

Project No: F0522

Title: Reproductive ecology of Atka mackerel, *Pleurogrammus monopterygius*, in Alaska

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Project Summary: Atka mackerel support a multi-million dollar commercial fishery and play a key role in the marine ecosystem of the Aleutian Islands. This study represents an ongoing research effort examining aspects of Atka mackerel reproductive ecology which will be directly applicable to estimates of spawning biomass, recruitment, stock dynamics, and distribution patterns. In 2004, spatio-temporal patterns in distribution were examined with respect to spawning condition and habitat use for nesting sites. Additionally, Atka mackerel embryos were incubated at different temperatures at the Alaska Sea Life Center to allow the construction of developmental series. This information is essential since egg development at low temperatures in deeper waters could extend the spawning season dramatically and influence distribution patterns. Variability in female maturity schedule was examined and it is proposed to estimate variability of realized fecundity that also directly affects reproductive output and estimation of female spawning biomass. Male spawning biomass might influence reproductive success as much as female spawning biomass due to nest guarding. Egg cannibalism as a mating strategy could maximize individual reproductive success and minimize the energetic costs associated with nest tending in males.

Specific objectives of this study are to: 1) analyze additional years of spatio-temporal distributions by reproductive stage, 2) expand embryonic developmental series over finer sampling scales and broader temperature range; 3) determine parentage of egg batches 4) evaluate egg cannibalism using genetic techniques; 5) investigate spatio-temporal variation in reproductive output (maturity schedule, realized fecundity); 6) determine fecundity and egg caloric content of successive batches spawned in captivity

Progress summary: Following is summary of progress made for the specific objectives:

1) *Analyze additional years of spatio-temporal distributions by reproductive stage.*
 In September 2005, 408 gonad samples were collected at Amchitka Island, Tanaga Pass and Petrel Bank, along with data on sex ratio and length frequency. Collections were made during the spawning season, since an analysis of previous data collected in 2002 at Seguam pass showed the greatest segregation by size and maturity stage during this time.

Spatio-temporal maturity patterns at Seguam pass in 2002 (NPRB project 417 final report) suggest either most mature females depart the only area open to commercial fishing at Seguam Pass during the September fishing season and/or recruitment of young fish occurs in the area outside of Seguam pass open the commercial fishery.

An analysis of length frequency data from the fishery data 1991-2005 indicated that the area at Petrel Bank may be similar to the Seguam pass area outside the trawl exclusion zone where juvenile fish dominate the catch (Figure 1). This was in contrast the remaining areas of the central Aleutian Islands (NMFS statistical area 542) where the fishery length distribution shows larger size groups caught. The analysis also showed that the Atka mackerel catch taken from the Petrel Bank area comprises 25-30% of the total Atka mackerel catch across all areas since 1999 (Figure 2). The relatively large percentage of juvenile fish taken from Petrel Bank may explain the shift in selectivity of the Atka mackerel fishery toward smaller fish in recent years noted in the Atka mackerel stock assessment.

We are continuing the description of the male reproductive cycle using histological methodology, with the male Atka mackerel samples collected in March, May and June 2005.

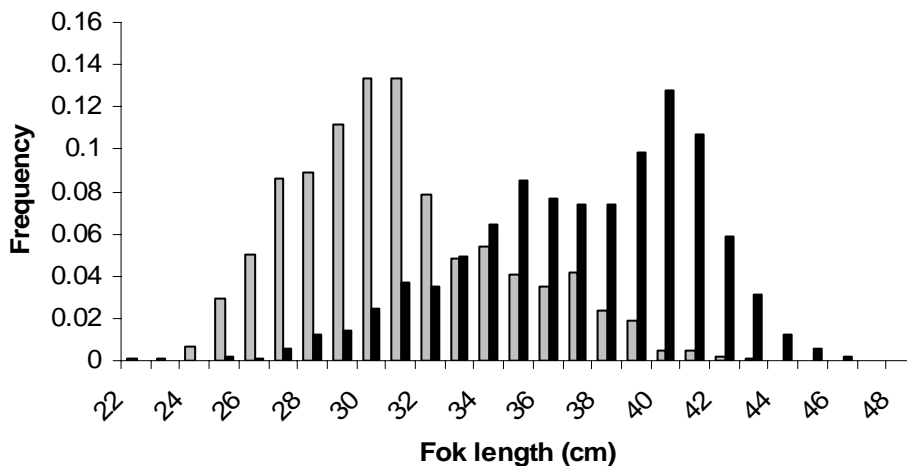


Figure 1. Percent length frequencies of Atka mackerel caught at Petrel Bank (Gray bars) compared to inside critical habit in area 542 (black bars).

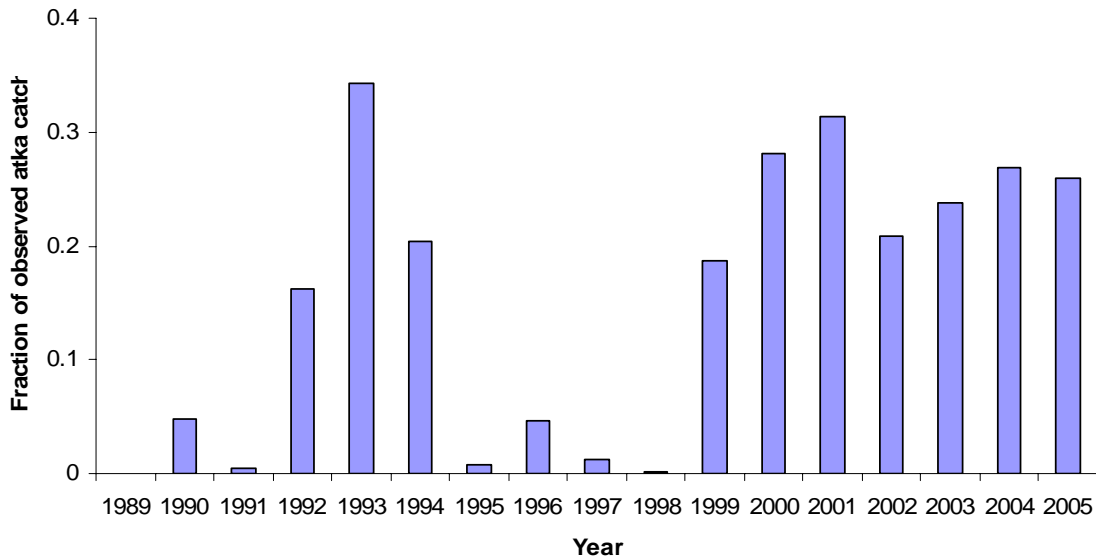


Figure 2. Fraction of total observed Atka mackerel catch which is caught in Petrel Bank by year.

2) *Expand embryonic developmental series over finer sampling scales and broader temperature range.*

For the 2006 breeding season, submersible cameras and recording equipment have been reinstalled in the study aquarium at the Alaska SeaLife Center. Equipment was upgraded to better document Atka mackerel spawning behavior and now consists of two color cameras. Incubation regimes have been established at 2°C and 12°C to examine the effect of extreme temperatures on embryo development. Additional egg batches will be incubated at 7°C. An IACUC annual renewal for 2006 has been submitted to the Alaska SeaLife Center’s IACUC for review.

In 2006, Atka mackerel spawning at the Alaska SeaLife Center began July 23 and continued until October 5. A total of 21 separately deposited egg masses were produced by 2 male and 4 female Atka mackerel between July 23 and September 21, 2006; these egg masses were removed from the study aquaria for incubation experiments, fecundity and caloric studies, and genetic analysis. At least two additional egg masses were documented as being cannibalized during the same time frame. On September 21, 2006 one male died and the remaining male and 4 females produced 5-7 egg masses, which were either cannibalized or sampled for later genetic analysis.

To date, incubation and sampling are completed for experiments at 15°C, 12°C and 7°C; only the incubation at 2°C is ongoing. Preliminary results from the completed incubation experiments for three egg batches suggest that at 15°C proper development and hatching did not occur. Four egg masses incubated at 12°C had an average time until first hatch of 39.14 days, and three egg masses incubated at 7°C had an average time until first hatch of 70.84 days. Three egg masses at 2°C have been incubating for over 165 days and are continuing to develop.

3) *Determine parentage of egg batches.*

Spawning event summer 2004, “small” tank

Thirteen egg masses, produced by two males and four females in captivity at the Alaska SeaLife Center in 2004, were genotyped using DNA microsatellite markers to determine parentage. We genotyped 96 eggs per clutch for the first two clutches and determined that a single pair of parents was responsible for each clutch and that a single male dominated spawning events (Table 1). These results were not consistent with those observed for egg masses collected in the field, where multiple parentage is very common, and we attribute them to the controlled conditions for mating in captivity (e.g. small tank, limited numbers of parents). We elected not to exhaustively sample the remaining clutches and instead analyzed 24 embryos from each. Behavioral observations showed that Male 2 held the territory for the first half of the spawning season, but was then replaced by Male 1 as the guardian male. Male 2 completely monopolized matings before being displaced from the territory, yet he continued to sire all embryos in all but one of the egg masses subsequently produced in the nesting territory, most likely as the result of alternative reproductive tactics. Some observations were made of the second male performing spawning movements at night, and this may represent sneaking behavior. We also observed variation in the realized fecundity of the females; the four females produced between 1 and 6 egg masses.

Lengths and weights were collected for Atka mackerel broodstock. Natural markings from the 6 known males were documented to later be used for identification of males guarding territories.

Table 1. Parentage assessment of egg masses produced in captivity in 2004.

Egg mass	Collection Date	Male	Female
A	2004	2	B
C	2004	2	A
D	2004	2	A
E	2004	1 (~90%), 2 (~10%)	D
G	2004	2	B
H	2004	2	D
J	2004	2	C
K	2004	2	B
L	2004	2	D

X	2004	2	A
1	2004	2	B
2	2004	2	B
3	2004	2	B

Spawning event 2005, “large” tank

We genotyped developing embryos from 11 Atka mackerel egg clutches produced at the Alaska SeaLife Center “Bird Exhibit” in 2005 to assess parentage and reproductive behavior. Clutches were collected from two different territories at three different time periods. In both cases a single guardian male fertilized all eggs in its territory including (in one case) clutches sampled two weeks apart. Preliminary results (Table 2) indicate a polygynous mating system with up to five females contributing eggs within an egg mass. Females also contributed to multiple clutches; two females deposited eggs in four clutches, two contributed eggs to two clutches, and the remaining five females contributed eggs to one clutch each. However, none of the clutches contained egg masses from two different females that were physically adhered. In all cases where more than one female contributed to a clutch, the eggs from different females were physically separated in different egg masses. Females did not appear to be limited to one territory or male, thus we conclude they have a polygynous mating system.

Results from captive fish in this exhibit suggest that in Atka mackerel, mating is random and involves one fish of each gender per egg mass. Captive males hold territories for some time period (at least several weeks) and fertilize all eggs within that territory, exhibiting the polygynous strategy documented in other greenlings. In these species females mate and distribute multiple clutches of eggs with nesting males, perhaps maximizing their reproductive potential by diluting the risk of egg predation and by selecting guardian male (e.g., color, size) or nest characteristics that reduce mortality. Crow et al. (1997) found that ~40% of kelp greenling (*Hexagrammos decagrammus*) nests contained clutches from multiple females and DeMartini (1987) reported similar proportions for painted greenling.

Table 2: Parentage analysis in the large tank in 2005.

Egg mass	Territory	Collection Date	Male	Female
B	1	8/25/2005	25	9
C	1	8/25/2005	25	14
J	1	8/25/2005	25	22, 23
I	1	8/25/2005	25	14, 16, 18, 19, 23
O	1	9/6/2005	25	14
Q	1	9/6/2005	25	14
R	6	10/14/2005	8	23
U	6	10/14/2005	8	24
X	6	10/14/2005	8	9, 13
Y	6	10/14/2005	8	19
Z	6	10/14/2005	8	23

4) *Evaluate egg cannibalism using genetic techniques.*

Highly polymorphic DNA markers were used to assess parentage of embryos consumed by five adult Atka mackerel of each gender. Gut contents contained both single eggs and one or two partial egg masses (Table 3). Most of these egg masses consisted of batches of developing full and half-sib embryos produced by multiple (3 - 8) parents. All female cannibals were excluded as the mother of embryos they had eaten, thus indicating heterocannibalism. Similarly, four of five males in spawning coloration were excluded as sires of cannibalized embryos, with the exception of one male cannibal, determined to be the sire of two half-sib families detected in one egg mass, thus documenting filial cannibalism by male Atka mackerel. However, this male sired only 22 % of the embryos genotyped in the egg mass, which contained a minimum number of eight parental genotypes. It is unknown if he was the attendant male or an adjacent territory holder. The complex polygamous mating system inferred from preliminary analyses of partially cannibalized egg clutches suggest that sneaked fertilizations and nest raiding by males may be common behaviors in this species. It seems highly improbable that females would exhibit filial cannibalism so we will focus on parental determination of 10 partial egg masses from male cannibals to get a better estimate of the frequency of this behavior in natural populations.

Table 3. Genetic assessment of patterns of cannibalism in male and female Atka mackerel.

Cannibal	# partial egg masses consumed	minimum # of parents			cannibalism type H = heterocannibalism F = filial cannibalism
		mass 1	mass 2	indeterminate*	
♂ 1	2	8	4		H, F. ♂ 1 sired two half-sib families (22% of all cannibalized embryos)
♂ 3	indeterminate			?	H
♂ 5	indeterminate			?	H
♂ 6	2	3	3		H
♂ 8	2	2	3		H
♀ 1	2	6	5		H
♀ 3	1	8			H
♀ 4	indeterminate			2	H
♀ 5	indeterminate			6	H

Further analysis of cannibals and egg masses collected during the summer of 2006 will provide additional data.

5) *Investigate spatio-temporal variation in reproductive output (maturity schedule, realized fecundity).*

Maturity at age and length analysis for the 146 samples collected in 2004 has been completed. The results were compared with results from previous years (1992-1994, 2002, and 2004). The data were compared using a generalized linear model with area and time period as factors (S-Plus, Veneables and Ripley, 1994).

When comparing all years, maturity at age did not vary by INFPC area ($p = 0.40$) (Figure 3). Maturity at age was marginally significantly different by time period ($p=0.053$; Figure 4). However, maturity at length varied significantly by area ($p << 0.0001$; Figure 5) and time period ($p << 0.0001$, Figure 6).

It appears that female maturity for Atka mackerel is determined by age and not size. At age 4, most females will be mature (50% age at maturity is 3.5 years) regardless of their size at this age. A model that predicts changes in year class strength was developed in collaborations with Jim Ianelli (AFSC). It showed that changes in year-class strength can cause annual variation in length at 50% maturity of up to 2cm, even if maturity at age and growth remains constant (Fig 7). A manuscript of these results is in internal review.

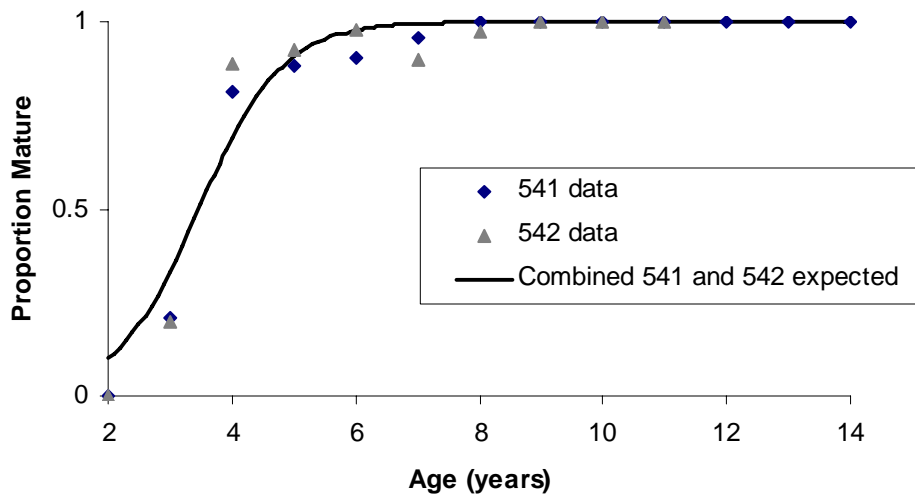


Figure 3. Proportion mature at age by INFPC area.

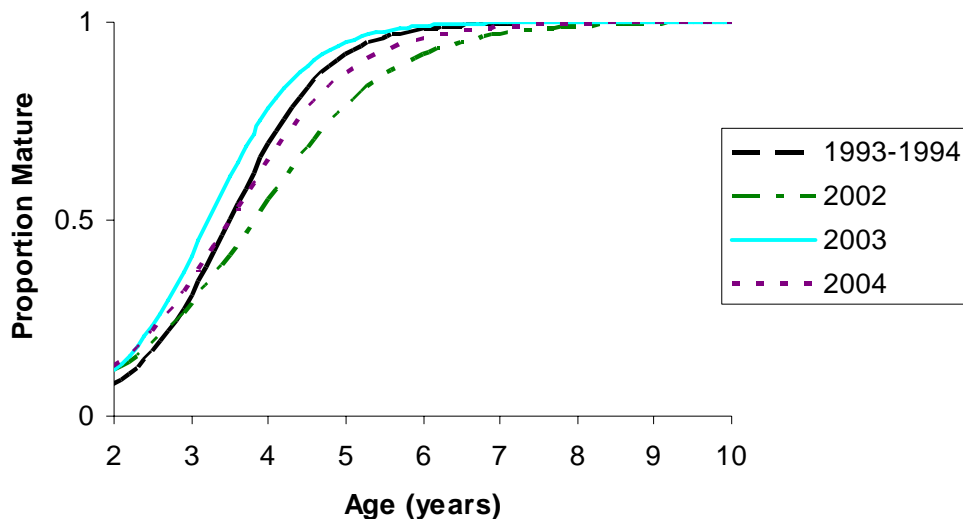


Figure 4. Proportion mature at age (INFPC areas 541 and 542 combined) by time period.

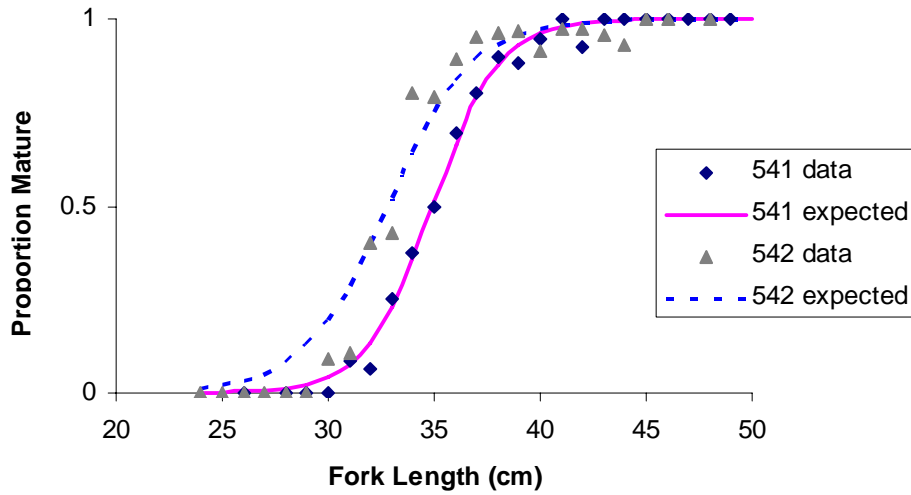


Figure 5. Proportion mature at length for INFPC areas 541 and 542.

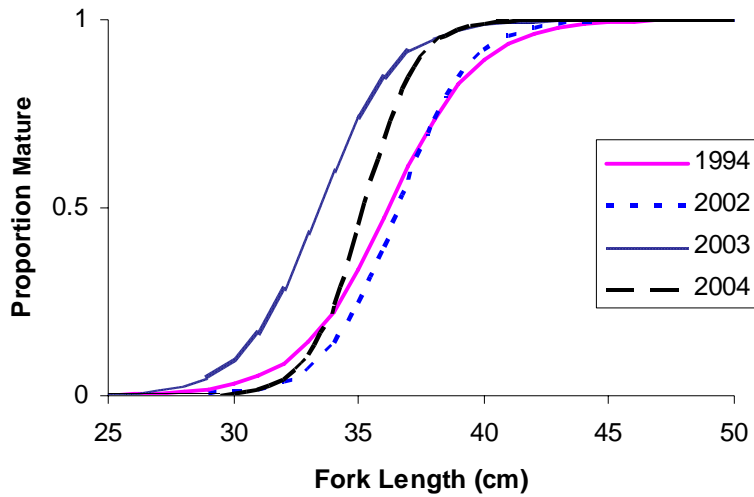


Figure 6. Proportion mature at length over time for INFPC area 541.

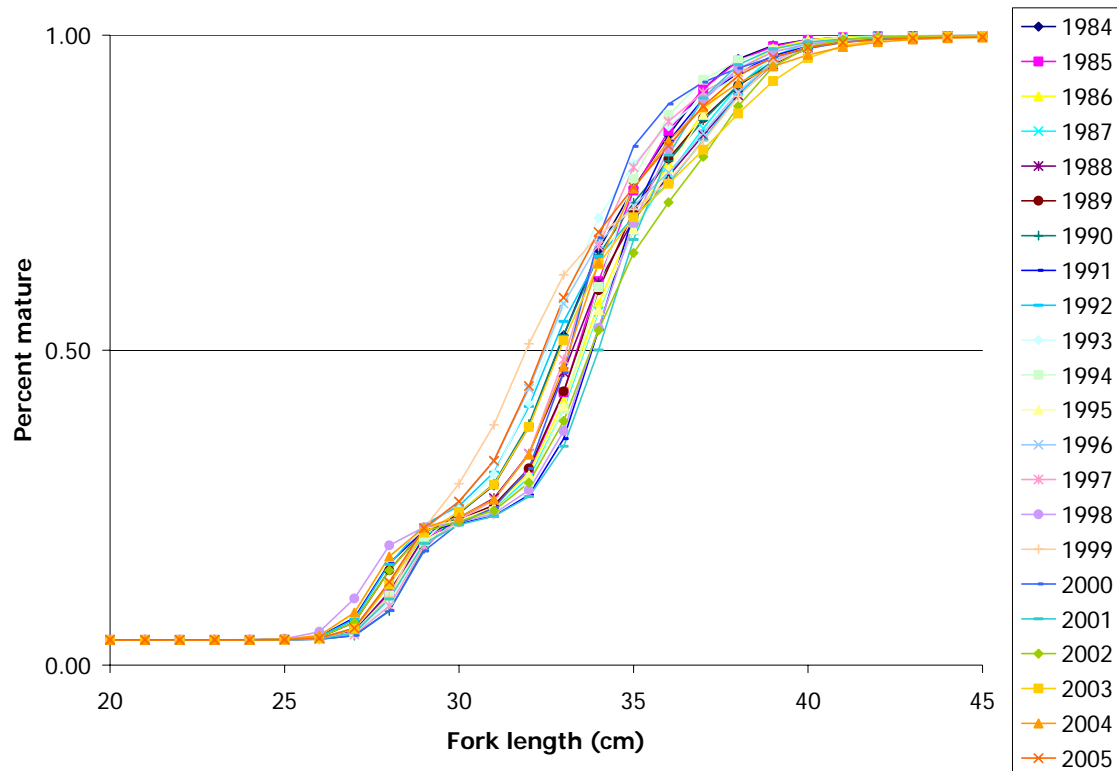


Figure 7. Model predicted proportion mature by length for 1984 – 2005.

6) *Determine fecundity and egg caloric content of successive batches spawned in captivity.*

Female gonad samples were collected from the 2005 Gulf of Alaska trawl survey, and from September in 2005 aboard the FV *Seafisher*. Those samples will be used to determine the methodology for estimating egg energetic content.

Researchers at the Alaska SeaLife center collected samples for fecundity and egg caloric analysis and shipped subsamples to Seattle. Spawning of eight (3.5.0) captive Atka mackerel began 7/13/05 at the Alaska Sealife Center and yielded forty separately deposited egg masses. Lengths and weights have been collected from 2.4.0 Atka mackerel broodstock. Gravimetric sampling was performed on each egg mass to determine number of eggs per egg mass. Sub samples for each egg mass were preserved for genetic analysis which will be used to determine maternal parentage.

A bomb calorimetry pilot study indicated 1.5 g wet weight of Atka mackerel embryos are required to determine caloric content. Embryo subsamples from the Alaska SeaLife center have been reweighed, an approximately 1.5 gram sample set aside for caloric content work, and the remainder of the embryos were separated and counted. Batch fecundity of egg masses was estimated gravimetrically and compared to estimates of batch fecundity from ovaries collected in the wild.

The number of embryos per batch collected at the Alaska SeaLife center did not significantly differ from batch fecundity estimates for wild fish prior to spawning (t-test, $p=0.95$). One interesting note is that several of the egg masses collected in captivity were much smaller than the estimates from wild fish from pre-spawning ovaries. This could be explained by either egg cannibalism prior to removal from the tank, or by the deposition of eggs from one female in different nests during a spawning event. Genetic parentage analysis is planned and may answer this question. A preliminary analysis showed that batch fecundity did not decrease over the course of the spawning season (Figure 8). Genetic parentage analysis will determine if batch size of individual females varies by batch order.

Bomb calorimetry estimates have begun and are in progress at the University of Washington.

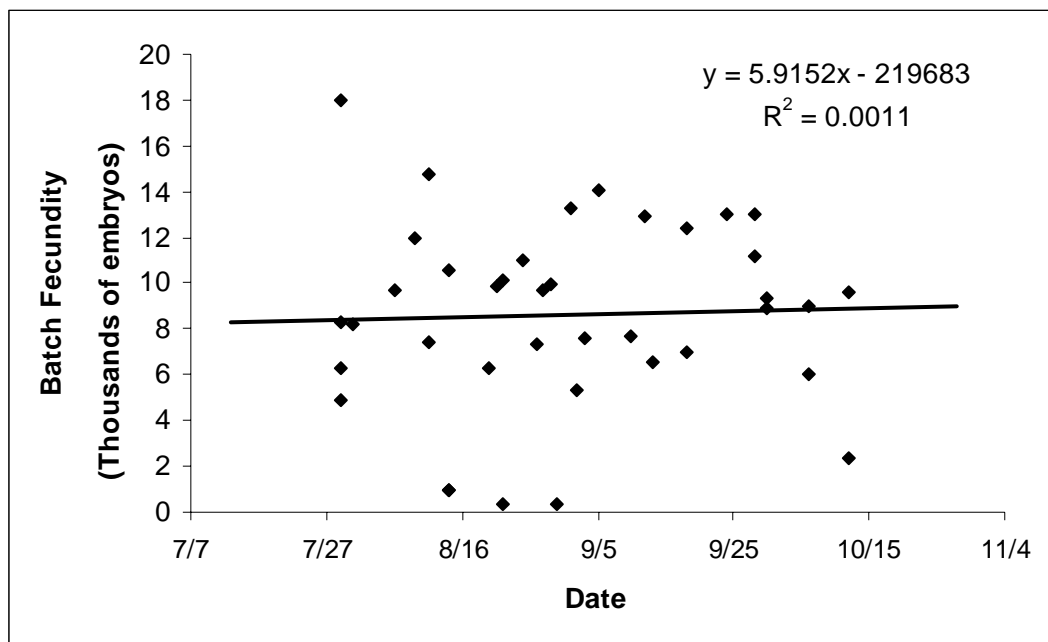


Figure 8: Batch fecundity by spawning date for batches spawned in 2005 at the Alaska Sealife Center.

Outreach:



Fabrication and construction of a new exhibit highlighting NPRB funded Atka mackerel research has been implemented at the Alaska SeaLife Center. The exhibit utilizes a CPU driven 48" plasma screen television and is located next to the Atka mackerel exhibit. Although operating software and content have not been finalized, initial public feedback has been very positive.

Presentations:

Guthridge, J. L., N. Hillgruber, and R. Lauth (2006). Embryonic development of Atka mackerel and the effect of temperature. AFS Juneau Student Symposium. April 2006 (Oral presentation)

Guthridge, J. L., N. Hillgruber, and R. Lauth (2006). The effect of temperature on hatch time for Atka mackerel. 14th Western Groundfish Conference, Newport, Oregon. January/February 2006 (Poster)

Guthridge, J. L., N. Hillgruber, and R. Lauth (2006). The effect of temperature on hatch time for Atka mackerel. Marine Science in Alaska: 2006 Symposium. January 2006, Anchorage, Alaska. (Poster)

Cooper, D., and S. F. McDermott (2006). Atka mackerel reproductive biology, Temporal and spatial variation in Atka mackerel maturity schedule. Marine Science in Alaska: 2006 Symposium. January 2006, Anchorage, Alaska. (Poster)

McDermott S. F. (2006). Current research of Atka mackerel at the Alaska Fisheries Science Center. Multicultural Initiative in the Marine Sciences (MIMSUP event), Alaska Fisheries Science Center.

Spies, I.S. and M. Canino. (2006) Atka mackerel reproductive biology, Genetic assessment of cannibalism and the mating system of Atka mackerel. Marine Science in Alaska: 2006 Symposium. January 2006, Anchorage, Alaska. (Poster)

Spies, I.S. and M. Canino. (2006) “Its elementary, dear Watson”; How genetics can provide clues to population structure, cannibalism, and the mating system of Atka Mackerel. Science in the Sound Speaker Series, Highline Community College. May, 2006, Seattle, WA. (Oral presentation; http://flightline.highline.edu/mast/06-Speaker_listing.htm).