2011

Effects of Maternal Growth on Fecundity and Egg Quality of Wild and Captive Atka Mackerel

Susanne F. McDermott
National Marine Fisheries Service, susanne.mcdermott@noaa.gov

Daniel W. Cooper
National Marine Fisheries Service

Jared L. Guthridge
Alaska SeaLife Center, 301 Railway Avenue, Seward, Alaska

Ingrid B. Spies
National Marine Fisheries Service

Mike F. Canino
National Marine Fisheries Service

See next page for additional authors

Authors
Susanne F. McDermott, Daniel W. Cooper, Jared L. Guthridge, Ingrid B. Spies, Mike F. Canino, Pamela Woods, and Nicola Hillgruber

Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science 3:324–335, 2011

ISSN: 1942-5120 online
DOI: 10.1080/19425120.2011.608592

SPECIAL SECTION: ATKA MACKEREL

Effects of Maternal Growth on Fecundity and Egg Quality of Wild and Captive Atka Mackerel

Susanne F. McDermott* and Daniel W. Cooper
National Marine Fisheries Service, 7600 Sand Point Way Northeast, Seattle, Washington 98115, USA

Jared L. Guthridge
Alaska SeaLife Center, 301 Railway Avenue, Seward, Alaska 99664, USA

Ingrid B. Spies, Mike F. Canino, and Pamela Woods
National Marine Fisheries Service, 7600 Sand Point Way Northeast, Seattle, Washington 98115, USA

Nicola Hillgruber
School of Fisheries and Ocean Sciences, University of Alaska–Fairbanks, 17101 Point Lena Loop Road, Juneau, Alaska 99801, USA

Abstract

Trade-offs in energy allocation between growth and reproduction can result in variations in reproductive potential in fish with differing growth patterns. Spawning biomass is often used as a proxy for reproductive potential on the assumption that fecundity is directly proportional to body weight. We examined variations in the reproductive potential of Atka mackerel *Pleurogrammus monopterygius* by studying the effect of differential growth and condition patterns on fecundity, atresia, and egg energy. Fecundity and egg energy were determined for fish from two geographic areas, Seguam Pass and Amchitka Island, Alaska, and compared with those of fish held in captivity. These Atka mackerel showed distinct differences in growth and condition, with weight at length and length at age being the highest among captive fish, intermediate among fish from Seguam Pass, and lowest among fish from Amchitka Island. Realized fecundity showed that on average captive fish spawned seven batches, fish from Seguam Pass six batches, and fish from Amchitka Island five batches. For wild fish, potential and realized fecundity at length or age was significantly higher at Seguam Pass than at Amchitka Island, whereas the fecundity-at-weight relationship did not differ by area, suggesting that weight is a better predictor of fecundity than length or age. Atresia and batch fecundity by length or weight did not differ by area, suggesting that the variation in fecundity is better explained by the variation in batch number than by batch size. Oocyte dry weight was higher for captive fish than for wild fish, whereas batch order did not significantly affect oocyte dry weight. Increased potential fecundity, realized fecundity, and oocyte quality in Atka mackerel females were strongly related to body size, indicating that growth differences and maternal feeding success impact the fecundity and oocyte quality of Atka mackerel. Therefore, changes in growth and condition patterns need to be taken into account to accurately estimate the reproductive potential of this species.

The importance of quantifying reproductive potential as a measure of the productivity of a fish stock has long been recognized (Ricker 1954; Murawski et al. 2001; Morgan and Rideout 2008). Spawning biomass is a parameter defined in fisheries management and life history theory as a measure of reproductive potential based on the usually strong correlation between population fecundity and spawning biomass. The fecundity of fish populations has been demonstrated to vary between areas

Subject editor: Gary Duker, National Oceanic and Atmospheric Administration, Alaska Fisheries Science Center, Seattle

*Corresponding author: susanne.mcdermott@noaa.gov
Received August 21, 2010; accepted March 2, 2011

and years (Kjesbu et al. 1998; Kraus et al. 2002; Kennedy et al. 2008, 2010). These authors suggest that there is a trade-off between allocating energy to growth and allocating it to reproductive output. In an environment in which food is scarce, mature fish tend to grow more slowly because most of the energy is allocated to reproductive output. In an environment of severely reduced productivity, not only growth but often the reproductive output of the population can be reduced. For some species, such as yellowfin sole *Limanda aspera*, regional growth differences seem to have little effect on fecundity–length relationships (Nichol and Acuna 2001). However, changes in realized fecundity have been linked to feeding or maternal condition in Atlantic herring *Clupea harengus* (Ma et al. 1998; Kurita et al. 2003; Kennedy et al. 2010), Atlantic cod *Gadus morhua* (Kraus et al. 2002), and European plaice (also known simply as plaice) *Pleuronectes platessa* (Kennedy et al. 2008). These results suggest that body condition, and therefore stored energy reserves, influence reproductive output and contribute to annual fluctuations in fecundity.

Internal regulation of individual fish fecundity appears to occur at two critical points during a fish's reproductive cycle: at the beginning of oocyte development and toward the end of the spawning season. The first involves the number of oocytes that will be developed during any given spawning season and is related to the condition of the fish at the beginning of the reproductive cycle. Once the oocytes to be spawned in the following season have begun development, estimation of their number will give the potential fecundity for that year (Kennedy et al. 2008). Traditionally, this has been used to estimate the reproductive output for a given year. Potential fecundity has been shown to be closely related to female body weight for most fish species, and the annual variation in potential fecundity is usually tied to the annual variation in fish weight or body condition (Kennedy et al. 2008). After recruitment to the developing cohort is complete, the oocytes are subject to down-regulation, which reduces potential fecundity through atresia (atretic oocytes are reabsorbed without being spawned). This usually occurs during vitellogenesis, when most of the energy is deposited into the oocytes, and causes realized fecundity (the actual number of eggs spawned) to be lower than potential fecundity. The extent of atresia is hypothesized to be determined by the amount of energy available to females at the time of reproduction (Rijnsdorp 1990; Kennedy et al. 2007, 2008). In some batch-spawning species, however, atresia might occur at the end of the spawning season, when whole batches of oocytes are reabsorbed. This has often been characterized as typical for species that exhibit nondeterminate fecundity, such as the northern anchovy *Engraulis mordax* and Pacific sardine *Sardinops sagax* (Hunter and Goldberg 1979; Macewicz et al. 1996). However, Atka mackerel *Pleurogrammus monopterygius* seem to exhibit this trait even though their fecundity is determinate (McDermott et al. 2007).

Another measure of reproductive output is the energy content of oocytes. Oocytes must provide energy for embryo development and to sustain the larvae until first feeding. Oocyte quality (size or energy content) has been positively correlated with larval survival in Atlantic cod (Marteinsdottir and Steinarsson 1998), black rockfish *Sebastes melanops* (Berkeley et al. 2004), and haddock *Melanogrammus aeglefinus* (Probst et al. 2006). Oocyte energy decreases with successively spawned batches in some species (Pauly and Pullin 1988; Kjesbu et al. 1992; Kennedy et al. 2008). Little is known about the energy content of Atka mackerel oocytes. To understand the relationship of maternal condition and reproductive output in Atka mackerel, we need to examine the maternal influence on oocyte energy content.

Atka mackerel females spawn multiple batches of demersal eggs. Their eggs are rather large (>2 mm) and the oocytes develop in batches throughout the spawning period, much like fish with indeterminate fecundity. However, all of the oocytes to be spawned in a given season are developed to the early yolked stage early in the season and potential fecundity can be estimated. McDermott et al. (2007) estimated Atka mackerel fecundity from collections made in 1993 and 1994 and found that up to 27% of developing oocytes were not spawned but reabsorbed by the females through atresia. Atresia was predominantly found at the end of the spawning season, when whole batches were often reabsorbed. Atresia was almost negligible during the oocyte development phase at the beginning of the spawning season. However, the temporal and spatial variability of fecundity, atresia, and oocyte energy content has not previously been studied.

Atka mackerel have been described as exhibiting a size cline from east to west, with larger size at age in fish at Seguam Pass than at Amchitka Island (Lowe et al. 2007). Atka mackerel occur in localized aggregations along the Aleutian Island chain, and based on recent tagging studies (McDermott et al. 2005) adult fish do not move much once they have settled into their adult habitat. Therefore, it is assumed that differences in Atka mackerel sizes are due to area-specific growth patterns and not to migration patterns. In this study we examined the potential effect of these area-specific growth patterns and condition on the fecundity, atresia, and oocyte quality of Atka mackerel. The fecundity of wild fish populations collected in two different areas was compared with that of fish in captivity at the Alaska SeaLife Center in Seward. Additionally, the oocyte energy content of wild fish was described and compared with that of captive fish. These captive fish provided a unique opportunity to estimate realized fecundity directly by counting the spawned eggs and comparing the results with estimates of realized fecundity from wild fish that were derived from prespawning specimens. In addition, with captive fish, it was possible to examine the potential effect of batch order on oocyte energy content.

The objectives of this study were to examine how growth and condition affect realized fecundity and oocyte energy by (1) estimating the potential and realized fecundity of wild Atka mackerel for two geographic areas with different growth rates, (2) estimating the realized fecundity of captive Atka mackerel and comparing it with the population estimates of the wild fish, and (3) measuring and comparing the oocyte energy content of captive and wild fish.

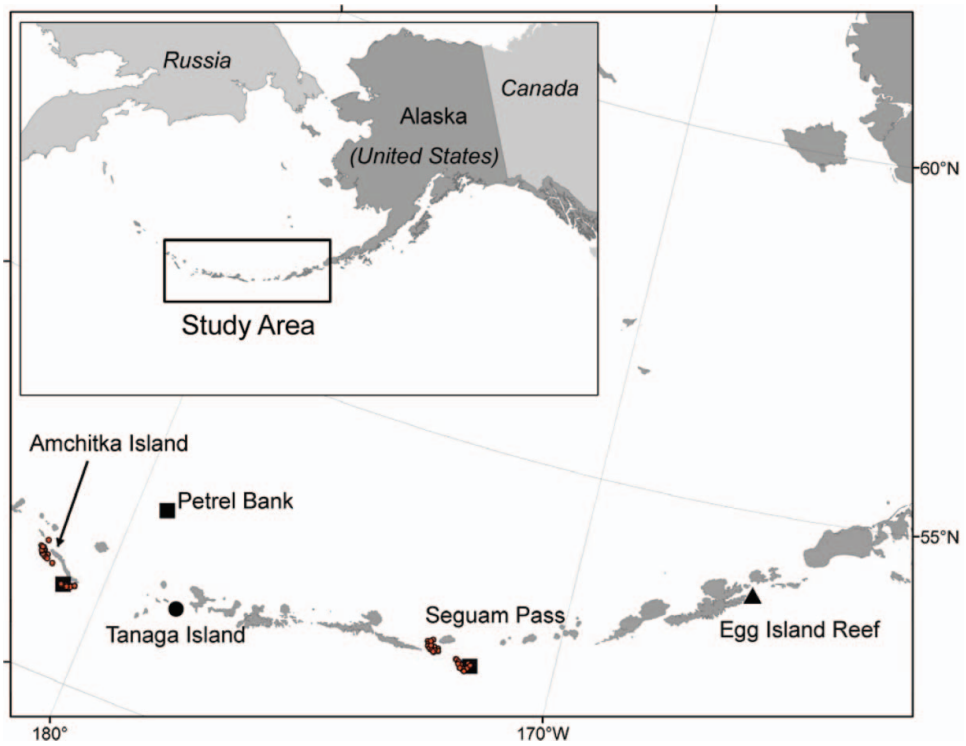

FIGURE 1. Locations at which samples of wild and captive Atka mackerel females were collected. Red dots mark the locations at Seguam Pass and Amchitka Island at which wild fish were collected for fecundity analysis during 2002 and 2003. Other symbols mark the locations at which Atka mackerel that had been held in captivity and used for egg dry weight analysis were collected. The triangle indicates the collection site of two of the females (F32 and F33) held in captivity, the circle the collection site of three females (F1, F2, and F4) held in captivity and wild females used in egg dry weight analysis, and the squares the collection sites of wild females used in egg dry weight analysis.

METHODS

Study area and data collection.—All specimens used for estimation of fecundity in the wild were collected during National Marine Fisheries Service (NMFS) chartered Atka mackerel tag–release and recovery cruises. The fish used in this study were collected at Seguam Pass in 2002 (NMFS management area 541) and Amchitka Island in 2003 (NMFS management area 542) (Figure 1). In both areas prespawning, spawning, and postspawning ovaries were collected from July through October for a total of 208 samples (Table 1). All wild specimens for the oocyte quality analysis were collected during the Atka mackerel spawning season in August and September 2005 aboard the commercial fishing vessel FT *Seafisher* from several locations in the Aleutian Islands (Figure 1). The sampling locations were combined into two geographic areas based on similar growth patterns: the eastern Aleutians (Seguam Pass) and central Aleutians (Petrel Bank, Tanaga Island, Amchitka Island). For fecundity and oocyte energy analysis of captive fish, two females were captured near Tanaga Island in October 2002 and three at Egg Island Reef in September 2004 (Figure 1).

Sample collections.—Catches of Atka mackerel were brought on board using bottom trawl gear. For each research haul, five females were randomly collected for age and maturity samples. Each fish was measured to the nearest centimeter and weighed to the nearest gram. Ovaries and otoliths were extracted. The otoliths, which were used for age determination, were patted dry, stored in vials, and hydrated with 50% alcohol in the laboratory. Ovaries were stored in a 10% buffered-formalin solution for at least 6 months. Ovary formalin weight was determined in the laboratory to the nearest 0.001 g.

TABLE 1. Number of fecundity samples in each maturity stage per area, year, and month.

Area	Year	Month	Potential fecundity (prespawning)	Batch fecundity (pawning)	Atresia (spent)
Seguam Pass	2002	Jun–Jul	75		
		Aug		8	
		Oct		7	26
Amchitka Island	2003	Jul	40	8	
		Oct			44
Total			115	23	70

The five females for the captivity experiment were held in 1-m^3 running-seawater tanks aboard the vessel until arrival in Dutch Harbor, where they were transferred into coolers with oxygenated seawater. From Dutch Harbor the fish were transported by air and land to the Alaska SeaLife Center. Immediately upon arrival the fish were transferred into live tanks and held captive for the remainder of the study.

Age determination.—Ages were assigned by the NMFS Alaska Fisheries Science Center (AFSC) age and growth laboratory using the otolith reading procedures outlined by Anderl et al. (1996).

Fecundity of wild fish.—Atka mackerel have been shown to regulate fecundity by reabsorbing one or more batches of oocytes at the end of the spawning season (McDermott et al. 2007) rather than during oocyte development. As a result, prespawning specimens were used for the estimation of potential fecundity and postspawning specimens were used for the estimation of atresia. This made it impossible to estimate realized fecundity directly for individual females and it was instead derived by subtracting predicted atresia at length from predicted potential fecundity at length. The methods for estimating fecundity are described in detail in McDermott et al. (2007) and only an overview and deviations from those methods are presented here.

Since it was established that there were no differences in maturity stages or oocytes per gram of ovary tissue between left and right ovaries (McDermott et al. 2007), cross sections for histological processing were taken from one of the ovaries while subsamples of whole oocytes for the fecundity estimation were taken from the other ovary. Maturity stages were determined for all specimens using histological methods (hematoxylin and eosin stain) and the classification described in McDermott and Lowe (1997). Fecundity and the number of atretic oocytes were estimated with the gravimetric method, that is,

$$F = \frac{W}{w}N, \tag{1}$$

where F = fecundity, W = total ovary weight, w = subsample weight, and N = number of oocytes in the subsample.

Only prespawning specimens (ones containing no postovulatory follicles in the histological sample) were used to estimate potential fecundity by counting all oocytes that showed a distinct ring around the nucleus in the whole-oocyte subsample. It has been shown in previous studies (McDermott et al. 2007) that Atka mackerel establish a reservoir of oocytes in the oil droplet stage that most likely will not get spawned in the current spawning season but form the reserve for the following year. All oocytes in the oil droplet stage and more advanced stages were initially counted for fecundity because it was not possible to distinguish oil-droplet-stage oocytes (stage 4) from vitellogenic oocytes (stage 5). It was assumed, however, that only oocytes in the vitellogenic stage and above were to be spawned during this spawning season. To distinguish the two stages, histological slides of 20 prespawning specimens were randomly selected and stage 4 and 5 oocytes were measured to estimate the size distributions of each stage. The number of stage 4 oocytes was then estimated using the proportion of stage 4 oocytes that did not overlap in size with stage 5 oocytes. Methods for separating these oocyte stages are described in detail in McDermott et al. (2007). Potential fecundity was then defined as the number of oocytes per female in stage 5 and later stages.

Batch fecundity was defined as the number of oocytes spawned by an individual female in one batch-spawning event. To estimate batch fecundity, the hydrated oocytes to be spawned as a batch needed to be clearly distinguished from the rest of the oocytes in the ovary. None of the prespawning ovaries had hydrated batches developed enough to be clearly distinguished from the rest of the oocytes, so we used specimens in the spawning stage (i.e., that had already spawned at least one batch). We assumed that the variability in batch fecundity due to batch order was small enough to be ignored (based on the results in this paper from the captive fish fecundity study).

Atresia was estimated from postspawning specimens by counting all atretic oocytes present in the subsamples of spent ovaries. Relative fecundity was defined as fecundity divided by somatic body weight.

The fecundity–length relationship was defined as $F = aL^b$, with F representing potential fecundity, realized fecundity, batch fecundity, and atresia. The fecundity–weight relationship was assumed to be linear. Linear regressions were fitted to the $\log_e$ transformed fecundity–length data and the fecundity–weight data using S-plus generalized linear models with area as a factor. When area was determined not to be significant, the data were pooled and a single regression was fitted to all data.

Fecundity of captive fish.—For the fecundity and oocyte energy analysis of captive fish, egg masses were collected and the parentage of egg masses was determined to estimate the batch fecundity and yearly potential fecundity for each female. Captive females were held in an exhibit (an approximately 11,300-L tank) at the Alaska SeaLife Center. Fish were generally fed to satiation three times per week. Feed was primarily squid *Doryteuthis opalescens*, capelin *Mallotus villosus*, silversides *Menidia menidia*, herring *Clupea pallasii pallasii*, and krill *Euphausia superba*. Temperature (nearest 0.1°C) was recorded an average of 14 times per month. Fork length was measured for three spawning females 1 month prior to the start of the spawning season in 2005. The fork lengths of the other two spawning females in 2005 is unknown; however, it was estimated by interpolating between the fork lengths at capture and those in June 2006 using the growth trajectories from the first three females. Atka mackerel began spawning in the exhibit in 2004. Five females spawned in the exhibit in 2005, and four of the same females spawned in 2006 (Table 2). Egg masses were collected soon after spawning (generally within 12 h) and weighed to the nearest 0.001 g. Subsamples of the egg masses were removed, weighed, and frozen to estimate fecundity and measure energy content at a later time. In 2006, high water turbidity caused suspected partial cannibalism of the final six egg masses, so

TABLE 2. Fecundity, length, and weight of female Atka mackerel spawning in captivity in 2005 and 2006.

	2005					2006				
Female	Batches spawned	Mean batch fecundity (thousands)	Total fecundity (thousands)	FL	Weight (g)	Batches spawned	Mean batch fecundity	Total fecundity	FL	Weight (g)
F1	12	10.5	127.0	52	2,700	9	13.8	123.9	54	2,670
F2[a]	6	7.6	45.7	52	2,745					
F3	6	9.6	58.1	52	2,700	7	8.1	[b]		
F4	7	10.0	70.3	45	<1,900	6	13.5	[b]	47	1,900
F5	6	5.8	34.6	43[c]	<1,840	6	4.3	[b]	45	1,840

[a]Female F2 died prior to spawning in 2006.
[b]Not available due to suspected cannibalism.
[c]Estimated from length in 2006 and growth trajectories of other captive fish.

these were not sampled for fecundity or egg energy. Otoliths were removed from dead captive fish to determine length at age. Otoliths were analyzed using standard procedures by the Age and Growth Program at the Alaska Fisheries Science Center. The eggs in the fecundity subsamples shipped frozen from the Alaska SeaLife Center to the Alaska Marine Science Center laboratory in Seattle. There they were thawed and counted, and batch fecundity was estimated by the gravimetric method. After the maternity of each egg mass was determined using genetics, batch number, batch order, batch fecundity, and total realized fecundity were determined for each spawning female.

Parentage of egg masses spawned in captivity.—DNA from captive females and spawned egg masses was analyzed to determine egg mass parentage. Fin clips were collected nonlethally from all adult Atka mackerel at the Alaska SeaLife Center and preserved in 95% nondenatured ethanol. Egg masses (minus the subsamples used for egg energy analysis and fecundity in this study) were incubated to late-stage larvae in another experiment and then similarly preserved. Genomic DNA was extracted with DNeasy tissue kits according to manufacturer's instructions (Qiagen, Inc., Valencia, California), except that 50 μL of elution buffer was used for the eggs. Two microsatellite loci (*Pmo70* and *Pmo152*; Spies et al. 2005) were found to be sufficiently polymorphic to identify all possible parents. The conditions for polymerase chain reaction amplifications of microsatellites were as described in Spies et al. (2005). Genotyping was conducted on a 4200 LI-COR DNA analysis system (LI-COR Biotechnology, Lincoln, Nebraska) and analyzed with LI-COR Saga Generation 2 genotyping software.

Egg energy and dry weight of captive fish.—The specimens used for this analysis were the same as the ones used for fecundity in captive fish. All collection procedures, age determination, and parentage analysis are described above.

Captive fish eggs were thawed and separated using forceps into countable groups of one to several eggs. Thirty eggs with intact chorions were dried at 55°C for 16–22 h. Three subsamples of 30 eggs were weighed after drying for 16, 23, and 39 h, and egg weight did not differ significantly from 16 to 39 h. After drying, the eggs were recounted and weighed (nearest 0.0001 g). The energy density of the eggs was measured using a Parr 1425 semimicro bomb calorimeter (Parr Instruments, Moline, Illinois). The dried eggs were placed directly into the sample cup and not pelletized. Energy per egg (EE) was calculated as

$$EE = (ED \times Wt)/NE, \quad (2)$$

where ED = energy density, Wt = the dry weight of the egg, and NE = number of eggs bombed.

Oocyte energy and dry weight for wild fish samples.—Oocytes were collected from females in the wild to compare oocyte quality between the captive and wild fish. Prespawned oocytes (oocytes that had begun hydration) were used for two reasons: (1) to obtain maternal data and batch order data for the oocytes and (2) to provide oocytes at maximum energy content to compare with the oocytes spawned in captivity (which were collected soon after spawning). Females were visually screened for the presence of hydrated oocytes. One lobe of each ovary was frozen for later oocyte energy measurement, and the other lobe was preserved in 10% formalin buffered with sodium bicarbonate for histological analysis to determine a rudimentary batch order. Fork length and weight were recorded for each female, and otoliths were removed for age determination.

After storage in 10% buffered formalin, the ovarian tissue samples of the wild fish were embedded in paraffin, sectioned to a width of 4 μm, and stained with hematoxylin and eosin. Histology sections were analyzed with a light microscope to verify that the most advanced batch of oocytes had reached the early hydration stage (McDermott and Lowe 1997). This ensured that the oocytes contained their maximum energy content (Gunderson 1997). The rudimentary batch order of the most advanced batch was also determined by histology. Batch order was placed into one of three categories: first, middle, or last. The first batch was defined as the most advanced batch when ovaries did not show any evidence of previous spawning (no postovulatory follicles). The middle batch was defined as the most advanced batch when ovaries contained both

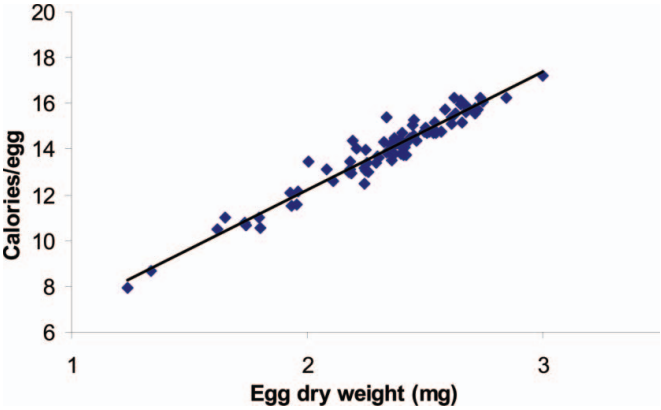

FIGURE 2. Relationship between energy content and dry weight for Atka mackerel eggs ($r^2 = 0.94$). Wild and captive fish samples were combined.

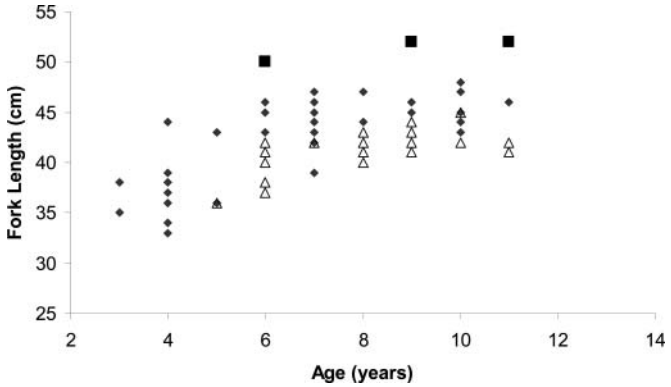

FIGURE 3. Length at age of three fish (squares) after 3 years in captivity at the Alaska SeaLife Center compared with that of fish from Seguam Pass (diamonds) and Amchitka Island (triangles). Note that the fish held in captivity were originally caught close to Amchitka Island.

evidence of spawning (postovulatory follicles) and vitellogenic and hydration-stage oocytes. The last batch was defined as the most advanced when ovaries only had postovulatory follicles and hydration-stage oocytes.

The frozen ovary lobes were thawed and 30 intact oocytes of the most advanced stage were separated from the ovary using forceps. Oocyte energy for 30 wild females was measured using the same methods as for captive fish. Oocyte dry weight predicted energy content well for both oocytes and eggs ($r^2 = 0.94$; Figure 2) and was therefore used as a proxy to compare the egg quality of wild and captive females, and to test for relationships between maternal characteristics and oocyte quality in wild fish. For each wild female, 30 oocytes were dried and weighed using the same drying procedure as for the captive egg masses.

Statistical analysis.—A two-factor analysis of variance (ANOVA) using rudimentary batch order (first, middle, or last) and oocyte source (captive or wild) was applied to oocyte dry weight data. Because captive fish each had multiple middle batches (which were not independent observations), the mean value of all middle batches for each captive female was used in the ANOVA to avoid pseudoreplication. Similarly, for wild fish the mean value by haul for each level of batch order was used in the ANOVA because females caught in the same trawl may have experienced similar conditions.

RESULTS

Length–Weight Relationships

Captive fish were larger at age than fish from their source population (Amchitka), indicating that growth rates increased in captivity (Figure 3). The lengths of wild fish ranged from 33 to 48 cm, whereas those of captive females ranged from 43 to 52 cm. Weight at length was also significantly higher in captive fish than in wild fish (Figure 4). The weight of wild fish ranged from 550 to 1,300 g, whereas the weight of captive females ranged from 1,380 to 2,750 g. Mean monthly temperature in the tank holding the captive fish ranged from 5.8°C in March to 9.9°C in October in 2005 and from 6.2°C in April to 10.5°C in October in 2006 (Table 3). Wild fish ovaries collected for oocyte weight were collected at bottom temperatures ranging from 4.3°C to 6.2°C.

Fecundity of Wild Fish

The linear regression model results showed that potential fecundity by length was significantly different between areas in both intercept ($P = 0.034$) and slope ($P = 0.028$). Batch fecundity ($P = 0.98$ for slope and 0.99 for intercept; Figure 5) and atresia ($P = 0.98$ for slope and 0.9 for intercept; Figure 6) by length were not significantly different for each area, so the data were pooled. Detailed regression parameters are given in Table 4. Realized fecundity was calculated by subtracting the estimated number of atretic oocytes at length from the potential fecundity estimate at length in each area (Figure 7). For an average female of 41 cm, potential fecundity (in thousands of oocytes) at Seguam Pass was estimated as 46.1 and realized fecundity

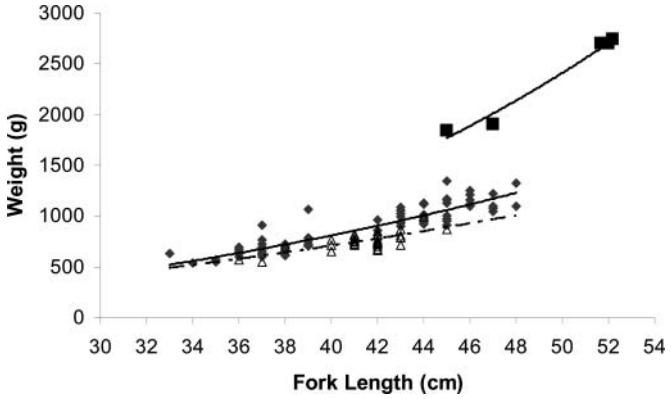

FIGURE 4. Weight (W)-at-length (L) relationships for Atka mackerel at Seguam Pass (diamonds and solid line; $W = 0.1762 \cdot L^{2.2861}$, $R^2 = 0.8542$), Amchitka Island (triangles and dotted line; $W = 0.5774 \cdot L^{1.9284}$, $R^2 = 0.5052$), and the Alaska SeaLife Center (squares and solid line; $W = 0.0251 \cdot L^{2.9329}$, $R^2 = 0.9704$). All measurements were taken from June to August.

TABLE 3. Mean monthly temperatures (°C) in the captive Atka mackerel tank in 2005 and 2006, by month.

Month	2005	2006
Jan	7.2	8.3
Feb	6.3	6.8
Mar	5.8	6.5
Apr	5.9	6.2
May	5.9	6.4
Jun	6.4	6.2
Jul	6.3	6.2
Aug	7.1	6.5
Sep	8.3	9.1
Oct	9.9	10.5
Nov	9.6	8.5
Dec	8.2	8.2

as 39.6. At Amchitka, potential fecundity for a 41-cm female was estimated as 38.0 and realized fecundity as 31.5. Batch fecundity was estimated to be 5.6 and atresia was estimated to be 6.6 for a 41-cm female in both areas. This indicated that Atka mackerel females reabsorb at least one batch of oocytes during their spawning season, decreasing batch number at Seguam Pass from 7 to 6 batches and that at Amchitka from 6 to 5 batches. Relative fecundity (fecundity per gram of body weight) was not significantly different by length or weight for each area ($P > 0.2$ for both slope and intercept). The fecundity–weight relationship did not differ by area ($P = 0.29$ for the intercept and 0.24 for the slope) and was combined (Figure 8). However, fecundity at age differed significantly by area ($P = 0.0001$; Figure 9). Females at Seguam Pass had a positive fecundity–age relationship, whereas those at Amchitka did not show any increase in fecundity by age and the slope was not significantly different from zero ($P = 0.34$). Relative potential fecundity by age showed similar trends, with females from Seguam Pass showing increases ($P = 0.0003$ for slope) and females at Amchitka showing nearly significant decreases ($P = 0.069$) (Figure 10).

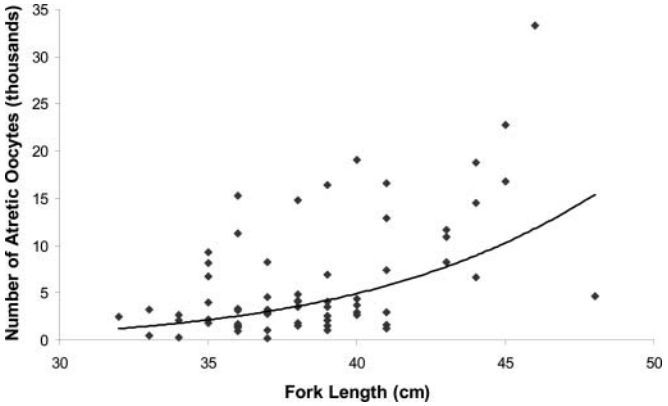

FIGURE 6. Observed atresia (diamonds) and predicted atresia (solid line) of wild fish. Data for Seguam Pass and Amchitka Island were combined.

Several of the fish showed high amounts of atresia; however, no significant relationship between relative atresia (atresia per gram of body weight) and specimen weight, length, or age were found. When the length–weight relationship of fish with a high occurrence of atresia (relative atresia greater than 10 oocytes per gram of body weight) was compared with that of fish with a low occurrence, no differences were found. It was therefore concluded that the amount of atresia per individual was not related to female body condition for this species.

Fecundity in Captivity

The genetic analysis successfully determined the female and male parent of each egg mass. Since each parent had a unique multilocus genotype, the parentage of each egg mass could be determined by excluding all but two possible parents. In 2005, captive females deposited 40 egg masses. Two very small egg masses (207 and 385 eggs each) were not fertilized and could not

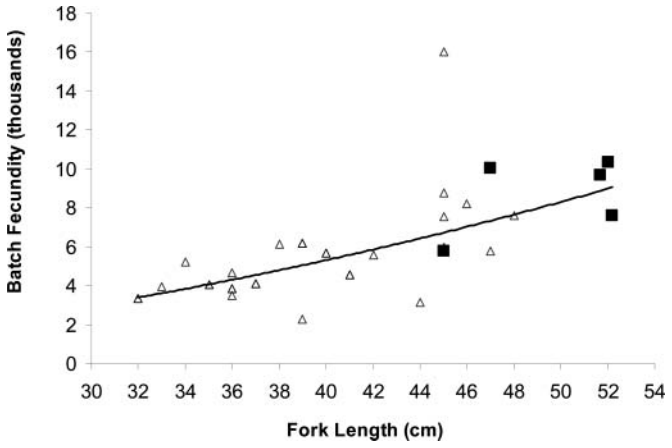

FIGURE 5. Batch fecundity at length (squares) of the five fish spawning in captivity in 2005 and wild fish from Seguam Pass and Amchitka Island combined (triangles and solid line).

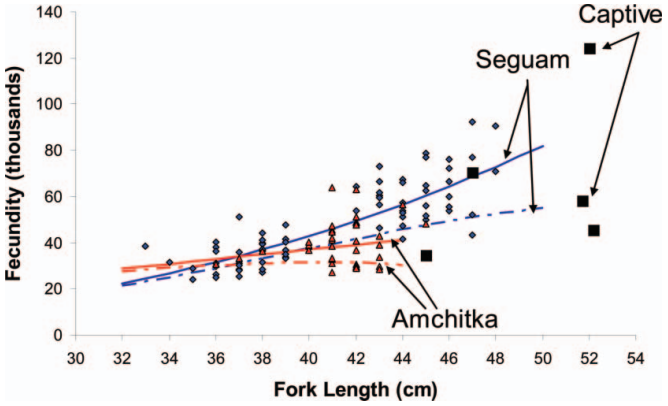

FIGURE 7. Estimated potential (solid line) and realized (dashed line) fecundity length regressions and data points for wild fish from Seguam Pass and Amchitka Island and realized fecundity for individual captive fish at the Alaska SeaLife Center(squares).

TABLE 4. Results of fecundity-at-length regressions, relative fecundity, and batch numbers for Seguam Pass and Amchitka Island and realized and batch fecundity for the captive fish at the Alaska SeaLife Center (ALSC). Abbreviations are as follows: n = sample size, a and b = the parameters of the linear regression equation, and P = the P-value for the slope of the linear regression. Fecundity for mean length is the estimated fecundity for the mean length using the length–fecundity regression equation, and average batch number is the average estimated batch number for each fecundity–length relationship.

Year	Area	Response Variable	Fecundity Type	n	a	b	R^2	P	Average relative fecundity	Mean weight (g)	Mean length (cm)	Fecundity for mean length (thousands)	Average batch number
					Wild fish								
2002	Seguam	Length	Potential fecundity	75	0.99	2.89	0.716	0.000	54.65	878	41	46.1	7.0
2003	Amchitka		Potential fecundity	40	590.81	1.12	0.044	0.196	51.91	760	41	38.0	5.8
2002, 2003	Seguam and Amchitka		Batch fecundity	23	2.84	2.04	0.358	0.003	6.83		41	5.5	
2002, 2003	Seguam and Amchitka		Atresia	70	0.00	7.11	0.356	0.000	9.63		41	6.6	
2002	Seguam		Realized fecundity						45.02	878	41	39.6	6.0
2003	Amchitka		Realized fecundity						42.28	760	41	31.5	4.8
2002, 2003	Seguam and Amchitka	Weight	Potential fecundity	115	−8,307.60	64.09	0.642	0.000					
2002	Seagum	Age	Potential fecundity	69	22,125.81	0.12	0.696	0.000					
2003	Amchitka		Potential fecundity	40	44,801.64	−0.02	0.024	0.342					
					Captive fish								
2005, 2006	ASLC		Realized fecundity	5					28.01	2,377	50	67	7.2
2005, 2006	ASLC		Batch fecundiy								50	9	

be incubated to determine parentage and thus were not included in the fecundity analysis. Two other egg masses were spawned on the same day by the same female and were combined into a single batch in this analysis. In 2005, the five captive females spawned a total of 37 fertilized batches. The number of batches spawned per female ranged from 5 to 12, with a mean of 7.4 (Table 2). Mean batch fecundity ranged from 5,770 to 10,584 (Table 2; Figure 5); realized fecundity ranged from 34,617 to 127,010 (Table 2; Figures 4, 6). In 2006, four females spawned 28 batches for a mean of 7 batches per female (Table 2).

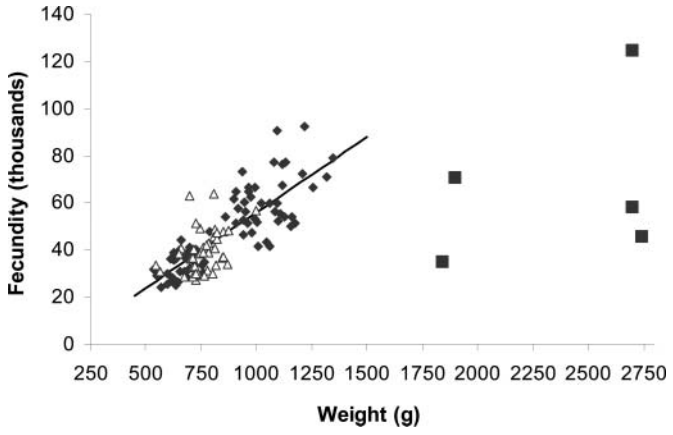

FIGURE 8. Realized fecundity at weight of the five females spawning in captivity in 2005 (squares) and estimated potential fecundity at weight of wild fish from Seguam Pass (diamonds) and Amchitka Island (triangles). Potential fecundity estimates were not significantly different by area ($P > 0.29$) and were therefore combined for estimating the trend line.

Egg Energy and Dry Weight

The energy content of batches spawned in captivity by the captive fish in 2005 ranged from 48.3 to 72.1 J/egg. The mean energy density for eggs (wet weight) was 5,680 J/g. The mean energy content of all batches varied significantly by female (ANOVA: $P < 0.001$; Figure 11).

The trend of egg energy content by batch order varied among individual captive females (Figure 12). Egg energy content declined with batch order in fish F4 in 2005. Egg energy also

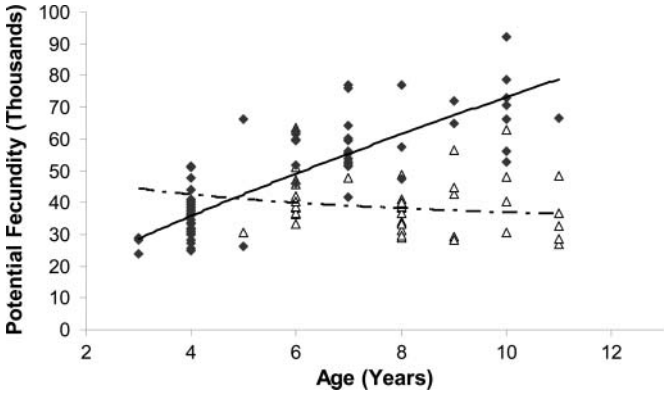

FIGURE 9. Potential fecundity at age of wild fish from Seguam Pass (diamonds) and Amchitka Island (triangles) and their respective trend lines (solid and dotted).

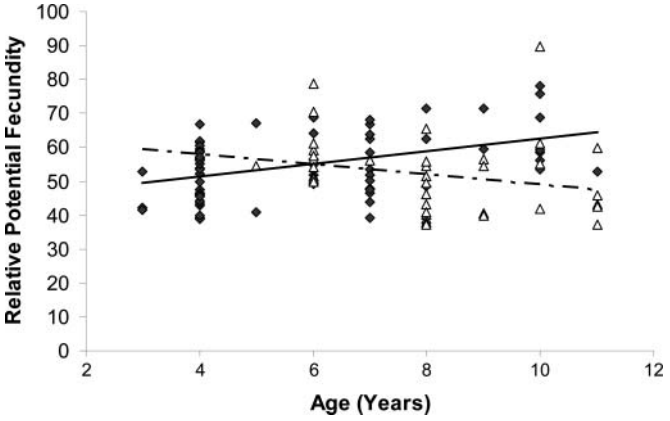

FIGURE 10. Relative potential fecundity of wild fish from Seguam Pass (diamonds) and Amchitka Island (triangles) and their respective trend lines (solid and dotted).

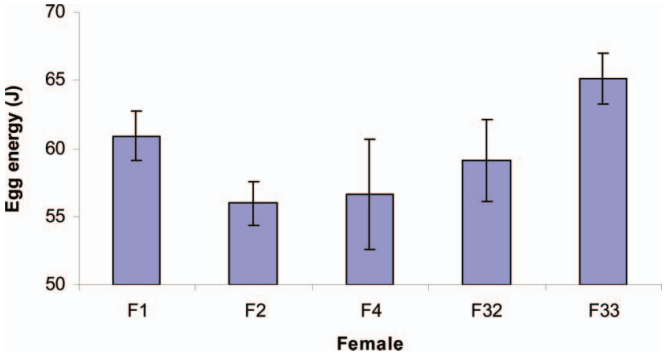

FIGURE 11. Mean egg energy content of all batches for the five females spawning in captivity in 2005. The error bars indicate the 95% confidence intervals around the means.

decreased with batch order over the first five batches in fish F1 in both 2005 and 2006. However, this female produced additional batches with higher energy contents in both years. No apparent pattern of egg energy with batch order was observed in the other females. Egg energy content did not differ by batch order in the first six batches of all five females in 2005 (ANOVA: $P = 0.18$).

Captive females had significantly heavier eggs than wild fish (ANOVA: $P = 0.014$; Figure 13); however, some wild females produced oocytes in the same dry-weight range as captive females (Figure 13). Captive female lengths ranged from 43 to 52 cm, and weights ranged from 1.38 to 2.75 kg. Wild female length ranged from 34 to 46 cm, and weights ranged from 0.4 to 0.99 kg. Maternal age (linear regression: $r^2 = 0.02$, $P = 0.16$) was not a significant predictors of oocyte dry weight in the wild fish.

DISCUSSION

The potential and realized fecundity–length relationships of the wild fish differed by area, whereas the fecundity–weight relationships did not differ by area. This indicates that

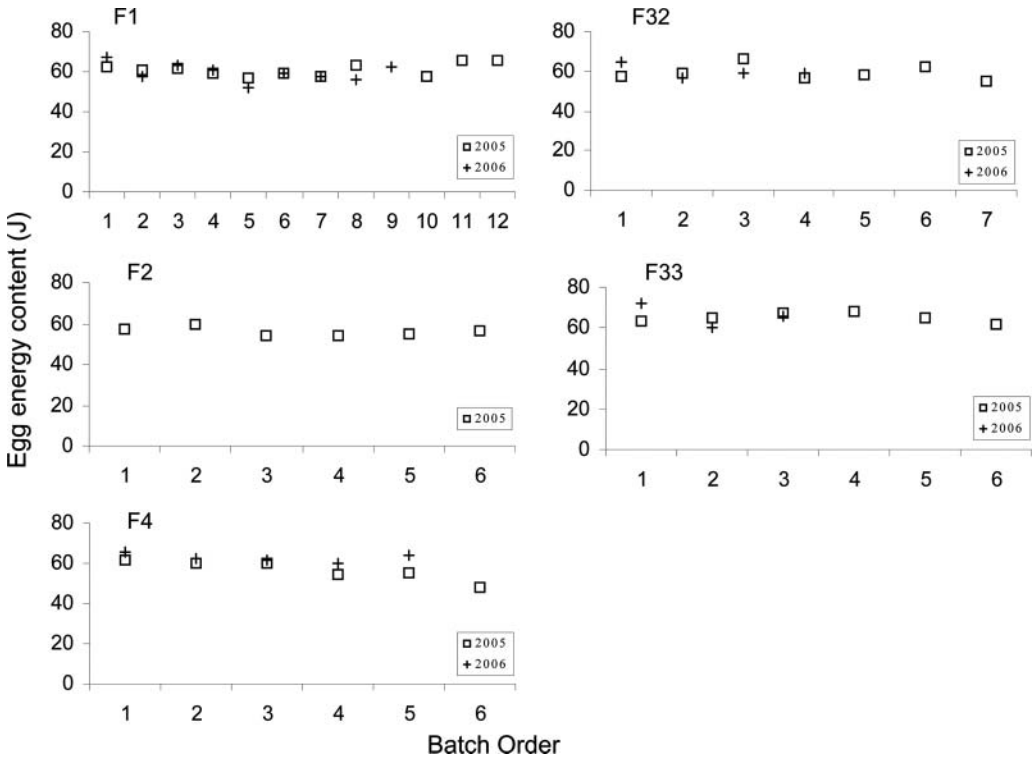

FIGURE 12. Mean egg energy content by batch order for all females spawning in captivity. Note that female F2 did not spawn in 2006.

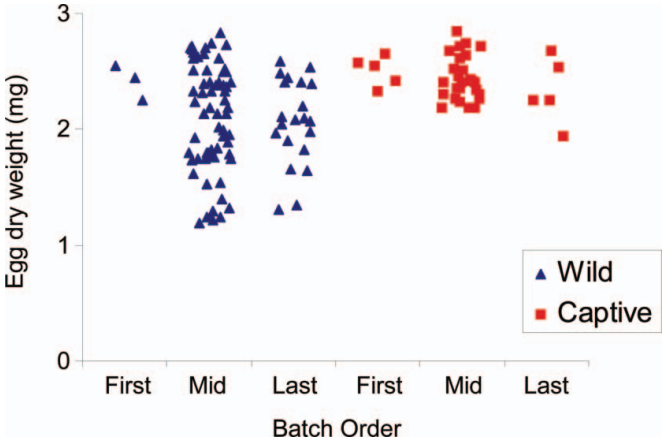

FIGURE 13. Mean egg dry weight by rudimentary batch order for wild Atka mackerel and five females spawning in captivity in 2005. The values on the *x*-axis are randomly scattered within each category to more clearly indicate all egg dry weight values.

body weight, and therefore body condition—rather than length—controls fecundity. The area-specific growth differences show that Atka mackerel not only have a greater length at age at Seguam Pass but also have a greater weight at length than the fish at Amchitka Island. It seems likely that the area-specific differences in fecundity by length are based on these area-specific growth differences.

Fecundity at age differed significantly between areas: the fish at Amchitka Island showed no trend (or a slight decrease) in the age–fecundity relationship, whereas those at Seguam Pass showed an increasing trend. Surprisingly, those trends still held true when relative fecundity was examined by age, indicating that the lack of increasing fecundity was not only correlated with the stunted growth of fish from Amchitka Island but also that mature females there produced fewer oocytes per gram of body weight as they got older. In contrast, mature fish from the Seguam Pass area showed increasing trends of oocytes per gram as they got older. These results might reflect differences in environmental conditions between these areas. Seguam Pass has been shown to provide better quality food for Atka mackerel than Amchitka Island (Rand 2007). Lower overall growth rates at Amchitka and lower weight at length seem to further support the hypothesis that fish there have less energy available for growth and reproduction once they reach adult sizes.

Since the samples for each area were collected during different years, temporal variation cannot be ruled out as a factor contributing to the differences in fecundity; however, this growth cline from east to west has been described consistently throughout the last decades for Atka mackerel populations in the annual stock assessment. Therefore, the authors believe that area-specific growth differences have a larger impact on Atka mackerel size than interannual variation in body condition. It can be argued that annual variation in condition influences fecundity as well and might affect atresia and therefore realized fecundity. This possibility, however, is beyond the scope of this study and should be examined in the future.

Atresia at the end of the spawning season in wild fish was significant, averaging about one batch of oocytes. This is slightly less than the estimates from samples taken throughout the Aleutian Islands in 1993 and 1994 (McDermott et al. 2007). Atresia could have been underestimated, since spent fish at Amchitka Island seemed to have already partially absorbed some of the atretic oocytes. This could also have contributed to high sample variance and the nonsignificant result for area-specific differences in atresia. Since the fish at Amchitka Island seem to spawn slightly earlier in the year than the fish at Seguam Pass, it is difficult to obtain samples that are at the same atretic state in both areas when sampling during a given time period such as a planned research cruise. Atresia, however, did not seem to be related to body condition. This suggests that the difference in fecundity between areas is brought on early in the development of the eggs (i.e., more oocytes are recruited into the developing cohort by fish of better condition). Atresia might be used at the end of the spawning season to regulate the release or resorption of the last batch to be spawned. This might be influenced by environmental conditions rather than the body condition of individual fish. Nevertheless, atresia seems to be an important component of Atka mackerel fecundity regulation and prevalent in samples of all years and areas examined.

Assigning parentage to egg masses using genetic techniques enabled us to derive fecundity estimates and egg energy measurements for females held in a common tank. Without genetic parentage assignment, females would either have had to be segregated or to have been tagged and constantly monitored to determine the parentage of egg masses. Either process would have added expense and may have altered spawning behavior.

The realized number of egg masses spawned by the captive fish was in the range of the estimated potential number of batches for wild fish at Seguam Pass. Similarly, the realized total fecundity at length for captive fish was similar to the potential fecundity estimates for wild fish there. These results seem to indicate that increased food availability promotes larger body sizes and increased realized fecundity. Of course, it cannot be determined whether the increased realized fecundity of the captive fish was due to more oocytes being developed (higher potential fecundity) or the absence of atresia. Future studies that include controlled feeding experiments of captive fish could shed light on this question.

Oocyte energy content and oocyte dry weight were highly correlated for both wild oocytes and captive eggs. Egg dry weight is easier to measure and seems to be a good metric for comparing the egg quality of Atka mackerel in the wild. The captive fish in this study had heavier eggs with higher energy content than the wild fish, and there was high variability in egg dry weight among wild females. Although other factors (such as temperature and year) cannot be completely ruled out as influences on egg energy content, this increase in the egg dry weight of the captive fish was most likely caused by feeding

differences between the captive fish, the fish at Seguam Pass, and the fish at Amchitka Island. The captive fish in this study were generally fed to satiation three times per week. In wild fish, food consumption peaks in the summer but declines by October, when the majority of stomach samples are empty (Rand 2007). Rand (2007) found that the fish at Amchitka Island generally consume less food and lower-quality food than those at Seguam Pass and linked the growth rates observed in those areas to food consumption. It can be argued, then, that the captive fish's dramatically increased growth rates and increased weight at length are also due to greater food consumption. An unexpected finding of this study—one that is attributable to the high weight at length of the captive fish—is that in spite of their higher fecundity by length captive fish showed a decrease in fecundity per gram of body weight (relative fecundity). Feeding success may be the cause of the higher realized fecundity at length of captive fish than wild fish, but at some point increased feeding success and increased weight do not seem to increase fecundity at weight. Similar results have been shown by other studies, where after reaching a critical condition relative potential fecundity no longer increased with increases in condition (Kjesbu 2009).

Our findings suggest that feeding success in the wild can influence the quality and quantity of reproductive output for Atka mackerel. Since this study has shown that the fecundity of Atka mackerel is better predicted by fish weight than by fish length and that fecundity at age can differ substantially on relatively small, local scales, it is of great importance to understand the spatial differences in growth and condition when estimating spawning biomass. Weight–length, length–fecundity, and age–fecundity relationships have been shown to differ between the Seguam Pass and Amchitka Island areas. Those locations represent populations in different management areas of the Aleutian Islands, suggesting that estimation of area-specific spawning biomass would be appropriate for this species.

In addition, Atka mackerel show a large amount of oocyte atresia that may be mediated by the environment. Realized fecundity may be higher in years with more food availability, while greater numbers of oocytes may be reabsorbed and the energy reallocated to females in years when food is scarce. Egg energy was higher in the well-fed captive fish than in the wild fish examined. It can be hypothesized that greater egg energy would increase embryo survival. This plasticity in reproductive output may be a contributing factor to year-class strength and recruitment success that has not previously been examined in many marine species, for which stock assessment models assume that the reproductive output per gram of female is constant. Variability in this parameter could indicate that spawning biomass alone is not enough to indicate the potential reproductive output for a given year and area. Further work is needed to examine this relationship in more areas and over longer time scales.

ACKNOWLEDGMENTS

We thank Richard Hocking (ASLC) for providing aquarium space and the assistance of aquarium staff, Jennifer O'Quin (ASLC) for sampling egg masses, and Madolyn Hollowed and Emily Gallichote for counting oocytes and measuring oocyte energy. David Beauchamp (University of Washington) provided us the use of a bomb calorimeter. Cascade Fishing Company graciously allowed us to collect ovaries aboard the *Seafisher*. We thank Susan Picquelle (AFSC) for statistical assistance and Daniel Nichol for comments. We also thank all the AFSC scientists involved in collecting samples during our research cruises, especially Kimberly Rand, Sandi Neidetcher, and Robert Lauth. We would like to thank the North Pacific Research Board for providing funds for this project (project 522). Reference to trade names does not imply endorsement by the National Marine Fisheries Service.

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.

Berkeley, S. A., C. Chapman, and S. M. Sogard. 2004. Maternal age as a determinant of larval growth and survival in a marine fish, *Sebastes melanops*. Ecology 85:1258–1264.

Gunderson, D. R. 1997. Trade-off between reproductive effort and adult survival in oviparous and viviparous fishes. Canadian Journal of Fisheries and Aquatic Sciences 54:990–998.

Hunter, J. R., and S. R. Goldberg. 1979. Spawning incidence and batch fecundity in northern anchovy, *Engraulis mordax*. U.S. National Marine Fisheries Service Fishery Bulletin 77:641–652.

Kennedy, J., J. E. Skæraasen, R. D. M. Nash, A. Thorsen, A. Slotte, T. Hansen, and O. S. Kjesbu. 2010. Do capital breeders like Atlantic herring (*Clupea harengus*) exhibit sensitive periods of nutritional control on ovary development and fecundity regulation? Canadian Journal of Fisheries and Aquatic Sciences 67:16–27.

Kennedy, J., P. R. Witthames, and R. D. M. Nash. 2007. The concept of fecundity regulation in plaice (*Pleuronectes platessa*) tested on three Irish Sea spawning populations. Canadian Journal of Fisheries and Aquatic Sciences 64: 587–601.

Kennedy, J., P. R. Witthames, R. D. M. Nash, and C. J. Fox. 2008. Is fecundity in plaice (*Pleuronectes platessa* L.) down-regulated in response to reduced food intake during autumn? Journal of Fish Biology 72:78–92.

Kjesbu, O. S. 2009. Applied fish reproductive biology: contribution of individual reproductive potential to recruitment and fisheries management. Pages 293–332 *in* T. Jakobsen, M. J. Fogarty, B. A. Megrey, and E. Moksness, editors. Reproductive biology and its implications for assessment and management. Wiley-Blackwell, Chichester, UK.

Kjesbu, O. S., H. Kryvi, S. Sundby, and P. Solemdal. 1992. Buoyancy variations in eggs of Atlantic cod (*Gadus morhua* L.) in relation to chorion thickness and egg size: theory and observations. Journal of Fish Biology 41: 581–599.

Kjesbu, O. S., P. R. Witthames, P. Solemdal, and M. G. Walker. 1998. Temporal variations in the fecundity of Arcto-Norwegian cod (*Gadus morhua*) in response to natural changes in food and temperature. Journal of Sea Research 40:303–321.

Kraus, G., J. Tomkiewicz, and F. W. Koster. 2002. Egg production of Baltic cod (*Gadus morhua*) in relation to variable sex ratio, maturity, and fecundity. Canadian Journal of Fisheries and Aquatic Sciences 59:1908–1920.

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. Journal of Sea Research 49:203–219.

Lowe, S., and coauthors. 2007. Stock assessment of Aleutian Islands Atka mackerel. *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.

Ma, Y., O. S. Kjesbu, and T. Jorgensen. 1998. Effects of ration on the maturation and fecundity in captive Atlantic herring (*Clupea harengus*). Canadian Journal of Fisheries and Aquatic Sciences 55:900–908.

Macewicz, B. J., J. J. CastroGonzalez, C. E. CoteroAltamirano, and J. R. Hunter. 1996. Adult reproductive parameters of Pacific sardine (*Sardinops sagax*) during 1994. California Cooperative Oceanic Fisheries Investigations Reports 37:140–151.

Marteinsdottir, G., and A. Steinarsson. 1998. Maternal influence on the size and viability of Iceland cod *Gadus morhua* eggs and larvae. Journal of Fish Biology 52:1241–1258.

McDermott, S. F., L. W. Fritz, and V. Haist. 2005. Estimating movement and abundance of Atka mackerel (*Pleurogrammus monopterygius*) with tag–release–recapture data. Fisheries Oceanography 14:113–130.

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

Morgan, M. J., and R. M. Rideout. 2008. The impact of intrapopulation variability in reproductive traits on population reproductive potential of Grand Bank American plaice (*Hippoglossoides platessoides*) and yellowtail flounder (*Limanda ferruginea*). Journal of Sea Research 59:186–197.

Murawski, S. A., P. J. Rago, and E. A. Trippel. 2001. Impacts of demographic variation in spawning characteristics on reference points for fishery management. ICES Journal of Marine Science 58:1002–1014.

Nichol, D. G., and E. I. Acuna. 2001. Annual and batch fecundities of yellowfin sole, *Limanda aspera*, in the eastern Bering Sea. U.S. National Marine Fisheries Service Fishery Bulletin 99:108–122.

Pauly, D., and R. S. V. Pullin. 1988. Hatching time in spherical, pelagic, marine fish eggs in response to temperature and egg size. Environmental Biology of Fishes 22:261–271.

Probst, W. N., G. Kraus, R. M. Rideout, and E. A. Trippel. 2006. Parental effects on early life history traits of haddock *Melanogrammus aeglefinus*. ICES Journal of Marine Science 63:224–234.

Rand, K. 2007. Longitudinal growth differences in Atka mackerel (*Pleurogrammus monopterygius*): using a bioenergetic model to identify underlying mechanisms. Master's thesis. University of Washington, Seattle.

Ricker, W. E. 1954. Stock and recruitment. Journal of the Fisheries Research Board of Canada 11:559–623.

Rijnsdorp, A. D. 1990. The mechanism of energy allocation over reproduction and somatic growth in female North Sea plaice, *Pleuronectes platessa* L. Netherlands Journal of Sea Research 25:279–289.

Spies, I. B., D. J. Brasier, T. L. O'Reilly, T. R. Seamons, and P. Bentzen. 2005. Development and characterization of novel tetra-, tri-, and dinucleotide microsatellite markers in rainbow trout (*Oncorhynchus mykiss*). Molecular Ecology Notes 5:278–281.