The reproductive cycle and sexual maturity of Atka mackerel, *Pleurogrammus monopterygius*, in Alaska Waters

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Abstract.—The reproductive biology and sexual maturity of Atka mackerel (*Pleurogrammus monopterygius*) in Alaskan waters were examined with data collected from commercial fishing vessels and National Marine Fisheries Service research surveys. The female reproductive system and ovarian development over time were described by using histological methods. The reproductive cycle is characterized by a period of slow development from January until May, a rapid growth period of vitellogenesis in June, and a protracted spawning period, July until October, during which three batches of eggs are spawned on average.

Length and age at maturity were calculated and compared for different subareas of the Aleutian Islands and Gulf of Alaska region. Size at 50% maturity was significantly different among the subareas,decreasing from east to west.

Lengths at 50% maturity were 38.24, 35.91, 33.55, and 33.64 cm in the Gulf of Alaska, eastern Aleutian Islands, central Aleutian Islands, and western Aleutian Islands, respectively. Age at maturity was not significantly different by area; Atka mackerel were found to reach 50% maturity at 3.6 years. Therefore, it was assumed that different sizes at sexual maturity were reflections of different growth rates in the respective geographic subareas.

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Atka mackerel, *Pleurogrammus monopterygius*, is a member of the greenling family (Hexagrammidae). It is distributed in Alaskan and Russian waters from the Gulf of Alaska to Kamchatka and is most abundant in the North Pacific Ocean, southern Bering Sea, and along the Aleutian Archipelago (Rutenberg, 1962). It has been of increasing commercial importance to the United States, with Alaskan catches averaging about 80,000 metric tons (t) in the last 3 years (valued at $14 million [ex-vessel] in 1993).

Recent information suggests that Atka mackerel play an important role in the Aleutian Islands and Gulf of Alaska ecosystems as forage for other groundfish, seabirds, and marine mammals, including the Steller sea lion (*Eumetopias jubatus*) which has been listed as a threatened species under the U.S. Endangered Species Act (Kajimura, 1984; Livingston et al., 1993; NMFS[1]). Despite the value of the species to commercial fisheries and other piscivores, many aspects of its life history and ecology are poorly understood. Furthermore, information and data available suggest behaviors and distribution patterns unique among Alaska groundfish.

During much of the year, Atka mackerel are pelagic but migrate annually from the lower edge of the continental shelf to shallow coastal waters where they spawn demersally. In eastern Kamchatka waters, the spawning migration begins at the end of May and peaks in the middle of June (Zolotov, 1993). Spawning peaks June through September, but may occur intermittently throughout the year (Gorbunova, 1962; Zolotov, 1993). Atka mackerel spawn their eggs in rock crevices or among stones, which are guarded by brightly colored males until hatching occurs (Gorbunova, 1962; Zolotov, 1993). Females are reported to spawn an average of three batches per season with at least a 2-week hiatus between subsequent spawnings (Zolotov, 1993). Batches of eggs in different phases of development were found inside one nest, suggesting a promiscuous mating system

[1] NMFS. 1995. Status review of the U.S. Steller sea lion (*Eumetopias jubatus*) population. Natl. Mar. Mamm. Laboratory, Natl. Mar. Fish. Serv., NOAA, 7600 Sand Point Way NE, Seattle, WA 98115, 61 p.

with polygyny in the males and polyandry in the females (Zolotov, 1993). The adhesive eggs hatch in 40–45 days, releasing planktonic larvae that have been found up to 800 km from shore (Gorbunova, 1962). Preliminary analyses of fishery and survey data suggest evidence of sex segregation during the spawning period. Males presumably remained on the spawning grounds guarding the nests, whereas females were found in exploitable concentrations farther offshore in high current areas such as island passes.[2]

The Atka mackerel resource in the Aleutian Islands appears to be in excess of 0.5 million t.[3] Owing to a lack of a strong market for the product, and insufficient biological information that prompted conservative catch recommendations, it was lightly exploited through the 1980's. Catch recommendations depend on an accurate knowledge of abundance which is based on the biology, distribution, and population dynamics of the species. The expansion of the fishery has greatly intensified the need for accurate estimates of life history parameters. However, to date most of the life history information available on Atka mackerel has been obtained in Russian waters (Gorbunova, 1962; Rutenberg, 1962; Zolotov, 1993); there is little or no information on the reproductive cycle, behavior, and ecology of Atka mackerel in U.S. waters. Because its distribution appears to be closely related to its reproductive life history, information on the reproductive cycle and spawning behavior of Atka mackerel off Alaska could lead to a better understanding of its localized movement patterns. This information is necessary to improve surveys for biomass estimates which will result in more accurate stock assessments and provide better long-term management of the fisheries. Of particular importance are parameters governing the reproductive potential of the stock, i.e. maturity at age, which is a direct input into the stock assessment model and is required to estimate female spawner biomass.

This paper presents the results of a study that was undertaken to examine the reproductive biology of Atka mackerel. Female gonads and otoliths were collected, gonads examined histologically, egg stages and maturity stages defined, and the reproductive cycle was described. Ages were estimated from otoliths. The gonad somatic index (GSI) and the mean egg stage per month were used as indicators of ovarian development over time. Population parameters such as length and age at 50 % maturity were determined and compared between different geographical areas.

Methods

Few opportunities existed for the collection of biological samples of Atka mackerel other than aboard commercial fishing boats or National Marine Fisheries Service (NMFS) research surveys. Consequently, sample collection was restricted to periods when the fishery was open and when the NMFS surveys were conducted.

Data and sample collection

The data and samples analyzed in this study were collected from 1992 through 1994 in 1) the Gulf of Alaska and 2) the Aleutian Island Region by observers and research scientists aboard commercial fishing vessels and NMFS research boats, respectively (Fig. 1). For purposes of collection and analysis, the study region was subdivided into four geographical subareas: western Aleutians, central Aleutians, eastern Aleutians, and the Gulf of Alaska.

The total number of gonad samples collected was 978. Monthly sample sizes ranged from a low of 30 in August to a high of 196 in June (Table 1). Otoliths were also collected from 537 of the sampled fish. Overall sampling effort by area was fairly even. However, sampling effort in each area by month was strongly dependent on the location of the seasonal fishing effort in winter, spring, and fall. Winter samples were available only from the eastern Aleutians, whereas spring and summer sampling took place in all areas. The only fall samples taken were in October from the Gulf of Alaska. Samples collected on research cruises were taken from June through August throughout most of the areas. Since the sampling scheme for samples on commercial vessels did not differ from the sampling scheme on research boats, all data were combined. However, commercial catches were obtained by directly targeting certain locations or schools, whereas the survey catches were obtained by sampling at randomly stratified stations. Therefore the age and size composition of the commercial catch may reflect a more uniform population structure because most commercial boats target schools of adult fish.

There were insufficient samples to distinguish annual differences, therefore all samples were pooled by month and subarea for the determination of length

[2] Fritz, L. W. 1995. Alaska Fish. Sci. Center, Natl. Mar. Fish. Serv., Seattle, WA 98115. Personal commun.

[3] Lowe, S. A., and L. W. Fritz. 1995. Atka Mackerel. *In* Stock Assessment and Fishery Evaluation Report for the Groundfish Resources of the Bering Sea/Aleutian Island Regions as Projected for 1996. North Pacific Management Council, P.O. Box 103136, Anchorage, AK 99510.

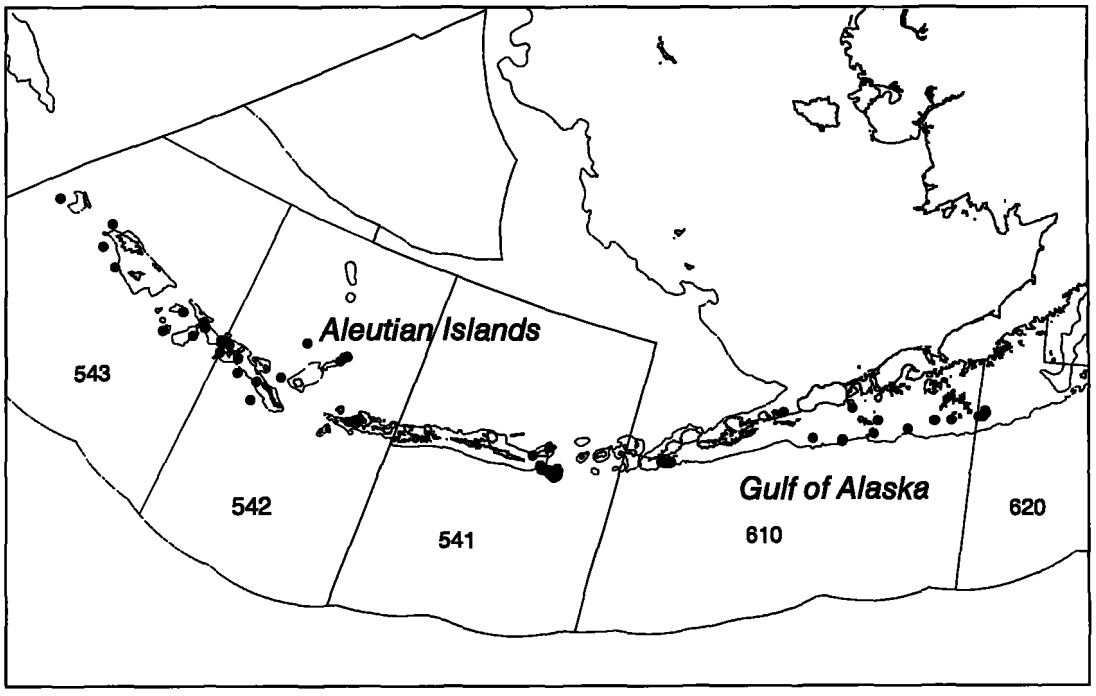

Figure 1

Haul locations for Atka mackerel ovary samples; 541 = eastern Aleutians, 542 = central Aleutians, 543 = western Aleutians, 610 and 620 = Gulf of Alaska.

Table 1

Number of samples of Atka mackerel, *Pleurogrammus monopterygius*, collected from 1992 to 1994 by month and area.

Month	Eastern Aleutians	Central Aleutians	Western Aleutians	Gulf of Alaska	Total
January	85	0	0	0	85
February	55	0	0	0	55
March	68	1	9	71	149
April	0	12	71	0	83
May	0	52	45	0	97
June	62	0	72	62	196
July	0	84	83	16	183
August	0	20	10	0	30
September	0	38	0	0	38
October	0	0	0	62	62
Total	270	207	290	211	978

and age at maturity and pooled by month only for the description of the reproductive cycle (Table 1).

Atka mackerel were collected from subsamples of individual trawl tows. Collections were stratified by size of individual fish. No more than five fish per sex in each 1-cm size group were collected within each subarea during a sampling cruise. Each selected fish was measured to the nearest centimeter and weighed to the nearest 0.1 kg. In most cases, the stomach was emptied before weighing the individual fish. The ovaries were excised and placed in labeled cloth bags in a 10% buffered formalin solution. Sodium acetate (20 g per liter of formalin solution) was used as a buffer. Weights of fresh ovaries were taken and recorded to the nearest gram for 254 specimens collected during the 1994 bottom trawl survey of the Aleutian Islands. In addition to the ovary samples, otoliths were collected opportunistically from sampled specimens. Ages were determined from otoliths by the Alaska Fisheries Science Center Age and Growth Unit using the surface-reading and break-and-burn technique (Chilton and Beamish, 1982).

Table 2

Definition of oocyte stages of Atka mackerel based on major histological characteristics.

Oocyte stage		Mean oocyte size (μm) (range)	Major histological characteristics
1	Early perinucleus	55 (30–80)	Small oocyte with hematoxylin-positive cytoplasm. Nucleoli on the outer margin of nucleus.
2	Late perinucleus	147 (117–176)	Oocyte becoming larger, cytoplasm lighter, nucleoli still present.
3	Cortical alveoli	230 (216–255)	Cortical alveoli present as a ring on the outer margin of the cytoplasm. Cortical alveoli appear as white droplets since they do not stain in H&E. The zona radiata can be seen developing as a thin, pink layer. Cytoplasm in center of oocyte appears granular.
4	Oil droplet stage	490 (313–628)	Oil droplets appear first on inner margin of cytoplasm and then start to fill out the inner half of the oocyte. Zona radiata thickens, nucleoli are still present in nucleus, granulosa cells in tight circle around zona radiata.
5	Yolk globule stage	677 (549–843)	Eosin-positive yolk droplets appear between the inner layer of oil vesicles and the outer layer of cortical alveoli, giving the oocyte a three-layered appearance. Vacuoles appear in oil droplet or cortical alveoli layer. Cytoplasm around nucleus granular, staining eosin-positive. With further development, yolk droplet zone and oil droplet zone may fuse together. Zona radiata thickens and oocyte increases in size.
6	Migratory nucleus	944 (686–1,294)	Yolk platelets form by the fusion of smaller yolk droplets. Oil droplet and yolk platelet zone have fused, with cortical alveoli still on the margin of the oocyte. Nucleus in the center loses its shape (nuclear membrane gets dissolved) and migrates towards the micropyle.
7	Early hydration	1,277 (999–1529)	Zona radiata thickens to almost twice the thickness characterizing migratory nucleus stage. Oocyte increases rapidly in size. Yolk fuses to uniform, pink mass (H&E stain) in center of oocyte, with still some large yolk platelets surrounding it. The margin of the cytoplasm does not stain, nucleus is no longer visible.
8	Late hydration	1,932 (1,646–2,195)	Yolk fused to one mass in the center of oocyte, surrounded by nonstaining area. Oocyte still within follicle.
9	Ovulation	Same as in stage 8	Oocyte same as in stage 8, but oocyte no longer inside follicle and usually found within lumen of ovary.

Histological preparation

After storage for several months in formalin, the ovary pairs were reweighed and sections from the middle of one ovary were taken and processed for histological examination. The tissue samples were embedded in Paraplast and sectioned with a microtome to a thickness of 5 μm. All samples were routinely stained with hematoxylin and eosin (H&E). Selected samples were stained with Periodic Acid Schiff reagent (PAS) to identify carbohydrate complexes in cortical alveoli while other samples were sectioned frozen and stained with Sudan black in order to demonstrate the presence of oil droplets (Galigher and Kozloff, 1971). Oocytes in each ovary were subsequently classified into histological oocyte stages (Table 2). Postovulatory follicles and atretic oocytes were also recorded and classified according to the categories defined by Hunter and Macewicz (1985).

Mean oocyte stage per month

Each ovary was classified to the most advanced oocyte stage present using the histological criteria summarized in Table 2. Mean oocyte stage per month was determined by summing the individual specimen's oocyte stages (most advanced) by month and dividing the sum by the number of specimens collected in that month as follows:

$$\bar{e}_j = \frac{\sum_{i=1}^{n_j} e_{ij}}{n_j},$$

where $\bar{e}_j$ = mean oocyte stage in month j;
$e_{i,j}$ = the most advanced oocyte stage of specimen i in month j; and
n_j = number of specimens in month j.

The estimated variance (s^2) of the mean egg stage was determined using the formula:

$$S\bar{e}_j^2 = \frac{\sum_{i=1}^{n_j}(e_{ij} - \bar{e}_j)^2}{n_i(n_i - 1)}.$$

Size measurement of oocytes

Oocyte diameters were measured from histologically prepared ovary sections using a compound microscope with an ocular micrometer. Random measurements were taken by measuring oocytes along multiple transect lines across the section. Only oocytes that touched the transect line and which had been sectioned through the nucleus were measured. For each oocyte stage a minimum of 15 oocytes per fish were measured from at least two individuals.

Length and age at 50% maturity

To minimize confusion between immature and resting fish (mature females with oocytes smaller than oocyte stage 4; see Table 2), only samples in which the oocytes of mature fish were in advanced oocyte stages (oocyte stages 4–9, Table 2) were used for the calculation of length and age at maturity, except for some samples collected in the Gulf of Alaska as discussed below.

The proportion of fish mature at length or age was estimated by fitting a logistic model to the observed proportion mature. The logistic equation used was:

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

where Y = proportion mature at length or age x;
α, β = model parameters to be estimated; and
x = fork length (cm).

Length or age at 50% maturity (L_{50}; Age_{50}) was calculated as $-\alpha/\beta$. The statistical program used was S-plus (Venables and Ripley, 1994). A general linear model with a binomial error distribution was applied with geographical area as a factor. The variance for the estimated L_{50} or Age_{50} was calculated using the delta method (Seber, 1982):

$$S^2(Age_{50}, L_{50}) = \frac{S^2(\hat{\alpha})}{\hat{\beta}^2} - \frac{2\hat{\alpha}S(\hat{\alpha})S(\hat{\beta})r}{\hat{\beta}^3} + \frac{\hat{\alpha}^2 S^2(\hat{\beta})}{\hat{\beta}^4},$$

where $S^2(L_{50}; Age_{50})$ = variance of the length or age at 50% maturity;
$\hat{\alpha}$ = estimate of α;
$\hat{\beta}$ = estimate of β;
r = correlation coefficient;
$S(\hat{\alpha})$ = standard error of $\hat{\alpha}$; and
$S(\hat{\beta})$ = standard error of $\hat{\beta}$.

Calculating gonad somatic index

Relative reproductive effort was expressed as a gonad somatic index (GSI), defined as the ratio of gonad weight to somatic body weight. In all cases the gonads were weighed after they had been preserved in formalin. For the samples that did not have weights for fresh gonads, fresh gonad weight was estimated with a linear regression using the samples for which both fresh weight and formalin-preserved weight of the gonads had been measured (n=254). The regression line was forced through the origin using:

$$y = cx,$$

where y = fresh weight of ovary;
x = formalin preserved weight of ovary; and
c = constant.

The GSI was calculated as:

$$\text{GSI} = \frac{G}{B} \times 100,$$

where GSI = gonad somatic index;
G = fresh gonad weight; and
B = somatic body weight (stomach empty, gonads removed).

Results

Definition of oocyte stages and maturity stages

Oocyte development was classified into nine oocyte stages based on major histological characteristics (Fig. 2, Table 2). The oocyte stages were then used to determine maturity stages.

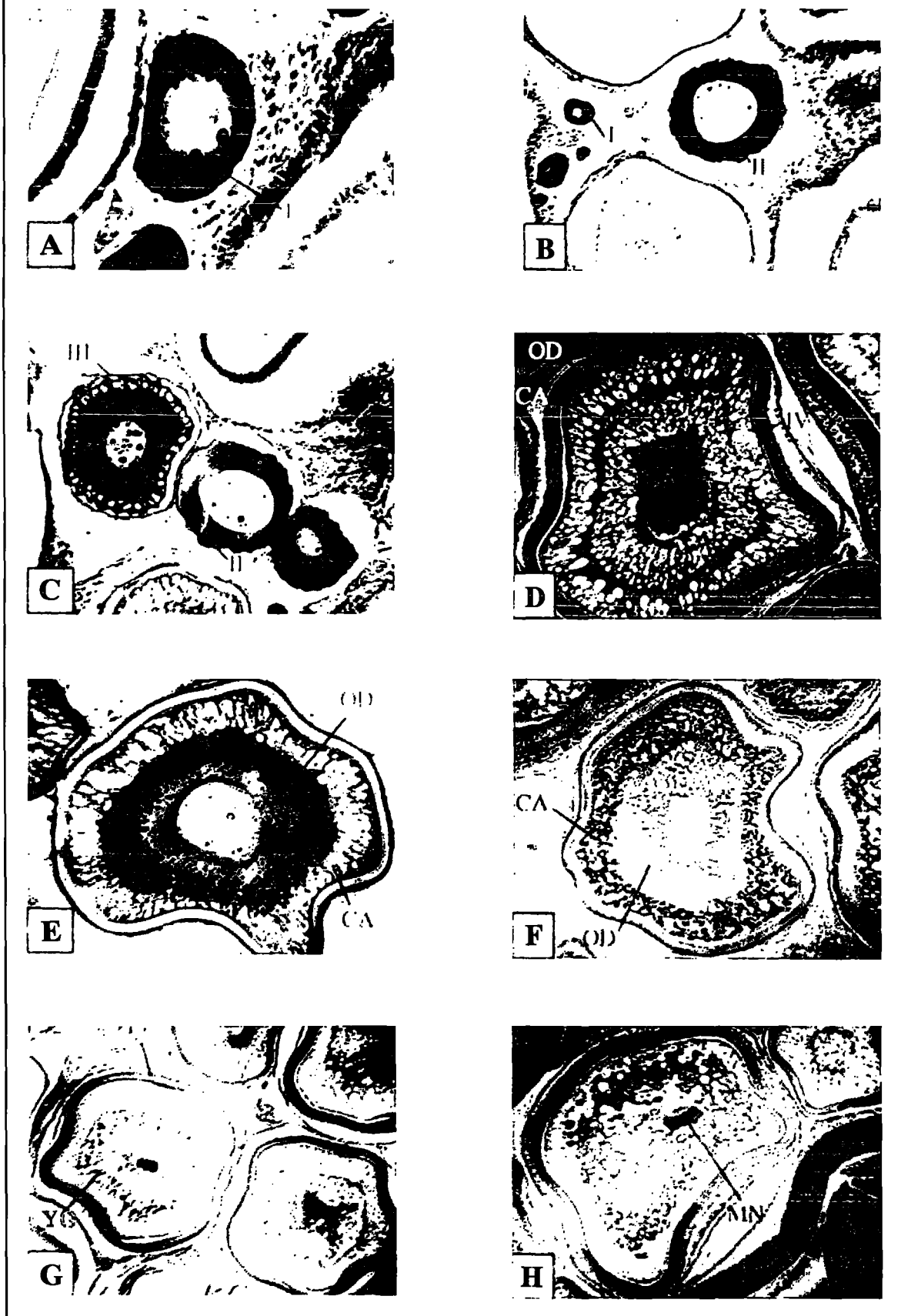

Figure 2

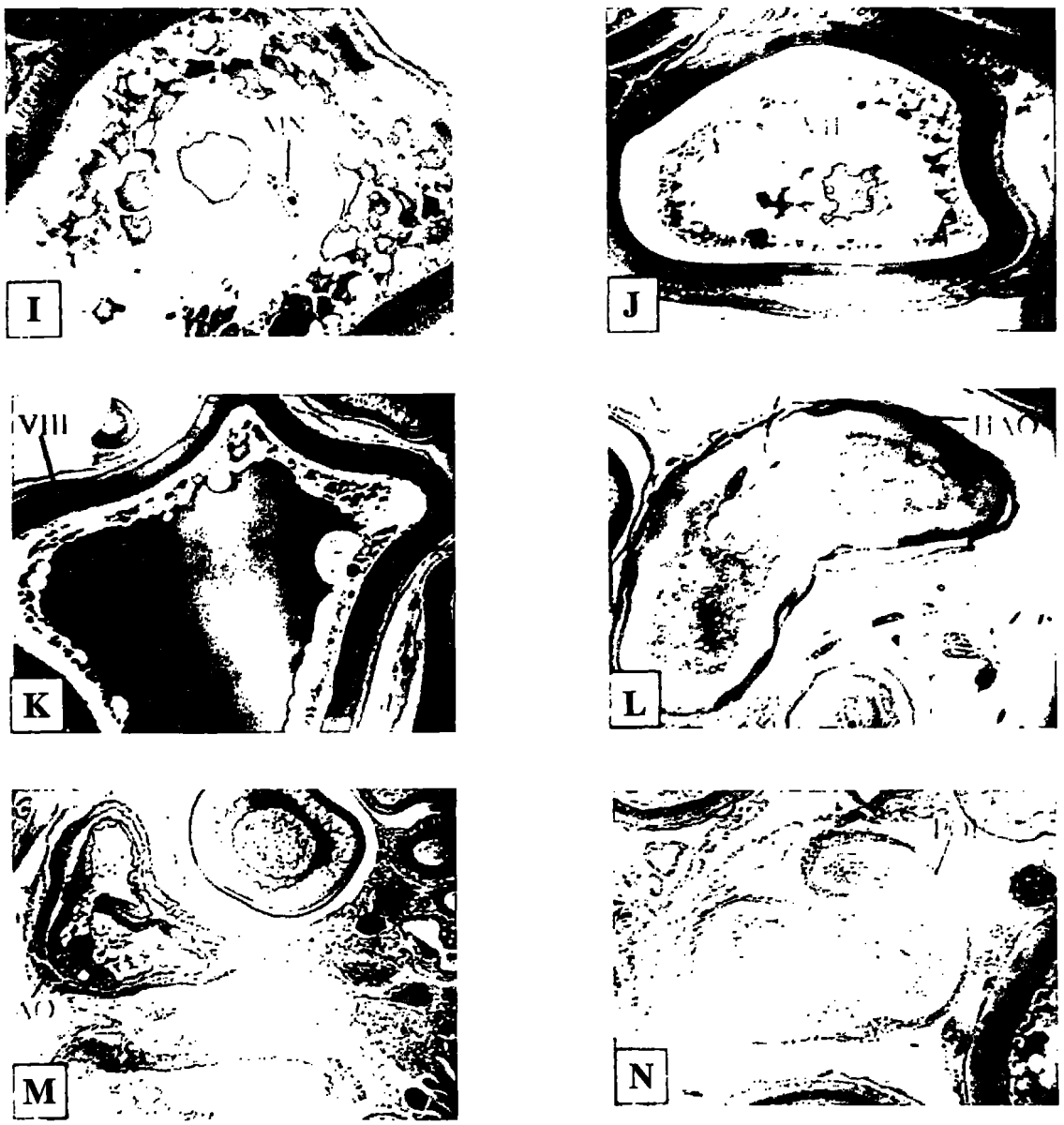

Figure 2

Histological cross sections of Atka mackerel ovaries stained with hematoxylin and eosin stain, except E and F: (**A**) cross section of ovary with early perinucleus oocyte (egg stage 1) (× 200); (**B**) cross section of ovary with late perinucleus oocyte (egg stage 2) (× 79); (**C**) cross section of ovary with late perinucleus oocyte (egg stage 2) and cortical alveoli stage (egg stage 3) (× 79); (**D**) cross section of ovary with oil droplet oocyte (egg stage 4), both cortical alveoli and oil droplets appear as clear droplets (× 200); (**E**) cross section of ovary with oil droplet oocyte (egg stage 4), oil droplets are staining deep black, cortical alveoli are clear (Sudan black) (× 200); (**F**) cross section of ovary with oil droplet oocyte (egg stage 4), cortical alveoli are staining PAS positive, oil droplets appear clear (PAS) (× 200); (**G**) cross section of ovary with vitellogenic oocyte (egg stage 5), yolk is staining eosin-positive (× 79); (**H**) cross section of ovary with early migratory nucleus stage (egg stage 6), yolk droplets fuse to yolk platelets (× 79); (**I**) cross section of ovary with late migratory nucleus oocyte, nuclear wall is disintegrated (× 200); (**J**) cross section of ovary with early hydrated oocyte (egg stage 7) (× 79); (**K**) cross section of ovary with late hydrated oocyte (egg stage 8) (× 79); (**L**) cross section of ovary with atretic hydrated oocyte (× 79); (**M**) cross section through ovary showing alpha atresia in a yolked oocyte (× 79); (**N**) cross section through ovary with post-ovulatory follicle (× 79). Roman numberals I–VIII=oocyte stages 1–8. AO=atretic oocyte; CA=cortical alveoli; HAO=hydrated atretic oocyte; MN=migratory nucleus; OD=oil droplets; POF=postovulatory follicle; and YG=yolk globules.

In order to define maturity stages, the most advanced oocyte stage in each specimen was used (Table 3). In most cases, oocytes in all stages up to the most advanced stage observed were present. For some of the spawning fish, however, stage 5 oocytes (vitellogenic) were absent. Since Atka mackerel are batch spawners (Zolotov, 1993), the number of advanced oocytes (egg stage 5 and larger) decreased with the number of batches spawned.

For the Aleutian Islands region, the ovaries of the mature females were far enough advanced to distinguish mature from immature fish by the presence of advanced oocyte stages (stages 5–9). Because of the timing of the collection of samples for the Gulf of Alaska, some of the maturity classification was done by comparing GSI values. Certain Gulf of Alaska samples showed a GSI that was almost an order of magnitude smaller than the GSI of the mature fish even though the oocytes appeared to be in a similar oocyte stage (stage 4, cortical alveoli and oil globules present). Because the GSI value was not continuous but showed a distinctive gap and because there was no evidence of yolk in the presumably immature ovaries, fish that belonged in the group with the lower GSI value were classified as immature. This GSI value coincided with the GSI value of the immature fish in the Aleutian Island region, and the age at maturity calculated also coincided with the age at maturity determined for the samples in the Aleutian Island region. However, until year-round samples for the Gulf of Alaska can be obtained, the possibility of the presumably immature fish spawning later in the year cannot be excluded.

Reproductive cycle

Since data were not available throughout the year in all of the areas, the data were pooled and compared by month only. Mean oocyte stage did not increase substantially from January until June, when most females possessed ovaries with stage 5 oocytes (vitellogenesis) (Fig. 3). Mean oocyte stage started to increase rapidly in June, peaked in August, and declined slightly in September. The mean GSI value

Table 3

Definition of maturity stages of Atka mackerel.

Maturity stage	Description	Most advanced oocyte stages
Stage 1: Immature	Ovary small with small oocytes. Oogonial nests, early and late perinucleus stages and cortical alveoli stage present. In some ovaries early oil droplet stage present.	Oocyte stages 1–3; early oocyte stage 4
Stage 2: Developing	Ovary increasing in size. Oocytes show oil droplets in advanced stage. Ovary wall thickens. Vascularization increases.	Oocyte stage 4
Stage 3: Vitellogenesis	Large visible eggs undergoing yolk development. Yolk globules present in oocytes. Wide range in oocyte diameter since oocytes from stage 1 through stage 5 are present.	Oocyte stage 5
Stage 4: Early hydration	Most advanced yolked oocytes are in migratory-nucleus and early hydration stage. Yolk is not completely coalesced in hydrated oocytes. Oocytes are present in stages 1–7	Oocyte stages 6 and 7
Stage 5: Spawning	Large oocytes visible at 2 mm. In advanced oocytes, yolk is completely coalesced. Number of yolked oocytes decreases as multiple batches are spawned. After first spawning, postovulatory follicles (POF) are present. In ovaries of fish that have spawned more than one batch, different stages of POF are distinguishable. In some cases proportion of vitellogenic oocytes decreases with the increase of hydrated oocytes. Ovaries are highly vascularized. Ovulated oocytes are found free-flowing in the center of the ovary.	Oocyte stages 8 and 9
Stage 6: Spent	Ovary appears flaccid and highly vascularized. Ovary shows abundance of late POF, and atretic hydrated oocytes. Healthy oocytes are all in early developing stage.	Oocyte stage 3 and 4, presence of postovulatory follicles and atretic hydrated oocytes. Atresia of oocyte stages 5–8.

reflected a similar pattern (Fig. 3), although a slight increase was noted from February through June, reflecting slow growth of oocytes during that time. The rapid increase from June through August suggests a rapid period of oocyte growth during vitellogenesis and hydration. The decrease in GSI after August reflects the loss of ovary weight due to spawning single batches, but it should be noted that the GSI in October is still higher than the GSI value in June, which suggests, that the fish might be still spawning their last batches. High variance in GSI and mean egg stage during the spawning period (July though October) could be attributed to batch spawning since most females were not spawning synchronously and the ovary weight and oocyte stages differed accordingly.

Examination of maturity stages over time indicated the same cycle with a long period of initial oocyte development, the appearance of vitellogenesis in June, and peak spawning in August (Fig. 4). Vitellogenesis progressed rather rapidly and was observed almost exclusively in June. However, vitellogenic eggs were found throughout most of the early hydration stage and during the spawning in some ovaries. It should be mentioned that in one cruise a few spawning fish were found in the central Aleutians in March and April 1992. While this was an oddity not observed in other years, it suggests that under certain circumstances fish can spawn as early (or late) as March.

In general, Atka mackerel develop their oocytes slowly in the oil droplet phase from at least January until May, with a gradual increase in oocyte size and ovary weight. Vitellogenesis starts in June and early migratory nucleus and early hydration is observed in July. Spawning individuals were observed from July until October with the peak in August, when the highest mean egg stage and GSI values were observed. Fish with ovaries having hydrated eggs in October were clearly spawning their last batch as they had many atretic hydrated oocytes, no vitellogenic, and few early hydrated oocytes present. Spent ovaries were found in September and October. Since no samples were collected in November and December, it is not clear how long the spawning season could last. However, by January all fish collected were in the early developing phase for the next year's cycle.

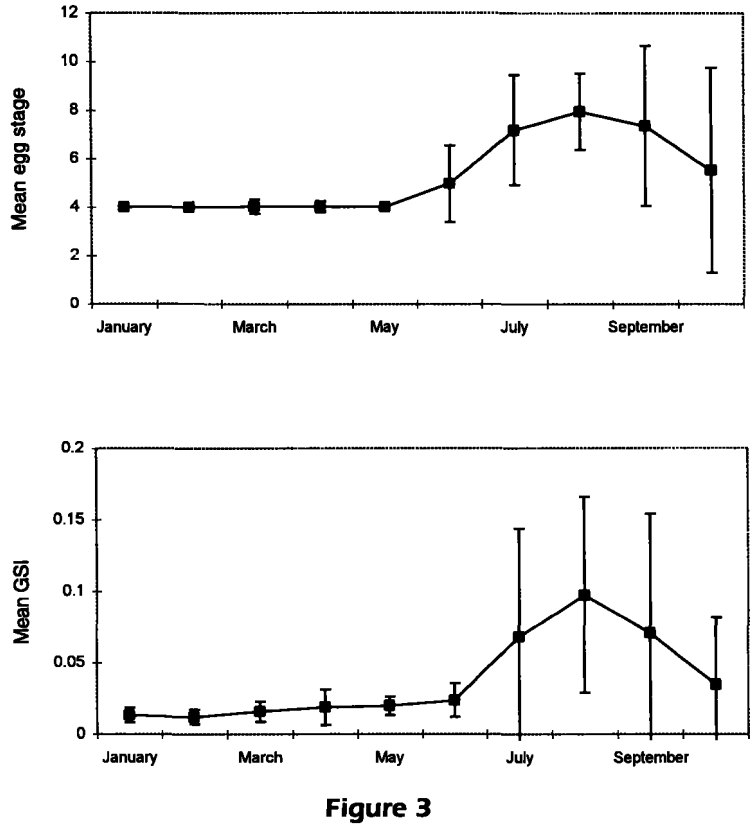

Figure 3

Mean oocyte stage and mean gonad somatic index (GSI) by month for mature Atka mackerel.

Size and age at 50% maturity

Size at 50% maturity ranged from 33 cm to 38 cm (Table 4). However, subarea was a highly significant factor ($P<0.001$), exhibiting a cline in the size at 50% maturity from east to west (Table 4, Fig. 5). Samples from the eastern areas reached 50% maturity at larger sizes. Length at 50% maturity in the Gulf of Alaska was 38.24 cm, while in the eastern Aleutian subarea the fish matured at 35.91 cm. Samples from the central and western Aleutian subareas matured at essentially the same size, 33.55 cm and 33.64 cm, respectively .

Age at maturity was not significantly different among the different Aleutian subareas ($P=0.66$) or between the Gulf of Alaska versus the Aleutian subareas combined ($P=0.69$), therefore the data were pooled. The age at 50% maturity (all areas combined) was 3.6 years for Atka mackerel (Table 4, Fig. 6).

Discussion

In order to make inferences about population parameters and biology, it is necessary to take representative samples of the population's true age and size

composition and sex ratio throughout their distribution. Due to the opportunistic nature of obtaining samples, only the portion of the population available to fisheries and research vessels was sampled. These are likely the larger animals, i.e. the mature individuals of the population. Therefore the results of length and age at maturity could be overestimated. Additionally, during the time of sex segregation the samples may be biased towards more females, since the males may be unavailable for sampling. Until the population distribution over time and space is better understood, it will be difficult to design sampling schemes that will yield unbiased population parameters.

Egg stage development for Atka mackerel is similar to that described for the masked greenling (*Hexagrammos octagrammos*) (Munehara et al., 1987; Munehara and Shimazaki, 1989). Oogenesis in Atka mackerel exhibited the following sequence:

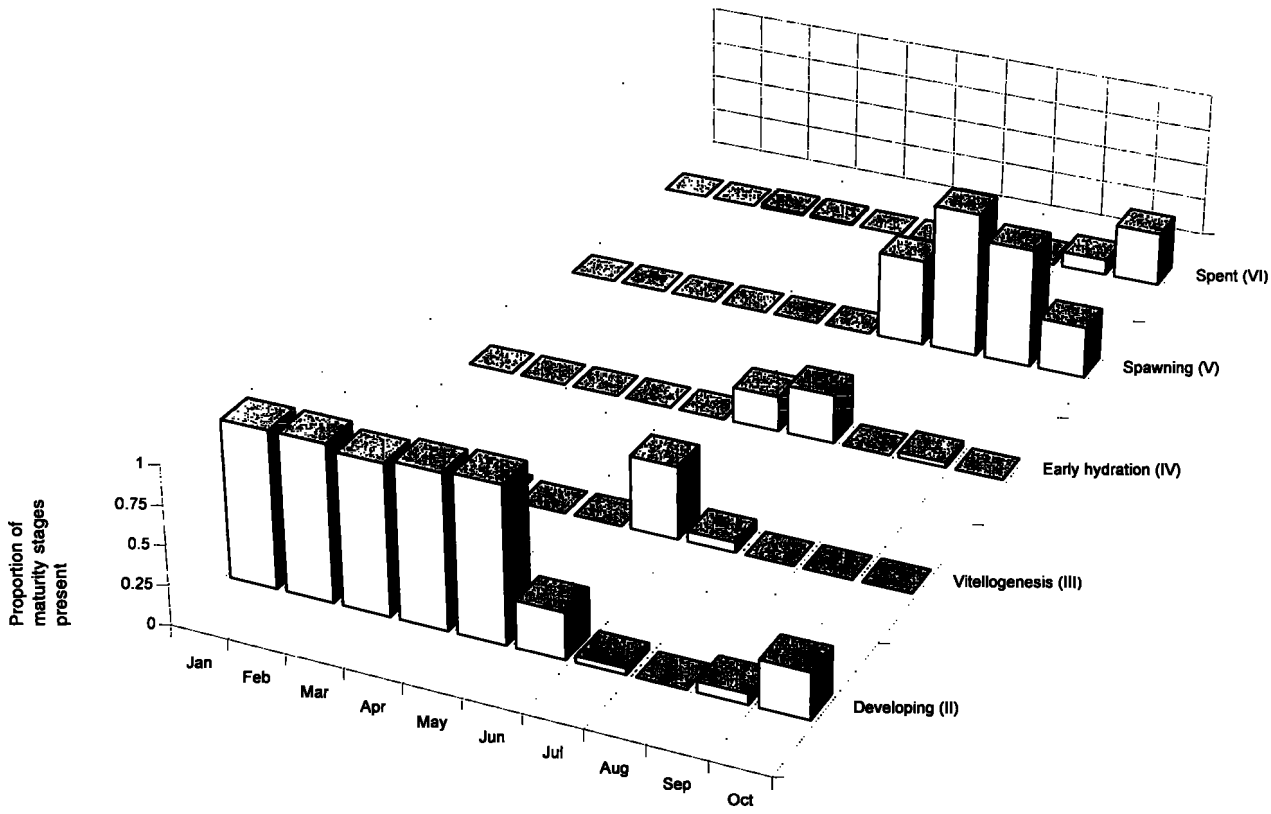

Figure 4
Maturity stage present by month for Atka mackerel.

Table 4
Length and age at maturity for Atka mackerel.

Area	$\hat{\alpha}$	$S(\hat{\alpha})$	$\hat{\beta}$	$S(\hat{\beta})$	L 50%	95% CI (low)	95% CI (upper)	Var (L 50%)
Gulf of Alaska	−27.16	3.69	0.71	0.09	38.24	36.27	40.21	1.00
Eastern Aleutians	−25.50	3.57	0.71	0.09	35.91	33.94	37.90	1.01
Central Aleutians	−23.83	3.67	0.71	0.09	33.55	31.12	36.57	1.54
Western Aleutians	−23.89	3.68	0.71	0.09	33.64	31.20	36.69	1.55
Area	$\hat{\alpha}$	$S(\hat{\alpha})$	$\hat{\beta}$	$S(\hat{\beta})$	**Age 50%**	**95% CI (low)**	**95% CI (upper)**	**Var (Age 50%)**
Areas combined	−7.33	0.87	2.03	0.22	3.60	3.40	3.81	0.01

the formation of cortical alveoli, followed by oil droplets, yolk accumulation, nuclear migration, and hydration (Fig. 2). The appearance of oil droplets after the formation of cortical alveoli and the coalescence of yolk before or during nuclear migration are features that have also been described for masked greenling (Munehara et al., 1987). Another feature that is similar to the masked greenling is that hydrated atretic oocytes were reabsorbed very slowly and could be found in the ovary for over 1 year.

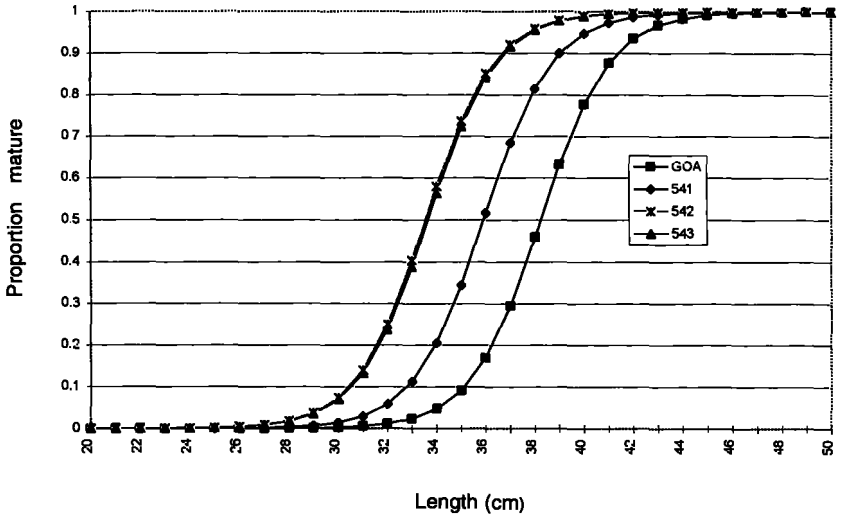

Figure 5

Length at maturity by geographical area for Atka mackerel; 541 = eastern Aleutians, 542 = central Aleutians, 543 = western Aleutians, GOA = Gulf of Alaska.

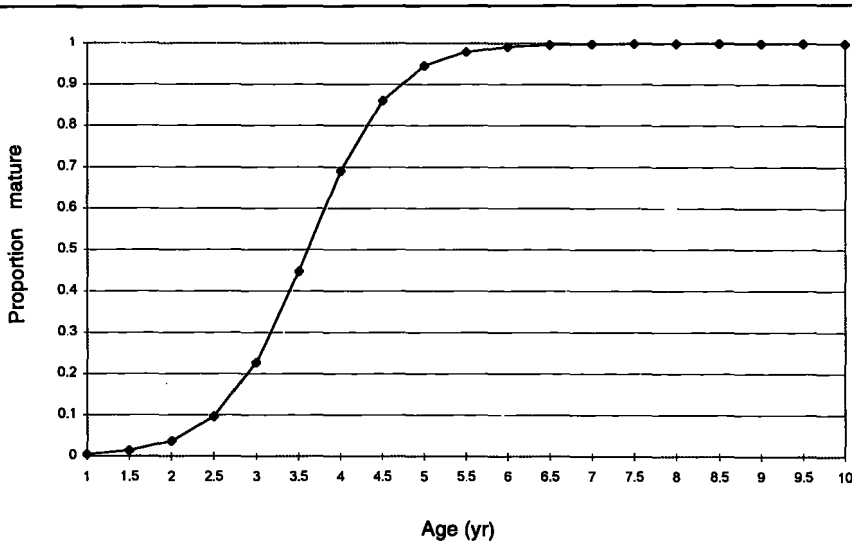

Figure 6

Age at maturity (all geographical areas pooled) for Atka mackerel.

The early maturation of the Atka mackerel ovary is characterized by an accumulation of oil droplets in the developing oocytes with a gradual increase in oocyte size over several months from January until May. Vitellogenesis is completed within 1 month, similar to the duration of vitellogenesis in masked greenling, but uncommonly short for most subarctic fishes (Munehara and Shimazaki, 1989).

The spawning period for Atka mackerel is extended and can last up to 4 months, from July through October. This relatively long spawning period can be attributed to the duration of time spent between the spawning of individual batches. Zolotov (1993) stated that the greater number of batches and the longer interval between their spawning corresponds to the longer duration of the reproductive period of Atka mackerel as compared with the arabesque greenling (*Pleurogrammus azonus*). The average spawning duration of 3 months found in this study is in agreement with the spawning duration reported for Atka mackerel in Kamchatka waters (Zolotov, 1993). However, the beginning of spawning in Alaska waters was observed in July lasting until October, whereas the spawning period in Kamchatka waters was described as starting in June and lasting until September (Zolotov, 1993). These differences may be attributed to year-to-year variations; however, different oceanographic conditions in Alaska versus Kamchatka waters may also be a contributing factor. There are not enough data to substantiate a seasonal cline in the timing of the reproductive cycle ranging from Kamchatkan waters to the Gulf of Alaska. The observation of a few spawning fish in March and April indicates that spawning times may be more variable than previously assumed. Data from several years were pooled in this study as the number of samples was insufficient to distinguish annual differences.

Reproductive timing and parameters can vary from year to year; this might be reflected in increased variance and range of the results in this study.

The spawning period during late summer and fall for Atka mackerel is earlier than that observed for the masked greenling (September through October; Munehara and Shimazaki, 1989), but later in the year than most other Alaska groundfish of commercial importance. Sablefish (*Anoplopoma fimbria*), Pacific halibut (*Hippoglossus stenolepis*), arrowtooth flounder (*Atheresthes stomias*), and flathead sole (Hippoglossoides elassodon) are reported to spawn in winter and early spring in the Gulf of Alaska, whereas walleye pollock (*Theragra chalcogramma*), Pacific cod (*Gadus macrocephalus*), Pacific ocean perch (*Sebastes alutus*), and rock sole (*Pleuronectes bilineatus*) were reported to have their spawning peak from spring to early summer in the Gulf of Alaska (NPFMC[4]). The life history feature of summer and fall spawning for Atka mackerel and other greenling species might be an adaptation to spawning large demersal eggs, the larvae of which enter the plankton at a larger size than larvae from pelagic eggs (Kendall and Dunn, 1985).

The differences by subarea for length at 50% maturity can be attributed to different growth rates by subarea, given that no age-at-maturity differences among geographical areas were found. Length-at-age curves in each management area revealed an increasing size at age from west to east (Lowe and Fritz[3]). The reasons for these different growth rates are unknown. It is not clear whether more favorable conditions such as food availability, or a more favorable temperature regime are contributing to a higher growth rate in the Gulf of Alaska and eastern Aleutian Islands subarea, or whether there are genetic differences in the populations. However, initial genetic studies suggest that there is little or no stock differentiation in Alaska (Winans[5]).

Analysis of fisheries data (Fritz[2]) indicated that in late summer and fall commercial hauls in many locations had a larger proportion of females than males. Sex segregation coincided with the spawning season (July through October) and supported the hypothesis that males were unavailable to the fishery, presumably guarding nests close to shore. Segregation of the Atka mackerel population by sex during the spawning season could also affect the results of summer trawl surveys used to assess population size if only a portion of the population is surveyed. More information on the location of nesting sites, behavior, and spawning distribution is necessary to understand the implications of population segregation on resource assessments.

Future research should be conducted on a more long-term basis for collection of maturity information, and larval and juvenile biology and distribution. Time and area gaps should be filled to understand the spatial and seasonal distribution patterns linked to spawning, crucial for assessing and managing this species appropriately.

[4] NPFMC. 1994. Fishery Management plan for the Alaskan Gulf of Alaska groundfish fishery. North Pacific Fishery Management Council, P.O. Box 103136, Anchorage, AK 99510.

[5] Winans, G. Northwest Fish. Sci. Center, Natl. Mar. Fish. Serv., NOAA, Seattle, WA 98112. Personal commun.

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Literature Cited

Chilton, D. E., and R. J. Beamish.
1982. Age determination methods for fishes studied by the groundfish program at the Pacific Biological station. Can. Spec. Pub. Fish. Aquat. Sci. 60, 102 p.

Galigher, A. E., and E. N. Kozloff.
1971. Essentials of practical microtechnique. Lea and Febiger, Philadelphia, PA, 531 p.

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

Gunderson, D. R., and P. H. Dygert.
1988. Reproductive effort as a predictor of natural mortality rate. J. Cons. Cons. Int. Explor. Mer. 44:200–209.

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(2):119–136.

Kajimura, H.
1984. Opportunistic feeding of the northern fur seal,

Callorhinus ursinus, in the eastern north Pacific Ocean and eastern Bering Sea. U.S. Dep. Commer., NOAA Tech. Rep. NMFS SSRF-779, 49 p.

Kendall, A. W., Jr., and J. R. Dunn.
1985. Ichthyoplankton of the continental shelf near Kodiak Island, Alaska. U.S. Dep. Commer., NOAA Tech. Rep. NMFS 20, 89 p.

Livingston, P. A., A. Ward, G. M. Lang, and M-S. Yang.
1993. Groundfish food habits and predation on commercially important prey species in the eastern Bering Sea from 1987 to 1989. U.S. Dep. Commer., NOAA Tech. Memo. NMFS-AFSC-11, 192 p.

Munehara, H., K. Shimazaki, and S. Mishima.
1987. The process of oogenesis in masked greenling, *Hexagrammos octogrammus*. Bull. Fac. Fish. Hokkaido Univ. 38(1):27–33.

Munehara, H., and K. Shimazaki.
1989. Annual maturation changes in the ovaries of masked greenling *Hexagrammos octogrammus*. Nippon Suisan Gakkaishi 55(3):423–429.

Rutenberg, E. P.
1962. Survey of the fishes of family Hexagrammidae. In Russian. (Trans. by Isr. Program Sci. Trans., 1970, p. 1–103. *In* T. S. Rass (ed.), Greenlings: taxonomy, biology, interoceanic transplantation. Available from U.S. Dep. Commer., Natl. Tech. Inf. Serv., Springfield, VA, as TT 69-55097.

Seber, G. A. F.
1982. The estimate of animal abundance and related parameters. Charles Griffin and Company, London, 654 p.

Venables, W. N., and B. D. Ripley.
1994. Modern applied statistics with S-plus. Springer Verlag, NY, 462 p.

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