$

where

$$p_l^{atr} = \frac{\hat{E}_l}{\hat{F}_l}, \quad (9)$$

where $\hat{D}_{il}^{real}$ = the batch number per specimen i at length l;
p_l^{atr} = the predicted proportion atretic at length l;
$\hat{E}_l$ = the predicted number of atretic eggs at length l; and
$\hat{F}_l$ = the predicted potential fecundity at length l.

The relationship between batch number and length was examined for both potential and realized fecundity with linear regression (S-plus).

Results

Data collection

Nine samples were collected after spawning events in October 1993 in NMFS statistical areas 542 (n=4) and 620 (n=5) (Table 1, Fig. 1). One hundred-fifty fish were collected from June through August in 1994 in NMFS statistical areas 541 (n=57), 542 (n=49), and 543 (n=44). Most (130) of these fish were in prespawning condition, i.e., contained no postovulatory follicles, and 20 had spawned at least one batch of eggs. Because the fish were collected during the NMFS Aleutian survey, which systematically moves from east to west along the Aleutian archipelago, all specimens in area 541 (Eastern Aleutian Islands) were considered prespawning fish Spawning commenced in late July in area 542 and by the middle of August all fish collected showed signs of spawning.

Location of tissue samples in ovaries

The effect of ovary lobe location or position within the ovary was not significant for either average egg size (P=0.07, 0.43, respectively) or mean number of eggs per gram of ovary tissue (P=0.07, 0.53, respectively). Maturity stage of ovary had a significant effect on both eggs per gram (P<0.0001) and average egg size (P<0.0001).

Separation of oil-droplet–stage oocytes (stage 4) from more advanced oocytes

There was no significant difference in mean egg size for stage-4 oocytes in pre- and postspawning fish (P=0.59)(Fig. 3B). We determined that all oocytes smaller than 525 μm that were measured were stage-4 oocytes (Fig. 3A). The proportion of stage-4 oocytes less than 525 μm ($\bar{p}$) was 0.755 based on samples of postspawning fish in 1993, with g_i = 1592 (the number of stage-4 oocytes that measured smaller than 525 μm), and m_i = 2110 (the total number of stage-4 oocytes measured). This proportion was treated as a constant when estimating the number of oocytes in stage 5 and larger.

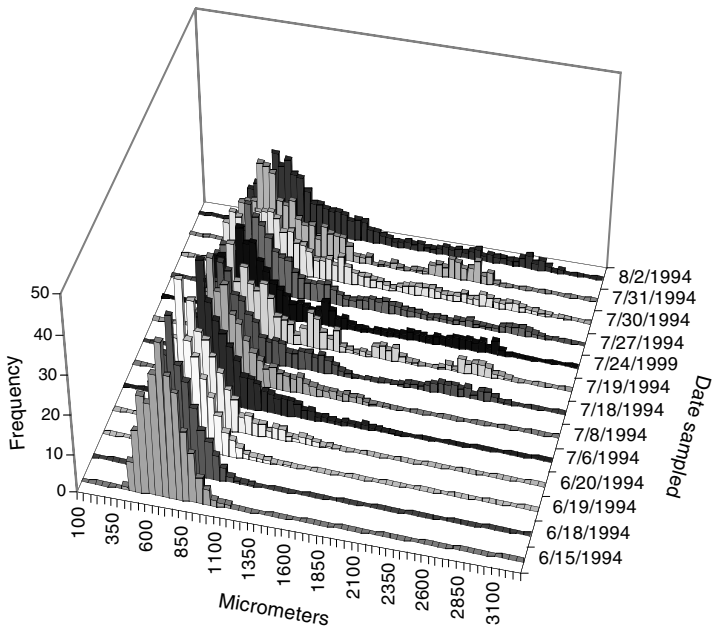

Figure 4

Atka mackerel (*Pleurogrammus monopterygius)* oocyte-size frequency distribution summarized by date for 1994. Oocyte-size frequencies were averaged per day.

Determinate versus indeterminate spawning

With the exception of hydrated eggs, Atka mackerel are characterized by a continuous oocyte-size distribution much like that of an indeterminate spawner (Fig. 4). Atka mackerel ovaries contain several stages of developing oocytes throughout the spawning season.

However, the length-fecundity relationship for the total number of oocytes decreased after the fish had spawned their first batch (Fig. 5A) and there was a significant difference in intercept and slope (P=0.01 and 0.001, respectively). When the length-fecundity relationship for oocytes in stage 5+ was examined, the potential fecundity also decreased after spawning (Fig. 5B), with a significant difference in intercept and slope (P=0.003 and P=0.009, respectively). The numbers of stage-4 oocytes did not appear to differ substantially before and after spawning for fish of comparable size (Fig. 5C) although the slope of the length-fecundity relationship differed significantly (P=0.012). Furthermore, there was no reduction in the number of stage-4 oocytes at comparable fish lengths for the nine spent fish collected late in the spawning season (October) versus prespawning and spawning fish collected in June–August.

Oocyte atresia

Incidence of oocyte atresia in prespawning and spawning fish was found to be low. Only 15 of the 150 ovaries examined showed any signs of atresia. Of these15 ovaries, high occurrence of atresia (more than 10% of oocytes affected) was found in 3, and low occurrence of atresia (less than 10% of oocytes affected) was found in 12. Therefore, atresia in ovaries of pre- and postspawning fish was not quantified further.

Atresia was found to be present in all of the nine ovaries of postspawning fish examined in the study and the number of atretic oocytes corresponded roughly with the number of ooccytes spawned in a batch (batch size). This finding indicates that Atka mackerel may use atresia to regulate reproductive output at the end of the spawning season.

Estimates of annual fecundity and batch fecundity

Length-fecundity parameters (a and b) for predicted fecundities for scenario 1 (oocytes ≥stage 4) and scenario 2 (oocytes ≥stage 5), as well as estimates of batch fecundity and atretic eggs are shown in Table 2 with their respective standard errors. Predicted potential fecundity for both scenarios is shown in Figure 6A.

The length-fecundity relationship for oocytes at stage 5+ is the most realistic because it appears that most stage-4 oocytes will not be spawned in the current season. Predicted potential and realized fecundity for stage 5+ oocytes are illustrated in Figure 6A with their respective confidence intervals. Because the estimates of potential fecundity were treated as data in the length-fecundity regressions, the variance estimates and confidence intervals are conservative. Data and model fit for the relationship of batch fecundity to length is shown in Figure 6B, and the data and model fit for the number of

Table 2

Atka mackerel length-fecundity coefficients derived with the equation $F = a\,L^b$, where F = fecundity and L = fish fork length (cm). SE = standard error of the mean. CI = 95% confidence intervals for predicted values of the mean. n = number of fish in sample.

	Constants					
	a		b			
Fecundity type	Estimate	SE	Estimate	SE	n	Estimate for 40-cm female (±95% CI)
Potential fecundity$_{total}$	0.5601	0.5067	3.0865	0.2409	130	49,321±2535
Potential fecundity$_{stage5+}$	2.3716	2.0913	2.6517	0.2352	130	41,994 ±2061
Number of atretic eggs	0.0013	0.0083	4.3303	1.6502	9	11,329 ±8802
Batch fecundity	0.1157	0.1923	2.9726	0.4536	33	6689 ±577
Realized fecundity$_{total}$						37,992±7873
Realized fecundity$_{stage5+}$						30,664 ±7730
	Mean value		SD			
Batch number potential$_{stage5+}$	6.13		1.35		33	6.13 ±2.64
Batch number potential$_{total}$	7.04		1.52		33	7.04 ±2.98
Batch number realized$_{stage5+}$	4.64		1.03		33	4.64 ±2.01
Batch number realized$_{total}$	5.6		1.15		33	5.33 ±2.25

atretric eggs in the ovary by length category is shown in Figure 6C. Average number of batches corresponding to potential and realized fecundity are shown in Figure 6D.

The average fork length for females during the 1994 NMFS survey was 40 cm (Lowe and Fritz, 1994). Potential fecundity (stage 5+) was estimated to be 41,994 eggs, and realized annual fecundity was estimated to be 30,664 eggs for a 40-cm female (Table 2). Batch fecundity for a 40-cm female was estimated to be 6689 eggs and the number of batches spawned showed no statistically significant relationship with length for both potential (P=0.35) and realized (P=0.75) fecundity (Fig. 6D). The estimated number of batches produced annually per female was calculated by using the grand mean and standard deviation for all specimens combined. The average number of batches of eggs for potential and realized fecundity was estimated at 6.1 and 4.5 batches per year, respectively, with corresponding 95% confidence intervals of ±2.64 and ±2.21 batches. This result would indicate that the average female has the potential to spawn about 6 batches, but may reabsorb 1–2 batches of eggs at the end of the season.

Discussion

The reproductive strategy of Atka mackerel and other hexagrammids has been characterized by low fecundity and large eggs, high parental care, and by larvae hatched at an advanced stage of development (Gorbunova, 1962). Potential fecundity for an average female Atka mackerel of 40 cm was 41,994 eggs for oocytes at stage 5+ and is higher than the estimates for Kamchatkan waters by Gorbunova (1962), who gave a range between 5000 and 31,000 eggs for a 52-cm female. Zolotov (1993) estimated potential fecundity to be 38,700 eggs (vitelline oocytes plus hydrated oocytes in first batch) off Kamchatka, which is also slightly lower than our estimate. Our batch fecundity estimate of 6689 eggs for an average female of 40 cm is similar to Zolotov's (1993) estimate of 6930 for a fish of the same size.

Atka mackerel are characterized by a continuous size distribution of oocytes much like that of indeterminate spawners. However, Atka mackerel have a distinct spawning season (July–October) during which they spawn batches containing a large number of eggs (Zolotov, 1993; McDermott and Lowe, 1997). This spawning pattern differs from that of typical indeterminate spawners that spawn a small number of eggs (in relation to the total number present) almost continuously for many months, as characterized by the northern anchovy (*Engraulis mordax*) (Hunter et al., 1985). Atka mackerel seem to lie somewhere in the middle of determinate versus indeterminate spawning fish. It appears that there is a potential to develop and spawn up to seven batches if all stage-4 oocytes are developed and spawned. Most of the stage-4 oocytes still remaining in the ovary during the spawning phase probably constitute the pool of oocytes to be spawned in the next season. However, those oocytes could be a reserve to be developed and spawned in highly productive years (i.e., during favorable spawning conditions). Estimates of fecundity based on oocytes at stage 5+ may be conservative if some of the stage-4 oocytes are

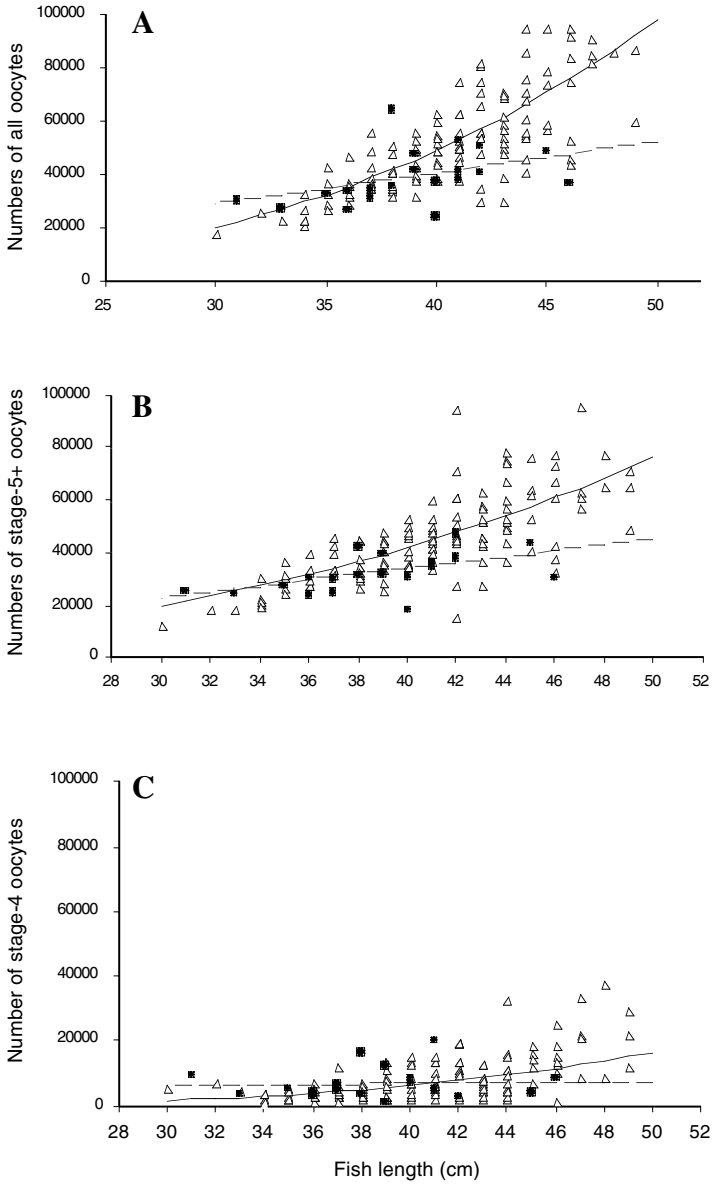

Figure 5

Fecundity of Atka mackerel (*Pleurogrammus monopterygius)* at the prespawning (clear triangles) and spawning (solid squares) phase for (**A**) total number of oocytes at stage 4 and above, (**B**) oocytes at stage 5+, and (**C**) for oocytes at stage 4 only. Regression lines for prespawning and spawning fish are indicated by solid and dashed lines, respectively.

developed and spawned late in the spawning season. However, knowledge of batch size, length of spawning season, and the spawning interval between batches (1–2 weeks) (Gorbunova, 1962; Zolotov, 1993; McDermott and Lowe, 1997), gives us confidence that our estimate of fecundity is realistic. Given that there are 14 days between batches, a 75-day incubation period (Lowe et al., 2003; McDermott, 2003), and that 4.6 batches are spawned annually, the spawning season would be 120 days, which is similar to that observed in the present study.

Conclusions

Prespawning Atka mackerel did not show much atresia during egg development; however high levels of atresia became apparent when ovaries of postspawning fish

were examined. Examination of ovaries of prespawning females alone would lead to the assumption that the potential fecundity is close to the realized fecundity. Atresia in postspawning Atka mackerel has been described in earlier studies (Gorbunova, 1962; Zolotov, 1993), where 400–500 atretic eggs per ovary and the prolonged presence of atretic eggs in the ovaries before reabsorption have been reported. However, this is the first study where atresia from recently spent ovaries has been included in the fecundity analysis in a quantitative manner. When recently spent ovaries were examined, it appeared that atresia had a major effect on potential fecundity and that an average of 1–2 batches were reabsorbed at the end of the spawning period in the ovaries examined. It should be noted that specimens with ovaries in the prespawning phase and specimens with recently spent ovaries were collected in different years. Atresia is likely to be related to feeding ecology, availability of appropriate substrate and environmental conditions for spawning, and could potentially change from year to year. Interannual variability of atresia should be examined in the future.

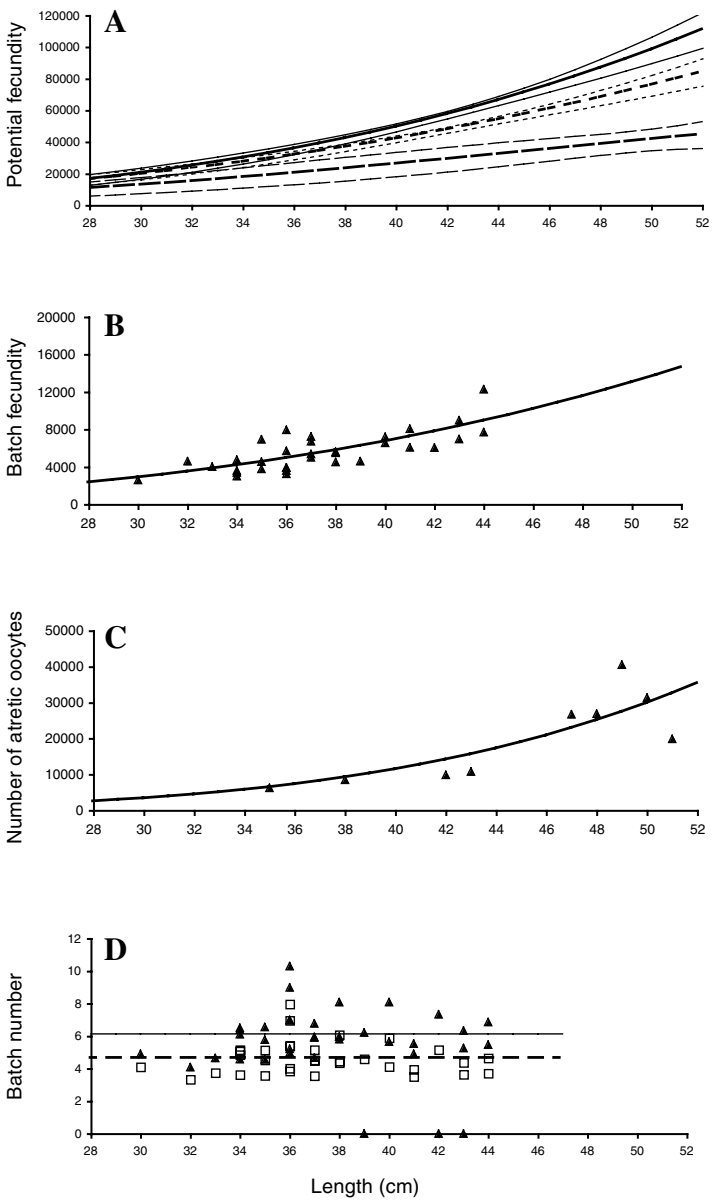

Figure 6

(**A**) Model fit and 95% confidence intervals for potential fecundity of Atka mackerel (*Pleurogrammus monopterygius)* at length for total number of oocytes (solid lines), stage-5+ oocytes (short dashed lines), and realized fecundity (long dashed lines). (**B**) Data and model fit (line) for Atka mackerel batch fecundity by length. (**C**) Data and model fit for number of atretic oocytes in spent ovaries of Atka mackerel by length. (**D**) Number of batches spawned by length for potential fecundity (solid triangles) and realized fecundity (open squares) and the estimated population means (solid line for potential fecundity and dashed line for realized fecundity) for Atka mackerel.

Acknowledgments

We thank G. Thompson and J. Ianelli for their statistical advice and F. Morado for his advice and assistance with histological work. We also thank all the observers and scientists who collected specimens and the commercial fishing industry for providing sampling platforms. G. Stauffer, B. Miller, A. Hollowed, S. Lowe, and S. Hinckley helped greatly by critically reviewing drafts of this paper. This research was supported by the Joint Institute for the Study of the Atmosphere and Ocean (JISAO) under NOAA Cooperative Agreement no. NA67RJ0155 (contribution no. 986).

Literature cited

Gorbunova, N. N.
1962. Spawning and development of greenlings (family Hexagrammidae). *In* Greenlings: taxonomy, biology, interoceanic transplantation (T. S. Rass, ed.), p. 1–103. Tr. Inst. Okeanol., Akad. Nauk. SSSR 59:118–182. In Russian (translated by Isr. Program. Sci. Trans., 1970). [Available from Natl. Tech. Inf. Serv., Springfield, VA, as TT 69-55097 S.]

Harðardóttir, K., O. S. Kjesbu, and G. Marteinsdottir.
2001. Atresia in Icelandic cod (*Gadus morhua* L.) prior to and during spawning. Report of the working group on modern approaches to assess maturity and fecundity of warm- and cold-water fish and squids (O. S. Kjesbu, J. R. Hunter, and P. R. Withames, eds.), 140 p. Institute of Marine Research, Bergen, Norway.

Hunter, J. R., N. C. H. Lo, and R. J. H. Leong.
1985. Batch fecundity in multiple spawning fishes. *In* An egg production method for estimating spawning biomass of pelagic fish: application to the northern anchovy, *Engraulis mordax* (R. Lasker, ed.), p. 67–77. U.S. Dep. Commer., NOAA Tech. Rep. NMFS 36.

Hunter, J. R., and B. J. Macewicz.
1985. Rates of atresia in the ovary of captive and wild northern anchovy, *Engraulis mordax*. Fish. Bull. 83:119–136.
2001. Improving the accuracy and precision of reproductive information used in fisheries. Report of the working group on modern approaches to assess maturity and fecundity of warm-and cold-water fish and squids (O. S. Kjesbu, J. R. Hunter, and P. R. Withames, eds.), 140 p. Institute of Marine Research, Bergen, Norway.

Kjesbu, O. S., J. Klungsøyr, H. Kryvi, P. R. Whitthames, and M. Greer Walker.
1991. Fecundity, atresia, and egg size of captive Atlantic cod (*Gadus morhua*) in relation to proximate body composition. Can. J. Fish. Aquat. Sci. 48: 2333–2343.

Kurita, Y., S. Meier, and O. S. Kjesbu.
2003. Oocyte growth and fecundity regulation by atresia of Atlantic herring (*Clupea harengus*) in relation to body condition throughout the maturation cycle. J. Sea Res. 49:203–219.

Lowe, S. A., and L. Fritz.
1994. Atka mackerel. *In* Stock assessment and evaluation report for the groundfish resources of the Bering Sea/Aleutian Islands regions, 11-1–11-43. North Pacific Fisheries Management Council, P.O. Box 103136, Anchorage, Alaska, 99510.

Lowe, S., J. Ianelli, H. Zenger, and R. Lauth.
2003. Stock assessment of Aleutian Islands Atka mackerel. *In* Stock assessment and evaluation report for the groundfish resources of the Bering Sea/Aleutian Islands regions, p. 711–776. North Pacific Fisheries Management Council, P.O. Box 103136, Anchorage, Alaska 99510.

Lowe, S., J. Ianelli, H. Zenger, and R. Reuter.
2002. Atka mackerel. *In* Stock assessment and evaluation report for the groundfish resources of the Bering Sea/Aleutian Islands regions, p. 609–667. North Pacific Fisheries Management Council, P.O. Box 103136, Anchorage, Alaska 99510.

Ma, Y., O. S Kjesbu, and T. Jørgensen.
1998. Effects of ration on the maturation and fecundity in captive Atlantic herring, (*Clupea harengus*). Can. J. Fish. Aquat. Sci. 55:900–908.

McDermott, S. F.
2003. Estimating abundance of a patchily distributed fish, Atka mackerel, *Pleurogrammus monopterygius*. Ph.D. diss., 149 p. Univ. Washington, Seattle, WA.

McDermott, S. F., and S. A. Lowe.
1997. The reproductive cycle and sexual maturity of Atka mackerel, *Pleurogrammus monopterygius* in Alaska waters. Fish. Bull. 95:321–333.

Nichol D. G., and E. I. Acuna.
2001. Annual batch fecundities of yellowfin sole, *Limanda aspera*, in the eastern Bering Sea. Fish. Bull. 99:108–122.

Nichol, D. G., and D. A. Somerton.
2002. Diurnal vertical migration of the Atka mackerel *Pleurogrammus monopterygius* as shown by archival tags. Mar. Ecol. Prog. Ser. 239:193–207.

Venables, W. N., and B. D. Ripley.
2002. Modern applied statistics with S-plus, 495 p. Springer-Verlag Inc., New York, NY.

Zolotov, O. G.
1993. Notes on the reproductive biology of *Pleurogrammus monopterygius* in Kamchatkan waters. J. Ichthyol. 33:(4):25–37.

Zolotov, O. G., and A. M. Tokranov.
1989. Reproductive ecology of hexagrammidae and cottidae in the Pacific waters of Kamchatka. J. Ichthyol. 3:430–438.