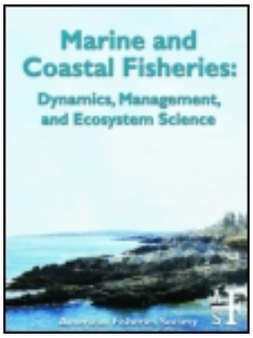

Taylor & Francis
Taylor & Francis Group

Marine and Coastal Fisheries

Dynamics, Management, and Ecosystem Science

ISSN: (Print) 1942-5120 (Online) Journal homepage: https://www.tandfonline.com/loi/umcf20

Spatial and Temporal Variability in Atka Mackerel Female Maturity at Length and Age

Daniel W. Cooper , Susanne F. McDermott & James N. Ianelli

To cite this article: Daniel W. Cooper , Susanne F. McDermott & James N. Ianelli (2010) Spatial and Temporal Variability in Atka Mackerel Female Maturity at Length and Age, Marine and Coastal Fisheries, 2:1, 329-338, DOI: 10.1577/C09-045.1

To link to this article: https://doi.org/10.1577/C09-045.1

Copyright Taylor and Francis Group, LLC

Published online: 09 Jan 2011.

Submit your article to this journal

Article views: 440

View related articles

Citing articles: 5 View citing articles

Full Terms & Conditions of access and use can be found at
https://www.tandfonline.com/action/journalInformation?journalCode=umcf20

Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science 2:329–338, 2010
© Copyright by the American Fisheries Society 2010
DOI: 10.1577/C09-045.1

[Special Section: Atka Mackerel]

Spatial and Temporal Variability in Atka Mackerel Female Maturity at Length and Age

DANIEL W. COOPER,* SUSANNE F. MCDERMOTT, AND JAMES N. IANELLI

National Marine Fisheries Service, Alaska Fisheries Science Center, 7600 Sand Point Way Northeast, Seattle, Washington 98115, USA

Abstract.—Spatial and temporal variability in maturity at length and maturity at age was examined for female Atka mackerel *Pleurogrammus monopterygius* in the eastern and central Aleutian Islands of Alaska. Postovulatory follicles (POFs) were evaluated as a potential character to distinguish spent mature fish from immature fish. We estimated that POFs remain in the ovaries for approximately 1 month after spawning, therefore allowing us to include some collections of recently spent fish for maturity estimates. Maturity-at-length data varied significantly among geographic areas and years, whereas maturity-at-age data failed to indicate differences. These results are probably attributable to different growth rates between the areas. An age-based model was developed to account for differences in year-class strengths, and modeling results showed that length at maturity could vary by as much as 4 cm over time because of variable recruitment. Maturity in Atka mackerel seems to be determined more by age than by somatic body size.

Maturity-at-age and maturity-at-length relationships are used in fisheries population dynamics to quantify reproductive output. Maturity at both age and length can vary spatially (Beacham 1983; Bowering 1989; Rochet 1998; Morgan and Colbourne 1999; Olsen et al. 2004) and temporally (Chen and Mello 1999; Morgan and Colbourne 1999; Barot et al. 2004; Hamatsu et al. 2004), causing error in estimates of reproductive output if a spatially and temporally fixed maturity relationship is used.

Commonly, either length or age is used to determine maturity in stock assessments. Although maturity is determined by a combination of age and length, one factor may be more influential than the other in determining maturity for a fish population (Stearns 1992). For stock assessment, selecting the determining factor (length or age) with less temporal and spatial variation would minimize error in reproductive output estimates.

Atka mackerel *Pleurogrammus monopterygius* currently represent the largest groundfish biomass in the Aleutian Islands, Alaska, and support a large-scale commercial trawl fishery. Atka mackerel females spawn an average of four batches per year (McDermott et al. 2007), and batches are estimated to be spawned 2–4 weeks apart (Zolotov 1993). McDermott and Lowe (1997) reported a constant age at 50% maturity (A_{50}) of 3.6 years for Atka mackerel throughout Alaska, but they documented decreasing length at maturity from east to west, which they attributed to differential spatial growth patterns. Temporal variability in Atka mackerel maturity at age or length has not been determined. Similar to many fish species, the magnitude of the incoming year-classes (annual recruitment) of Atka mackerel is highly variable (Lowe et al. 2008); however, the effect of year-class variation on maturity has not been studied.

To study the temporal and spatial variability associated with maturity at age and length in fish, it is necessary to distinguish spent females from immature females. One ovarian structure used to distinguish spent females from immature females is the postovulatory follicle (POF). Many reports describing POF degeneration indicate that POFs persist for 3 d or less (Hunter and Goldberg 1980; Goldberg et al. 1984; Hunter et al. 1986); therefore, Hunter et al. (1992) recommended avoiding sampling after spawning begins because POFs may not be identifiable and spent mature fish will be erroneously classified as immature. However, there are reports that POFs persist for months in fish from relatively cold waters, making maturity estimates possible from collections that include spent fish (Saborido-Rey and Junquera 1998; Narimatsu et al. 2005). Typical water temperatures during and after Atka mackerel spawning are approximately 4–11°C (Lauth et al. 2007).

Our objectives for this study were to (1) evaluate the use of POFs in maturity classification for postspawning Atka mackerel females; (2) use additional years of data to re-examine the conclusions of McDermott and Lowe (1997) that maturity at age is constant across areas, whereas maturity at length varies with spatial growth differences; (3) determine whether maturity at length or

Subject editor: Gary Duker, Alaska Fisheries Science Center, Seattle, Washington

* Corresponding author: dan.cooper@noaa.gov

Received August 10, 2009; accepted October 16, 2009
Published online October 4, 2010

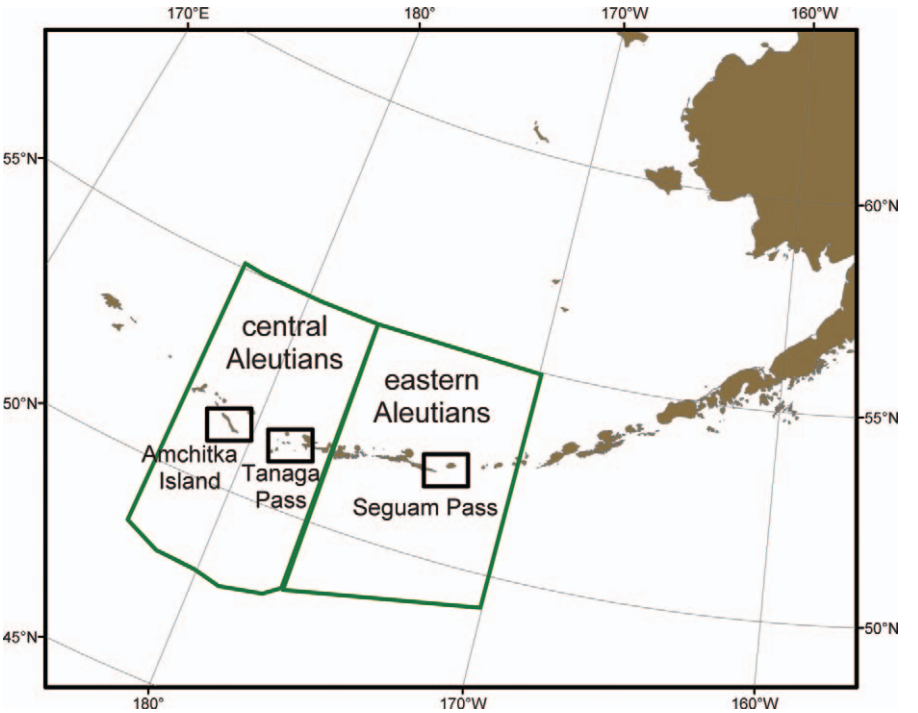

FIGURE 1.—Map of the study area, showing Atka mackerel female collection sites at Amchitka Island and Tanaga Pass (central Aleutian Islands [AI]) and Seguam Pass (eastern AI). National Marine Fisheries Service statistical area boundaries for the central and eastern AI are shown in green.

maturity at age (or both) varies temporally; and (4) model the effect of variability in annual population age composition on maturity at length.

Methods

Collection methods.—During 2002–2004, ovaries were collected aboard the National Marine Fisheries Service chartered vessel F/T *Seafisher* by using bottom trawl gear in the eastern Aleutian Islands (Seguam Pass) and the central Aleutian Islands (Tanaga Pass and near Amchitka Island; Figure 1). All cruises were conducted in October, coinciding with the end of the Atka mackerel spawning season (McDermott and Lowe 1997). Five females were randomly sampled from each trawl haul. Total weight (±2 g) and fork length (±1 cm) were recorded, and ovaries were removed and preserved in 10% formalin in seawater buffered with sodium bicarbonate. Otoliths were removed and stored in a 50% solution of ethanol. In addition to the samples collected for this study, the maturity data collected from both study areas in 1993

TABLE 1.—Number of female Atka mackerel used in the maturity analysis by time period and Aleutian Islands (AI) area.

Time period	Eastern AI	Central AI	Total
1993–1994[a]	62	142	204
2002	149	121	270
2003	169	203	372
2004	146	0	146
Total	526	466	992

[a] Data for 1993–1994 are from McDermott and Lowe (1997).

TABLE 2.—Schedule of female Atka mackerel mean fork length (cm) at age (L_a), standard deviation of length at age (σ_a), and maturity at age (φ_a) used for the model (from Lowe et al. 2005).

Age (years)	L_a	σ_a	φ_a
2	27.11	1.63	0.00
3	31.73	1.81	0.22
4	35.16	1.89	0.69
5	37.70	1.91	0.94
6	39.58	1.89	0.99
7	40.98	1.83	1.00
8	42.01	1.75	1.00
9	42.78	1.65	1.00
10	43.35	1.53	1.00
11	43.77	1.41	1.00
12	44.09	1.29	1.00
13	44.32	1.16	1.00
14	44.49	1.03	1.00
15	44.62	0.89	1.00

TABLE 3.—Equations used to generate the maturity at length shown in Figure 6 (σ_a = standard deviation of length at age [L_a]).

Description	Equation
Proportion at length i given age a	$p_{i,a} = \frac{1}{\sigma_a\sqrt{2\pi}}\exp\left(-\frac{(i-L_a)}{2\sigma_a^2}\right)$
Numbers at age (from Table 15.10 in Lowe et al. 2005)	N_a
Number at length	$N_i = \sum_{a=2}^{15} N_a p_{i,a}$
Maturity at length	$\varphi_i = \frac{\sum_{a=2}^{15} \varphi_a N_a p_{i,a}}{N_i}$

and 1994 by McDermott and Lowe (1997) were used to examine temporal variability in maturity (Table 1).

Histology.—After storage for 1–2 years, ovaries were removed from formalin and were soaked in freshwater for a minimum of 4 h before additional handling. The presence of residual unspawned ova within individual ovaries was observed macroscopically and was recorded. Residual unspawned ova are the few ova that were ready to be spawned but were not successfully expelled from the female. Residual unspawned ova are easily identified by the naked eye because they are relatively large (~2 mm) and blackish brown in color (compared with the rest of the ovary, which is pink or gray). They remain identifiable for a long period, and some persist in the ovaries for at least 1 year postspawning (McDermott and Lowe 1997).

A cross section was taken from the middle of one ovary, embedded in paraffin, sectioned at 4 μm, mounted on a slide, and stained with hematoxylin and eosin (McDermott and Lowe 1997). Ovary cross sections were examined at 40× and 100× magnification. Oocyte stages were determined, and the presence of POFs was recorded.

Maturity classification and postovulatory follicle evaluation.—Oocyte stages and maturity stages were defined by McDermott and Lowe (1997), and three stages of POFs were determined on the basis of descriptions by Hunter and Goldberg (1980). Spent females did not contain developing oocytes and were classified as mature based on presence of residual unspawned ova, POFs, or both. Residual unspawned ova are a reliable character for maturity, but they are not present in all mature females; therefore, they could not be used as a sole character to differentiate spent females from immature females. In females without residual unspawned ova, maturity determination was based solely on the presence of POFs. Because POFs are more ephemeral than residual ova, there is the potential for mature fish to have reabsorbed POFs and be erroneously assigned as immature fish. To reduce the magnitude of this error and to test the validity of POF presence as a maturity character, POF presence was examined in fish that were known to be mature based on the presence of residual unspawned ova. Ovary collections from a given year and area were considered suitable for maturity analysis when the percentage of known mature females (residual ova present) with identifiable POFs was high. It was assumed that these ovary collections were made soon enough after spawning so that the POFs were still present and identifiable within the ovaries of mature fish that did not contain residual unspawned ova.

Age determination.—Ages were assigned by the Alaska Fisheries Science Center's Age and Growth Program, which used otoliths according to the procedures outlined by Anderl et al. (1996).

Statistical analysis.—Generalized linear models (GLM) with binomial error distributions were applied to the proportion of females mature at each length and

TABLE 4.—Description of postovulatory follicle (POF) degeneration categories for Atka mackerel.

Degeneration category	Description
Early	Observed infrequently, and found most often in ovaries containing a batch of ova ready to be spawned. A convoluted structure composed of an outer layer of theca cells and an inner layer of granulosa cells surrounding a lumen. The theca cells are much thicker than the theca of a mature oocyte. The theca contains capillaries filled with erythrocytes. In most cases, the thick band of hypertrophied, columnar granulosa cells is separated from the theca and forms an inner ring of the POF. The granulosa layer is usually more convoluted than the thecal layer, and the two layers may not be in continuous contact. The granulosa nuclei are darkly staining and basally located in the columnar cells. The theca and granulosa cells are individually distinguishable.
Middle	The entire structure is about half the length of an early stage POF. A few erythrocytes may remain within the theca. The structure is much less convoluted. The granulosa cells form a continuous band within the theca, are reduced greatly in size, and are no longer columnar. The lumen is smaller but remains evident.
Late	The granulosa cells no longer form a continuous band inside the theca. The granulosa cells disappear until only the theca remains. There are no erythrocytes in the thecal layer. Individual theca cells can no longer be differentiated. The lumen may be largely occluded but remains apparent.

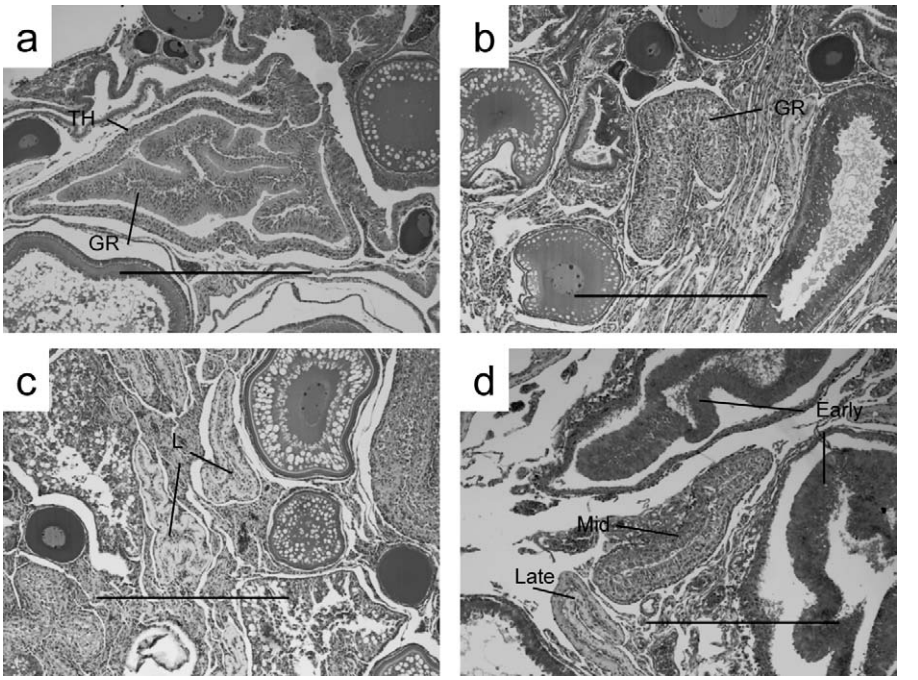

FIGURE 2.—Histological sections of Atka mackerel ovary, showing **(a)** an early stage postovulatory follicle (POF); **(b)** a middle-stage POF; **(c)** a late-stage POF; and **(d)** POFs of all three stages (scale bar = 1,000 μm; GR = granulosa; TH = theca; L = lumen).

age, with geographic area and time period as factors. The geographic areas were the eastern Aleutian Islands (Seguam Pass) and the central Aleutian Islands (Tanaga Pass and Amchikta Island). In most cases, each year represents a separate time period; however, 1993 and 1994 data were combined into one time period for the central Aleutian Islands as was done by McDermott and Lowe (1997). We tested the significance of the GLM terms by using the chi-square (χ^2) approximation test (Venables and Ripley 1997). The expected proportion of mature females at each length or age was determined by fitting the following logistic model to the observed data by using SPLUS (Insightful Corp., Seattle):

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

where Y = proportion mature at length or age x, α and β = parameters to be estimated, e = the base of natural logarithms, and x = fork length (cm) or age (years).

Estimating the effect of spatial growth differences on maturity at length.—The A_{50} was obtained from the combined data for both study areas. Using separate growth parameters for each area, the lengths at A_{50}

TABLE 5.—Number and percent of ovaries of known spent Atka mackerel females containing identifiable postovulatory follicles (POFs) by collection date and Aleutian Islands area (eastern or central).

Year	Region	Collection date	Known spent[a]	POFs present[b]	Percent[c]
2002	Eastern	1–3 Oct	25	25	100.0
	Central	4–10 Oct	56	53	94.6
2003	Eastern	21–30 Oct	46	46	100.0
	Central	8–20 Oct	112	108	96.4
2004	Eastern	9–14 Oct	52	50	96.2
	Central	16–22 Oct	90	63	70.0

[a] Number known to be spent because remnant ova were noted in the ovaries during processing for histology.
[b] Number of known spent females with identifiable POFs present in the histological section.
[c] Percent of known spent females that were correctly identified by POF presence.

TABLE 6.—Analysis of deviance from the generalized linear model of Atka mackerel female maturity at age for both Aleutian Islands areas and all time periods.

Added factor	Deviance	Residual df	Residual deviance	P (chi-square)
Null		965	1131.17	
Age	370.49	964	760.67	<0.00001
Area	0.71	963	759.97	0.400
Time period	3.73	962	756.24	0.0535

were estimated for each area by using the von Bertalanffy growth equation (von Bertalanffy 1938). The difference in these values was assumed to approximate the effect of spatial growth differences on maturity at length, and these values were compared with the lengths at 50% maturity (L_{50}) estimated from the maturity data for each area. The von Bertalanffy growth parameters were obtained from Lowe et al. (2008) and were estimated independently with data from fishery observers.

Maturity-at-length modeling.—A model was developed to determine the effect of population age composition on the maturity-at-length relationship

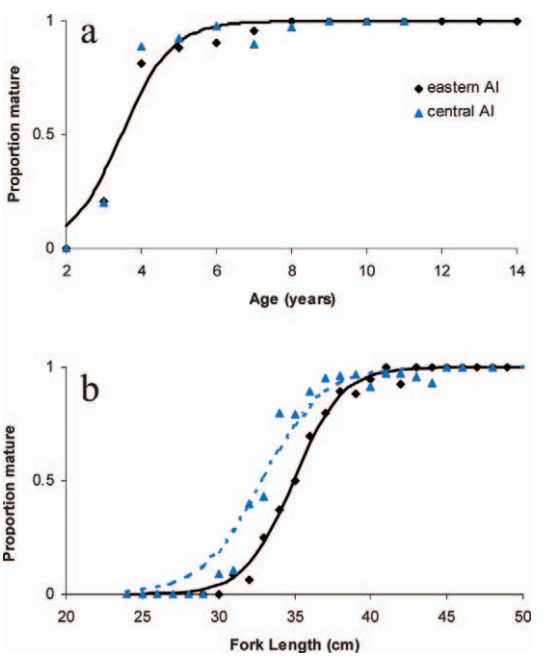

FIGURE 3.—Female Atka mackerel **(a)** maturity at age and **(b)** maturity at length for all time periods combined in two Aleutian Islands (AI) areas (black diamonds = eastern area; blue triangles = central area). The solid black line in (a) represents generalized linear model (GLM) results for both areas combined. The dashed blue line and the solid black line in (b) represent GLM model results for the central AI and eastern AI, respectively.

TABLE 7.—Maturity at length and maturity at age for female Atka mackerel in the eastern and central Aleutian Islands (AI) for all time periods combined (α, β = parameters from equation 1, s_α = standard error of α, s_β = standard error of β, A_{50} = age [years] at 50% maturity, L_{50} = fork length [cm] at 50% maturity).

Area	α	s_α	β	s_β	Estimate
Both areas combined	−5.18	0.44	1.49	0.11	$A_{50} = 3.47$
Eastern AI	−22.14	2.24	0.63	0.06	$L_{50} = 34.91$
Central AI	−16.59	1.85	0.51	0.05	$L_{50} = 32.84$

(Table 2, Table 3). This approach was designed simply to evaluate the extent to which a variable population age structure affects the observed maturity at length (under the assumption that growth and maturity at age were constant). The growth rate and the population age composition estimates used were from the Atka mackerel stock assessment by Lowe et al. (2005). The mean and variance of lengths given ages were used to produce a transition matrix where expected population length frequencies could be computed given estimated population numbers at age. Similarly, applying a maturity-at-age schedule (as from Lowe et al. 2005), the proportion of mature fish at each centimeter length increment could be calculated.

Results

Postovulatory Follicles

Three stages of POFs were described (Table 4; Figure 2). Atka mackerel oocytes contain oil droplets, which appear as clear, spherical objects when stained with hematoxylin and eosin

(McDermott and Lowe 1997); these oil droplets persist in vitellogenic oocytes undergoing beta-stage atresia. Postovulatory follicles do not contain oil droplets and can therefore be distinguished from advanced atretic oocytes. All three POF stages were present in some females (Figure 1d), indicating that POFs persist for at least two intervals between spawning events. Based on a reported interval of 2–4 weeks between batch spawning events (Zolotov 1993),

TABLE 8.—Analysis of deviance from the generalized linear model of Atka mackerel female maturity at length for both Aleutian Islands areas and all time periods.

Added factor	Deviance	Residual df	Residual deviance	P (chi-square)
Null		991	1159.49	
Length	407.02	990	752.46	<0.00001
Area	30.07	989	722.39	<0.00001
Time period	18.8774	988	703.51	0.000014

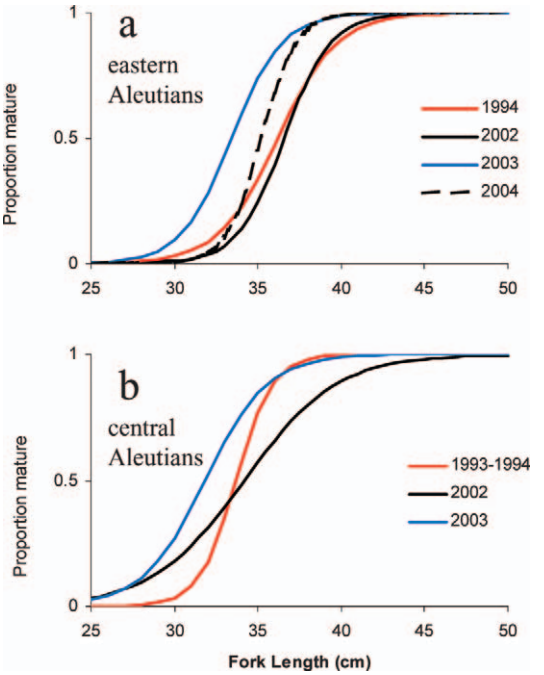

FIGURE 4.—Expected maturity at length in 1993–1994 (red line), 2002 (solid black line), 2003 (blue line), and 2004 (dashed black line) for Atka mackerel females in **(a)** the eastern Aleutian Islands and **(b)** the central Aleutian Islands.

POFs are estimated to be present for at least 4 weeks after spawning.

Postovulatory follicles were present in only 70% of females with residual eggs in samples taken from the central Aleutian Islands in 2004, indicating that sampling occurred too long after spawning to use POFs for reliable determination of maturity; consequently, these data were excluded from the analysis. Aside from the 2004 central Aleutian Islands data, POFs were present in 94–100% of known mature females in both areas during all years (Table 5), and these data were used in the maturity analysis.

Spatial Variability in Maturity

Maturity at age did not significantly vary between the study areas ($P = 0.40$), and a model was fitted to the combined data from both areas (Table 6; Figure 3a). Maturity at age was estimated to be 3.47 years (Table 7). Maturity at length did vary significantly by area ($P < 0.0001$; Table 8; Figure 3b). The L_{50} was estimated at 34.9 cm in the eastern Aleutian Islands and 32.8 cm in the central Aleutian Islands (Table 7). These L_{50} values were similar to the L_{50} values estimated from the von Bertalanffy equation using a combined A_{50} for both areas and area-specific growth parameters (L_{50} of 35.2 cm for the eastern Aleutian Islands and 32.5 cm for the central Aleutian Islands), indicating that spatial growth differences are great enough to cause the observed spatial differences in maturity at length.

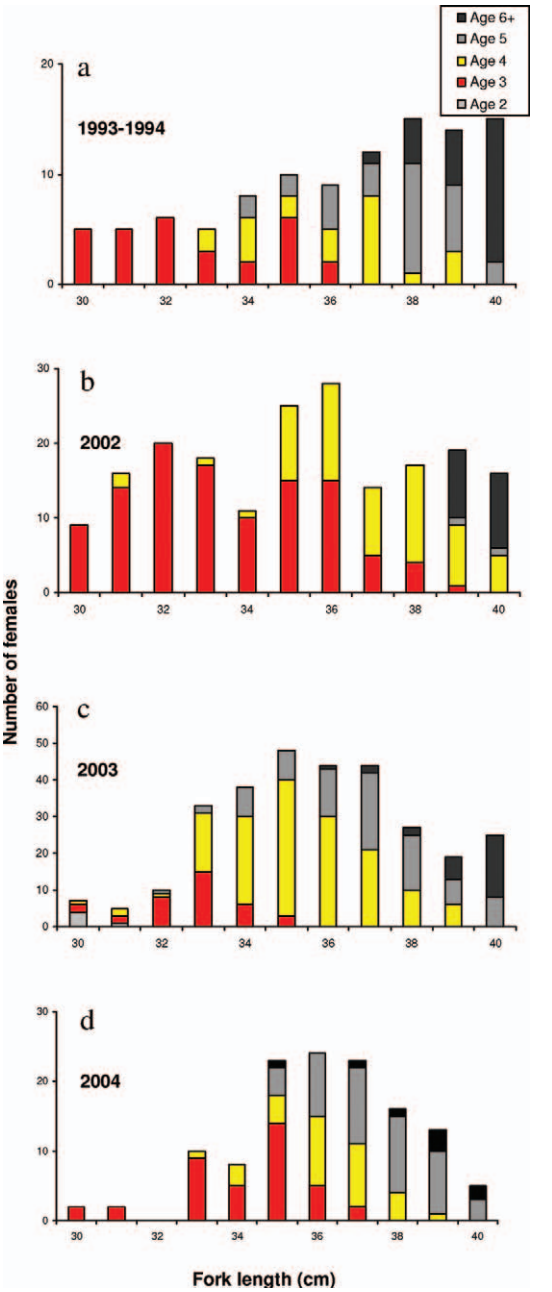

FIGURE 5.—Age composition of sampled female Atka mackerel within the fork length range (30–40 cm) encompassing the transition from immature to mature for the Aleutian Islands, Alaska, population: **(a)** 1993–1994, **(b)** 2002, **(c)** 2003, and **(d)** 2004.

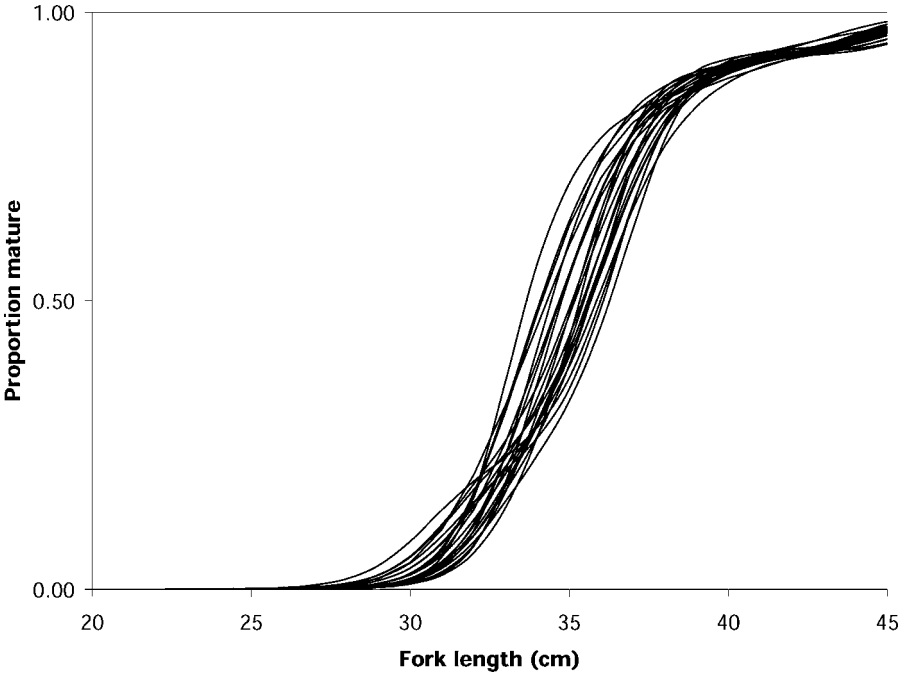

FIGURE 6.—Model results describing the effect of Atka mackerel year-class strength on the proportion of mature females at length in 1984–2005.

Temporal Differences in Maturity

Estimates of A_{50} ranged from 3.2 years in 2003 to 3.8 years in 2002; however, time period was not a statistically significant factor in maturity at age ($P = 0.053$; Table 6).

Length at 50% maturity varied significantly over time ($P < 0.0001$; Table 8); L_{50} was lowest in 2003 in both areas and was highest in 2002 (Figure 4).

Age Composition of Maturity Samples

The sampled Atka mackerel populations transitioned from immature to mature between 30 and 40 cm; in other words, females within this size range could be immature or mature. Females smaller than 30 cm were always immature, and females larger than 40 cm were almost always mature (Figure 3b). The age composition of 30–40-cm females varied with year-class strength (Figure 5). The relatively high percentage of age-3 fish collected in 2002 (Figure 5b) corresponded with the highest L_{50} values in both areas (Figure 4). In 2003, the relatively low percentage of age-3 fish (Figure 5c) corresponded with the lowest L_{50} values in both areas (Figure 4).

Length-at-Maturity Model

The model of the effect of year-class strength on maturity at length indicated that fluctuations in year-

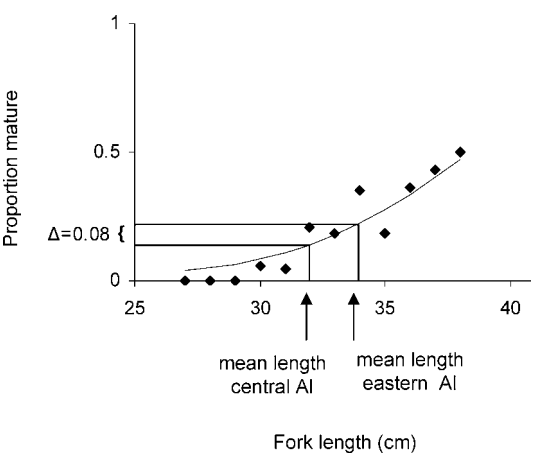

FIGURE 7.—Proportion of age-3 female Atka mackerel that were mature at each length; data are from the central and eastern Aleutian Islands (AI) areas (all time periods combined). Data points are denoted by black diamonds, and the solid line represents a logistic regression fit to the data. Arrows indicate the mean lengths of females collected in the central and eastern AI; the delta symbol (Δ) represents the difference in proportion mature between these lengths.

TABLE 9.—Postovulatory follicle (POF) reported durations for various species in relation to latitude and temperature (temp).

Species	Latitude (°)	POF duration (d)	Temp (°C)	Method[a]	Source
Ocean lightfish *Vinciguerria nimbaria*	0–5	1	Not reported	E	Stequert et al. (2003)
Pacific sardine *Sardinops sagax*	9	2	Not reported	E	Goldberg et al. (1984)
Yellowfin tuna *Thunnus albacares*	10	1	28–29	E	Schaefer (1996)
Skipjack tuna *Katsuwonus pelamis*	0–23	1	23–24	M	Hunter et al. (1986)
Nehu *Encrasicholina purpurea*	21	1	Not reported	E	Clarke (1987)
Northern anchovy *Engraulis mordax*	32–34	2	Not reported	M	Hunter and Goldberg (1980)
Carpenter seabream *Argyrozona argyrozona*	34	2	16	M	Brouwer and Griffiths (2005)
Atlantic menhaden *Brevoortia tyrannus*	35	1.5	19–20	M	Fitzhugh and Hettler (1995)
	35	5	15	M	Fitzhugh and Hettler (1995)
European pilchard *Sardina pilchardus sardina*	38–39	2.4	16.7–19.2	E	Ganias et al. (2003)
Rikuzen sole *Dexistes rikuzenius*	40–42	14–60	Not reported	E	Narimatsu et al. (2005)
Atlantic cod *Gadus morhua*	47	At least 90–120	Not reported	E	Saborido-Rey and Junquera (1998)
European flounder *Pleuronectes flesus*	53	30	Not reported	E	Janssen et al. (1995)
European plaice *Pleuronectes platessa*	55	60	Not reported	E	Barr (1963)

[a] M denotes fish held in a laboratory with POF duration measured from known spawn date and time; E denotes POF duration estimated by comparing POF presence with estimated spawn date or time.

class strength can cause L_{50} to fluctuate over time by as much as 4 cm, even if age at maturity and growth remain constant (Figure 6).

Combined Effect of Length and Age on Maturity

To examine the combined effects of age and length on maturation, a logistic model was fitted to observed maturity-at-length data for age-3 females. The proportion of mature fish increased with length for age-3 females (Figure 7).

Discussion

Atka mackerel maturity can be assigned on the basis of POF presence after some females are spent. Such a finding is important for this species because some mature females cannot be distinguished from immature females until June or July, and the earliest-spawning females are spent in August. By taking advantage of an extended POF persistence time in ovaries, samples for maturity can be collected as late as October, although October was too late in the central Aleutian Islands in 2004. The ability to determine maturity based on POF presence is important for this relatively remotely located species with limited sampling opportunities, and it may be important for other similar species. Postovulatory follicle duration seems to be closely related to water temperature. Fitzhugh and Hettler (1995) observed that POF duration in Atlantic menhaden *Brevoortia tyrannus* increased from 1.5 to 5.0 d when water temperature decreased from 19–20°C to 15°C, and there may be a general relationship with temperature among species as well. Published reports of POF duration indicated negative relationships with temperature and positive relationships with latitude, which is presumably related to temperature (Table 9).

Atka mackerel maturity seems to be more dependent on fish age than on fish length. Maturity at age did not vary temporally or spatially, whereas maturity at length was both spatially and temporally variable. These data support the conclusions of McDermott and Lowe (1997) that maturity at age is spatially constant, whereas maturity at length varies spatially with differential growth patterns. We confirmed that spatial growth differences are great enough to cause the observed differences in maturity at length between Atka mackerel females in the central and eastern Aleutian Islands.

Examination of maturity at length for age-3 females (Figure 7) may explain why maturity seems fixed with age, even though life history theory predicts that both age and length at maturity should vary with growth changes (Stearns 1992). Although length did affect the probability of maturity, the observed spatial length differences caused only small changes in the proportion of mature age-3 females (0.08 is the expected fraction). It seems likely that the observed spatial and temporal growth differences would cause small differences in maturity at age, but the differences were probably too small to be detected by our methodology.

The Atka mackerel stock assessment assumes that maturity at age is temporally and spatially constant (Lowe et al. 2008). This assumption seems robust within the observed ranges of growth rates in this study. For this species, age is a better (i.e., less temporally and spatially variable) predictor of maturity than is length, and a fixed maturity-at-age estimate used for stock assessment will cause less error in spawning biomass estimates over time than a fixed maturity-at-length estimate. It seems that variation in Atka mackerel maturity at length is at least partly due to the relative age composition of the population. Females mature between 30 and 40 cm; depending on

year-class strength, this length range could be dominated by either age-3 fish or age-4 fish. Because age-4 females are more likely to be mature than age-3 females, maturity at length shifts over time with changes in year-class strength caused by recruitment variability. For assessment purposes, it seems prudent to account for population maturity based on age. In many settings, length-based stock assessments assume that maturity is based on length independent of age (e.g., Thompson et al. 2007). Doing so for Atka mackerel would create bias in estimates of spawning stock biomass, which are critical for conservation and management recommendations. This is clearly a potential problem for similar species if similar length-based stock assessments are applied.

Acknowledgments

We thank Kimberly Rand and Sandi Neidetcher (Alaska Fisheries Science Center) for assistance with ovary collections, and we thank Martin Dorn (Alaska Fisheries Science Center) for discussions of the effects of length and age on maturity. Sandra Lowe, Dan Nichol, and Libby Logerwell (Alaska Fisheries Science Center) improved this article with thoughtful reviews. This study was partially funded by a grant from the North Pacific Research Board (Project Number 522).

References

Anderl, D. M., A. Nishimura, and S. A. Lowe. 1996. Is the first annulus on the otolith of the Atka mackerel, *Pleurogrammus monopterygius*, missing? U.S. National Marine Fisheries Service Fishery Bulletin 94:163–169.

Barot, S., M. Heino, L. O'Brien, and U. Dieckmann. 2004. Long-term trend in the maturation reaction norm of two cod stocks. Ecological Applications 14:1257–1271.

Barr, W. A. 1963. The endocrine control of the sexual cycle in the plaice, *Pleuronectes platessa* (L) I: cyclical changes in the normal ovary. General and Comparative Endocrinology 3:197–204.

Beacham, T. D. 1983. Variability in median size and age at sexual maturity of Atlantic cod, *Gadus morhua*, on the Scotian shelf in the northwest Atlantic Ocean. U.S. National Marine Fisheries Service Fishery Bulletin 81:303–321.

Bowering, W. R. 1989. Witch flounder distribution off southern Newfoundland, and changes in age, growth, and sexual maturity patterns with commercial exploitation. Transactions of the American Fisheries Society 1118:659–669.

Brouwer, S. L., and M. H. Griffiths. 2005. Reproductive biology of carpenter seabream (*Argyrozona argyrozona*) (Pisces: Sparidae) in a marine protected area. U.S. National Marine Fisheries Service Fishery Bulletin 103:258–269.

Chen, Y., and L. G. S. Mello. 1999. Growth and maturation of cod (*Gadus morhua*) of different year classes in the Northwest Atlantic, NAFO subdivision 3Ps. Fisheries Research 42:87–101.

Clarke, T. A. 1987. Fecundity and spawning frequency of the Hawaiian anchovy or nehu, *Encrasicholina purpurea*. U.S. National Marine Fisheries Service Fishery Bulletin 85:127–138.

Fitzhugh, G. R., and W. F. Hettler. 1995. Temperature influence on postovulatory follicle degeneration in Atlantic menhaden, *Brevoortia tyrannus*. U.S. National Marine Fisheries Service Fishery Bulletin 93:568–572.

Ganias, K., S. Somarkis, A. Machias, and A. J. Theodorou. 2003. Evaluation of spawning frequency in a Mediterranean sardine population (*Sardina pilchardus sardina*). Marine Biology 142:1169–1179.

Goldberg, S. R., V. H. Alarcon, and J. Alheit. 1984. Postovulatory follicle histology of the Pacific sardine, *Sardinops sagax*, from Peru. U.S. National Marine Fisheries Service Fishery Bulletin 82:443–445.

Hamatsu, T., K. Yabuki, and K. Watanabe. 2004. Decadal changes in reproduction of walleye pollock (*Theragra chalcogramma*) off the Pacific coast of northern Japan. Fisheries Oceanography 13(Supplement 1):74–83.

Hunter, J. R., and S. R. Goldberg. 1980. Spawning incidence and batch fecundity in northern anchovy, *Engraulis mordax*. U.S. National Marine Fisheries Service Fishery Bulletin 77:641–652.

Hunter, J. R., B. J. Macewicz, N. C. Lo, and C. A. Kimbrell. 1992. Fecundity, spawning, and maturity of female Dover sole, *Microstomus pacificus*, with an evaluation of assumptions and precision. U.S. National Marine Fisheries Service Fishery Bulletin 90:101–128.

Hunter, J. R., B. J. Macewicz, and J. R. Sibert. 1986. The spawning frequency of skipjack tuna, *Katsuwonus pelamis*, from the South Pacific. U.S. National Marine Fisheries Service Fishery Bulletin 84:895–903.

Janssen, P. A., J. G. D. Lambert, and H. J. Goos. 1995. The annual ovarian cycle and the influence of pollution on vitellogenesis in the flounder, *Pleuronectes flesus*. Journal of Fish Biology 47:509–523.

Lauth, R., S. McEntire, and H. Zenger. 2007. Geographic distribution, depth range, and description of Atka mackerel *Pleurogrammus monopterygius* nesting habits in Alaska. Alaska Fishery Research Bulletin 12(2): 165–186.

Lowe, S., J. Ianelli, M. Wilkins, K. Aydin, R. Lauth, and I. Spies. 2008. Stock Assessment of Bering Sea/Aleutian Islands Atka Mackerel. Pages 1119–1198 *in* Stock assessment and fishery evaluation report for the groundfish resources of the Bering Sea/Aleutian Islands regions. North Pacific Fishery Management Council, Anchorage, Alaska.

Lowe, S., J. Ianelli, H. Zenger, K. Aydin, and R. Lauth. 2005. Stock assessment of Bering Sea/Aleutian Islands Atka mackerel. Pages 757–820 *in* Stock assessment and fishery evaluation report for the groundfish resources of the Bering Sea/Aleutian Islands regions. North Pacific Fishery Management Council, Anchorage, Alaska.

McDermott, S. F., and S. A. Lowe. 1997. The reproductive cycle and sexual maturity of Atka mackerel, *Pleurogrammus monopterygius*, in Alaska waters. U.S. National Marine Fisheries Service Fishery Bulletin 95:321–333.

McDermott, S. F., K. P. Maslenikov, and D. R. Gunderson. 2007. Annual fecundity, batch fecundity, and oocyte atresia of Atka mackerel (*Pleurogrammus monoptery-*

gius) in Alaskan waters. U.S. National Marine Fisheries Service Fishery Bulletin 105:19–29.

Morgan, M., and E. B. Colbourne. 1999. Variation in maturity-at-age and size in three populations of American plaice. ICES Journal of Marine Science 56:673–688.

Narimatsu, Y., D. Kitagawa, T. Hattori, and H. Onodera. 2005. Reproductive biology of female Rikuzen sole (*Dexistes rikuzenius*). U.S. National Marine Fisheries Service Fishery Bulletin 103:635–647.

Olsen, E. M., M. Heino, G. R. Lilly, M. J. Morgan, J. Brattey, B. Ernande, and U. Dieckmann. 2004. Maturation trends indicative of rapid evolution preceded the collapse of northern cod. Nature (London) 428:932–935.

Rochet, M. 1998. Short-term effects of fishing on life history traits of fishes. ICES Journal of Marine Science 55:371–391.

Saborido-Rey, F., and S. Junquera. 1998. Histological assessment of variations in sexual maturity of cod (*Gadus morhua* L.) at the Flemish Cap (northwest Atlantic). ICES Journal of Marine Science 55:515–521.

Schaefer, K. M. 1996. Spawning time, frequency, and batch fecundity of yellowfin tuna, *Thunnus albacares*, near Clipperton Atoll in the eastern Pacific Ocean. U.S. National Marine Fisheries Service Fishery Bulletin 94:98–112.

Stearns, S. C. 1992. The evolution of life histories. Oxford University Press, New York.

Stequert, B., F. Menard, and E. Marchal. 2003. Reproductive biology of *Vinciguerria nimbaria* in the equatorial waters of the eastern Atlantic Ocean. Journal of Fish Biology 62:1116–1136.

Thompson, G., J. Ianelli, M. Dorn, D. Nichol, S. Gaichas, and K. Aydin. 2007. Assessment of the Pacific cod stock in the Eastern Bering Sea and Aleutian Islands area. Pages 209–328 *in* Stock assessment and fishery evaluation report for the groundfish resources of the Bering Sea/Aleutian Islands regions. North Pacific Fishery Management Council, Anchorage, Alaska.

Venables, W. N., and B. D. Ripley. 1997. Modern applied statistics with S-PLUS, 2nd edition. Springer-Verlag, New York.

von Bertalanffy, L. 1938. A quantitative theory of organic growth (inquiries on growth law, II). Human Biology 10:181–213.

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