Geographic variation in genetic and growth patterns of Atka mackerel, *Pleurogrammus monopterygius* (Hexagrammidae), in the Aleutian archipelago

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Abstract.—Atka mackerel, *Pleurogrammus monopterygius*, growth data differed significantly by area for length and weight characteristics, suggesting that local aggregations of this species develop differential growth patterns. We analyzed length-at-age and weight-length growth patterns from over 500 fish and 37 protein-coding gene loci to determine the relation among Atka mackerel stocks in the Aleutian Islands. However, the potential stock delineations based on the growth patterns were not supported by the genetic data. Atka mackerel showed a high degree of genetic variability. Variation was detected at 30 of 37 loci; 14 of the 30 loci were variable at the $P_{0.95}$ level. Average heterozygosity for 329 specimens was 0.137, an unusually high value for a marine fish. Between-sample variation among samples was extremely low (F_{ST}=0.004), suggesting considerable gene flow throughout the range represented by the samples. On the basis of the genetic data, we cannot reject the null hypothesis that our samples came from a single genetically homogenous population of Atka mackerel. We presume that gene flow occurs throughout the population through the dispersal of pelagic larvae and juveniles. We conclude that despite genetic homogenization, phenotypic variation in Atka mackerel adult life history stages warrants consideration by fishery managers.

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Atka mackerel, *Pleurogrammus monopterygius*, a member of the greenling family Hexagrammidae, is distributed throughout the north Pacific Ocean, the southern Bering Sea, and the Gulf of Alaska. The center of abundance of this semipelagic species is the Aleutian Islands.[1] Greenling larvae and fingerlings (25–30 mm) undergo a pelagic stage and assume an oceanic mode, during which time they reside in the surface layers of the open waters and migrate for considerable distances out to sea (Gorbunova, 1962). Adult (3+ years) Atka mackerel are pelagic during much of the year (in waters <200 m depth) but migrate annually to moderately shallow waters where they become demersal and spawn in areas of strong currents (Gorbunova, 1962). They have specific spawning site preferences and spawning has been observed in island passes in the Aleutian, Shumagin, and Commander Island archipelagoes (Turner, 1886; Rutenberg, 1962).

Historically, large inshore concentrations of spawning Atka mackerel have been the target of subsistence fisheries by native Aleuts (Turner, 1886). The first large-scale commercial catches in the Aleutian Islands and western Gulf of Alaska were taken by Russian fleets beginning in the early 1970s, followed by the Republic of Korea, and to a lesser extent, Japan in the early 1980s (Murai et al., 1981; Berger et al., 1986). Presently, a U.S. trawl fishery harvests Atka mackerel from the eastern Bering Sea and Aleutian Islands regions, with minimal catches from the Gulf of Alaska. From 1992 to 1994, catches averaged about 70,000 metric tons (t) (valued at 17 million U.S. dollars [exvessel] in 1994) and increased to 104,000 t in 1996.[1,2]

[1] Lowe, S. A., and L. W. Fritz. 1996a. Atka mackerel. *In* Stock assessment and fishery evaluation report for the groundfish resources of the Bering Sea/Aleutian Islands regions as projected for 1997, p. 369–420. North Pacific Fishery Management Council, 605 W. 4th Avenue, Suite 306, Anchorage, AK 99501-2252.

[2] Lowe, S. A., and L. W. Fritz. 1996. Atka mackerel. *In* Stock Assessment and Fishery Evaluation Report for the Groundfish Resources of the Gulf of Alaska as projected for 1997, p. 331–361. North Pacific Fisheries Management Council, 605 W. 4th Avenue, Suite, Anchorage, AK 99501-2252.

An analysis of morphological and meristic data by a Russian scientist indicated separate populations in the Gulf of Alaska and the Aleutian Islands.[3] The meristic study compared the number of dorsal, anal, and pectoral fin rays, total number of vertebrae, and number of gill rakers on the first gill arch from a sample of 100 fish collected off Kodiak Island in the Gulf of Alaska and the Rat Islands in the Aleutian Islands. The morphological study consisted of a statistical comparison of various partial fish body lengths as a percentage of fork length, by area. Lee (1985) also conducted a morphological study analyzing the covariance between four partial fish lengths and fork length by area and sex from samples taken from the Bering Sea, Aleutian Islands, and the Gulf of Alaska. The data showed some differences (although not consistent by area for each characteristic), suggesting a certain degree of reproductive isolation. On the basis of an analysis of variance of Aleutian Islands growth data with year, area, and sex as factors, Kimura and Ronholt (1988) found significant differences in weight and length-at-age of Atka mackerel from six different areas in the Aleutian Islands, indicating potential stock differentiation. Kimura and Ronholt (1988) suggested therefore that Atka mackerel appear to be distributed in localized groups or assemblages once they assume the more demersal phase of their life history. Recent analysis of Aleutian Islands Atka mackerel growth data by current fishery management areas shows a distinctive size cline, with length at age smallest in the western Aleutians and largest in the eastern Aleutians[1,2]

Differential growth by area can be an indication of stock delineations. The presumption for Atka mackerel, based on the morphological and growth analyses, was of at least a discontinuous distribution throughout the Aleutian Archipelago. Genetic tests are necessary to confirm separate stocks and help to further our understanding of the life history and distribution patterns of Atka mackerel. Information about the extent and nature of stock differences is also critical to improve stock assessments for long-term management of the Atka mackerel fisheries in the Gulf of Alaska and Aleutian Islands. To date, there have been no population genetics surveys of this species to determine the existence of discrete stocks.

A preliminary survey of allozymes from 40 individuals indicated a sufficient number of polymorphic loci to conduct a full study of the genetic population structure of this species (Winans et al., 1995). We report here 1) length-at-age and length-weight relations derived from samples taken throughout the Aleutian Archipelago and 2) a genetic survey of Atka mackerel from samples taken from four locations in the Aleutian Islands ranging from 169°W to 172°E (Fig. 1). Our null hypothesis is that there are no differences between samples taken along the Aleutian Archipelago, from Umnak Island in the east to Attu Island in the west.

[3] Levada, T. P. 1979. Comparative morphological study of Atka mackerel. Pac. Sci. Res. Inst. Fish. Oceanogr.5(TINRO), Vladivostok, U.S.S.R. Unpubl. manuscript, 7 p.

Materials and methods

Age, weight, and length data

Biological samples and length and weight information were collected during National Marine Fisheries Service (NMFS) triennial trawl surveys, June to August of 1993 and 1994, from the Gulf of Alaska and Aleutian Islands region, respectively. The sampling coincided with the summer spawning period of Atka mackerel (July to October; McDermott and Lowe, 1997). Random samples of Atka mackerel from the trawl survey catches were sorted by sex, and individual weight and fork-length data were collected. Length was estimated to the nearest one centimeter, and weight was estimated to the nearest gram with a platform scale when weather conditions allowed (Martin and Clausen, 1995). Age structures (sagittal otoliths) were collected by using a length-stratified sampling scheme of five fish per sex, per centimeter length category. An attempt was made to distribute the otolith collections over the entire survey area. Otoliths were placed in vials with 50% ethanol, and age was determined by personnel in the NMFS Age Determination Laboratory.

A total of 510 otoliths were collected and aged (Table 1). Otoliths were prepared by snapping each along the dorsal-ventral plane and passing the broken surface over a flame. The burnt cross-section was examined under a dissecting microscope and illuminated by reflected light (Anderl et. al, 1996).

Growth parameters were estimated by fitting the age-length data to the widely used von Bertalanffy (1938) growth equation:

$$l_t = L_\infty\left(1-e^{-K(t-t_0)}\right),$$

which expresses length at age t (l_t) as a function of three parameters: L_∞, K, and t_0. As age increases, length approaches L_∞, which is the mean asymptotic length. The slope of the von Bertalanffy curve continuously decreases with increasing age as l_t approaches the asymptotic length. This rate of decrease is described by K. The parameter t_0 is the theoretical time a fish would have been zero length. The

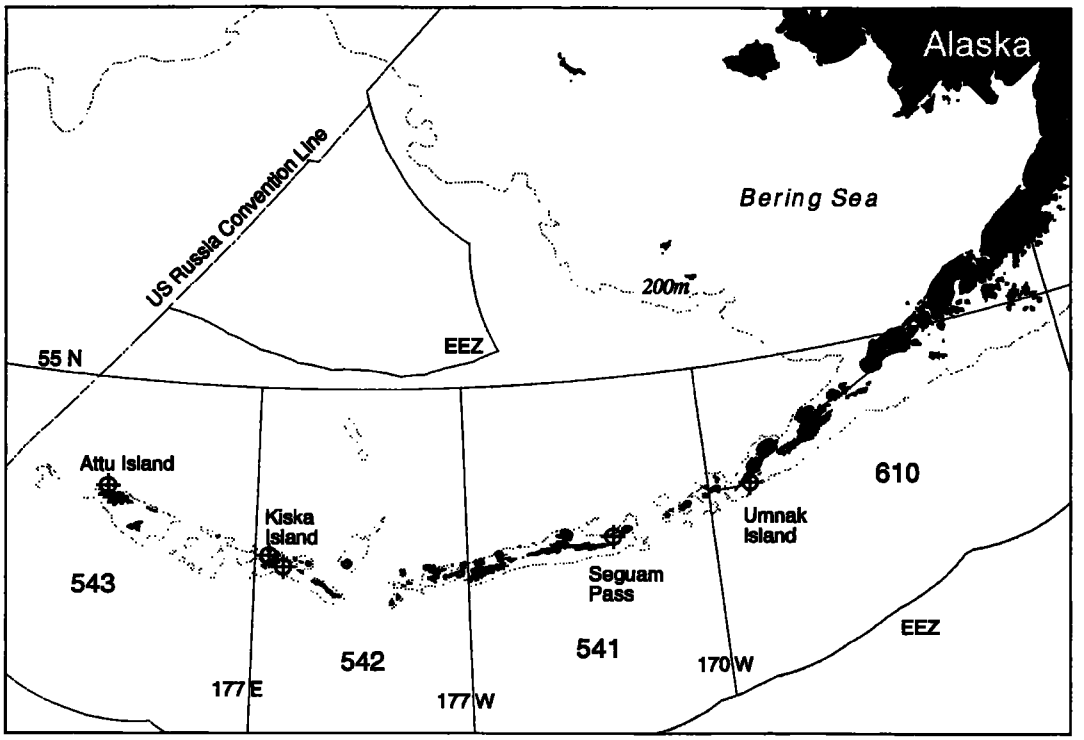

Figure 1

Locations of Atka mackerel sample collections in the western Aleutian (543), central Aleutian (542), and eastern Aleutian Islands (541), and western Gulf of Alaska (610) fishery management areas. The U.S. Exclusive Economic Zone (EEZ) is also shown.

growth parameters were determined with a nonlinear least squares procedure (FISHPARM[4]).

Similarly, length-weight relationships were estimated from the following equation:

$$w = al^b,$$

where weight (w) varies as a power (b) of length (l). The coefficients a and b were estimated for each of the four management areas with a nonlinear least squares procedure (FISHPARM[4]). On the basis of the work of Kimura and Ronholt (1988), who found that sex was not an important differentiating variable for growth in Atka mackerel, we present growth curves for the sexes combined.

The age-length and length-weight growth curves for the four management areas were estimated and compared with an F-test. To further test for the significance of the differences among areas, regardless of the fit to the von Bertalanffy or length-weight curves, a two-factor analysis of variance (ANOVA) was applied to the age-length and the length-weight data with SPLUS software (Chambers and Hastie, 1992). The age-length ANOVA included age and area as factors and an age × area interaction term, and

Table 1

Sample sizes of aged Atka mackerel otoliths from the Gulf of Alaska (area 610), eastern Aleutian Islands (area 541), central Aleutian Islands (area 542), and western Aleutian Islands (area 543) fishery management areas (Fig. 1).

Age (yr)	Gulf of Alaska (610)	Eastern Aleutian Islands (541)	Central Aleutian Islands (542)	Western Aleutian Islands (543)	Total
2	22	2	18	19	61
3	1	7	55	53	116
4	19	9	22	10	60
5	43	15	30	25	113
6	9	44	19	20	92
7	1	8	7	5	21
8	0	7	7	8	22
9	0	1	4	5	10
10	0	1	1	13	15
Total	95	94	163	158	510

[4] Prager, M. H., C. W. Recksiek, and S. B. Saila. 1987. Nonlinear parameter estimation for fisheries. Michael Prager, Old Dominion University, Dep. of Oceanography, Norfolk, VA 23508. Unpubl. documentation.

Table 2

Enzymes examined for allozyme variation. Enzyme commission (EC) numbers follow the IUBMBNC (1992). Tissues examined were muscle (M) and liver (L). Buffers used are described by Aebersold et al. (1987) except for the ACEN7 gel, which is an ACE7 gel with 0.015% beta-nicotinamide adenine dinucleotide added to the gel and which has cathodal electrode buffers.

Enzyme name	EC Number	Locus	Tissue	Buffer
Beta-*N*-Acetylgalactosaminidase	3.2.1.53	*bGALA**	L	ACE7
N-Acetyl-beta-glucosaminidase	3.2.1.30	*bGLUA**	L	ACE7
Aconitate hydratase	4.2.1.3	*AH-1**	M	ACE7
		*AH-2**	L	ACE7
Adenosine deaminase	3.5.4.4	*ADA**	M	TBE
Adenylate kinase	2.7.4.3	*AK**	M	ACE7
Alanine aminotransferase	2.6.1.2	*ALAT**	M	TBE
Alcohol dehydrogenase	1.1.1.1	*ADH**	L	ACE7
Aspartate aminotransferase	2.6.1.1	*AAT-1**	M	ACE7
		*AAT-2**	L	TBCLE, TBE
		*AAT-3**	M	TBCLE, TBE
Creatine kinase	2.7.3.2	*CK**	M	TBCLE
Esterase	3.1.1.-	*EST**	M	TBCLE
Enolase	4.2.1.11	*ENO**	M	ACE7
Fumarate hydratase	4.2.1.2	*FH**	M	ACEN7
Glucose-6-phosphate isomerase	5.3.1.9	*GPI-1**	M	TBCLE
		*GPI-2**	M	TBCLE
Glycerol-3-phosphate dehydrogenase (NAD$^+$)	1.1.1.8	*G3PDH-1**	M	ACEN7
		*G3PDH-2**	M	ACEN7
L-Iditol dehydrogenase	1.1.1.14	*IDDH**	L	TBCL
Isocitrate dehydrogenase (NADP$^+$)	1.1.1.42	*IDHP-1**	L	ACE7
		*IDHP-2**	M	ACE7
L-Lactate dehydrogenase	1.1.1.27	*LDH**	M	ACE7
Malate dehydrogenase	1.1.1.37	*mMDH**	M	ACEN7
		*sMDH-1**	ML	ACEN7
		*sMDH-2**	M	ACEN7
Mannose-6-phosphate isomerase	5.3.1.8	*MPI**	M	TBE
Peptidase-C	3.4.-.-	*PEP-C**	M	TBE
Phosphoglucomutase	5.4.2.2	*PGM**	M	TBCLE, ACE7
Phosphogluconate dehydrogenase (decarboxylating)	1.1.1.44	*PGDH**	M	ACE7
Phosphoglycerate kinase	2.7.2.3	*PGK**	M	ACE7
Proline dipeptidase	3.4.13.9	*PEPD**	M	TBE
Pyruvate kinase	2.7.1.40	*PK**	M	ACE7
Superoxide dismutase	1.15.1.1	*SOD**	L	ACE7
Triose-phosphate isomerase	5.3.1.1	*TPI**	M	TBE
Tripeptide aminopeptidase	3.4.11.4	*PEPB-1**	M	TBE, TC4
		*PEPB-2**	M	TBE

the length-weight ANOVA included length and area factors and a length × area interaction term.

Genetic data

Genetic samples were collected from four locations throughout the Aleutian Archipelago (Fig. 1). Sample sizes were as follows: Attu Island, n=74; Kiska Island, n=80; Seguam Pass, n=100; and Umnak Island, n=75. Muscle and liver tissues were collected from each specimen for protein electrophoresis and placed in the onboard freezers until they could be transferred to a freezer set at –80°C.

Genetic variability was examined by using starch gel electrophoresis as described by Aebersold et al. (1987). Initially, we examined 36 enzyme systems, of which 28 were clearly resolved. Those 28 enzyme systems revealed 37 loci. Tissue and buffer combinations for each enzyme are listed in Table 2. Nomenclature for loci and alleles followed Shaklee et al. (1990).

Genetic variability within samples was estimated as average heterozygosity (mean proportion of heterozygous loci per individual), the percentage of polymorphic loci per sample at the $P_{0.95}$ level (frequency of the common allele ≤0.95), and the average num-

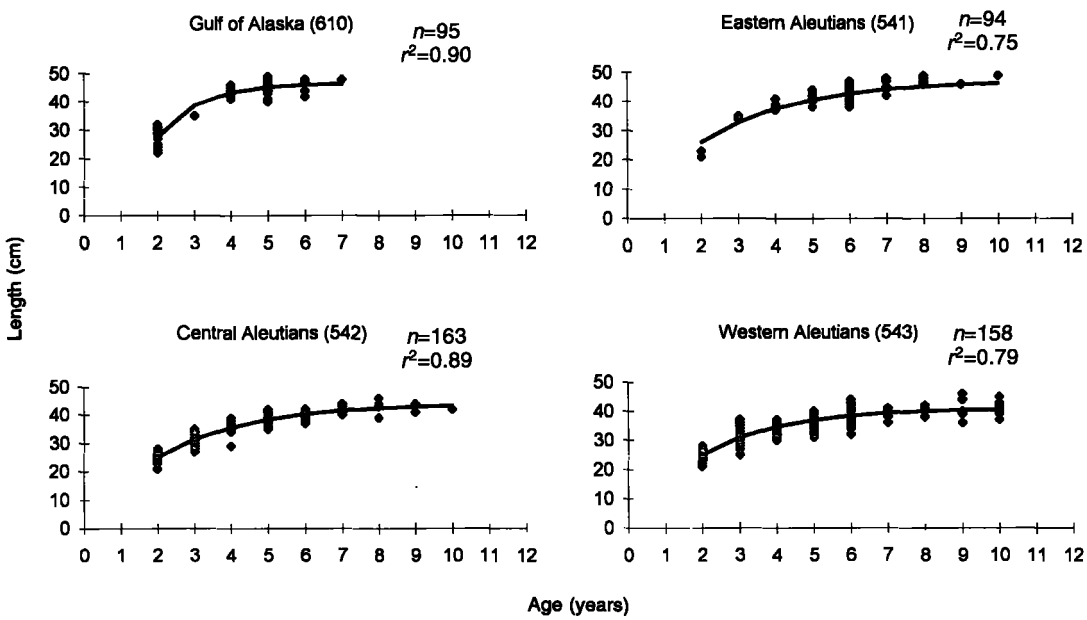

Figure 2

Atka mackerel age-length data by fishery management areas, collected from resource assessment surveys of the Gulf of Alaska and Aleutian Islands in 1993 and 1994, respectively. The fitted von Bertalanffy growth curves are plotted. Sample sizes (n) and the coefficients of determination (r^2) are given.

ber of alleles per locus. Samples were tested individually with chi-square analyses for conformance to expected Hardy-Weinberg proportions and as one pooled sample. The latter method tests the assumption that the samples are not different (i.e. represent one interbreeding population). Differences among samples were examined with Wright's fixation index F_{ST} and Nei's unbiased genetic distance statistic (Nei, 1978) and with standard chi-square contingency table analysis for the $P_{0.95}$ loci. Values of F_{ST} range from zero, indicating no population differentiation, to one, indicating fixation for alternate alleles. Genetic analyses were conducted using the BIOSYS-1 computer program (Swofford and Selander, 1981).

Results

Age, weight, and length data

Sample sizes were relatively small when stratified by area, ranging from 95 to 163. Sampled fish lengths ranged from 21 to 49 cm, ages from 2 to 10 years, and weights from 0.084 to 1.9 kg (Figs. 2 and 3). The relatively high coefficients of determination (r^2) indicated good fits to the von Bertalanffy and length-weight models (Figs. 2 and 3). An examination of the residuals also indicated no obvious patterns, and the variances of the residuals were homogeneous by age and area for the von Bertalanffy model, and by length and area for the length-weight model. The fitted growth curves for each management are shown together in Figures 4 and 5; Table 3 gives the estimated parameters and standard errors. The F-tests revealed that differences in the growth curves among areas were significant ($P<0.0005$) for both the age-length and length-weight data. Because of the low sample sizes for the Gulf of Alaska and eastern Aleutian Islands data, and low numbers of fish in the Gulf of Alaska greater than five years, these data were combined and fit to the von Bertalanffy model. An F-test to test for differences between these two specific data sets was highly significant ($P<0.0005$).

The results of the two-way factorial analysis of age-length and length-weight data were highly significant (P of $F \leq 0.0001$, Tables 4 and 5). To account for unequal sample sizes among factors, the ANOVA results in Tables 4 and 5 should be interpreted sequentially. The terms in the tables were added in the order presented, and the F-tests were given for each term in sequence. In addition, an ANOVA model was evaluated where the area factor was added first. The result of that F-test was also highly significant (P of $F \leq 0.0001$). An examination of the residuals from the age-length and length-weight ANOVA models showed

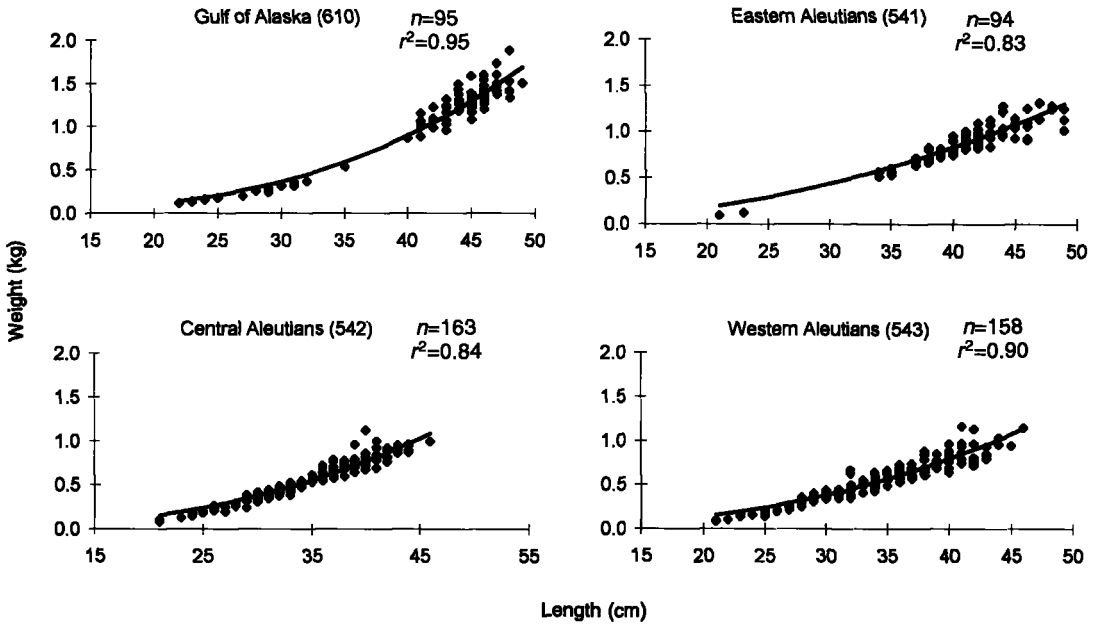

Figure 3

Atka mackerel weight-length data by fishery management areas, collected from resource assessment surveys of the Gulf of Alaska and Aleutian Islands in 1993 and 1994, respectively. The fitted weight-length curves are plotted. Sample sizes (n) and the coefficients of determination (r^2) are given.

no obvious patterns, and the variances of the residuals were homogeneous by age and area, and by length and area, for the age-length and length-weight ANOVA models, respectively.

In order to evaluate the ANOVA model assumption of equality of variances among factors, the distributions of the raw length data by age within each area were examined, and the length distributions at age among areas were compared (Fig. 2), and suggested that the variances do not appear different. Examination of the distributions of the raw weight data by length within each area, and a comparison of the weight distributions at length among areas (Fig. 3), also suggested fairly homogeneous variances. It is noted that the ANOVA model is robust to small departures from the assumption of equal variances (Neter et. al, 1985).

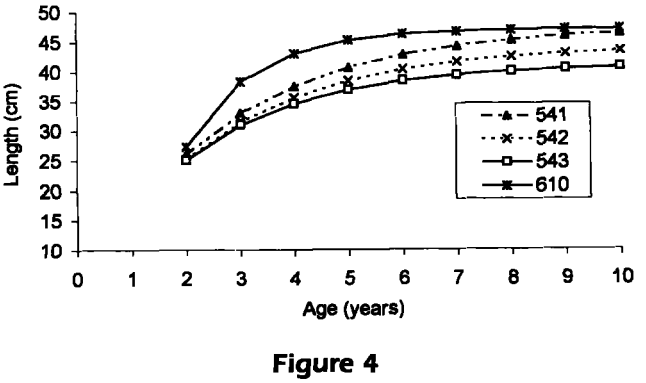

Figure 4

Estimated von Bertalanffy growth curves for Atka mackerel by fishery management area (541=eastern Aleutian, 542=central Aleutian, 543=western Aleutian Islands, and 610=western Gulf of Alaska) based on data collected from resource assessment surveys of the Aleutian Islands and Gulf of Alaska during 1993 and 1994, respectively.

Genetic data

Electrophoretic variation was observed at 30 of the 37 loci (Table 6). A majority of the variable loci (83%) had 2 to 4 alleles per locus. *IDHP-1**, *PEP-C**, and *PGK-1** had 5 alleles each, *AH-2** had 6 alleles, and *ADA** had 9 alleles. There were 14 $P_{0.95}$ loci; the frequency of the common allele at four of these loci (*ADA**, *AH-2**, *ALAT**, and *PEP-C**) was approximately 0.50.

One out of the 120 tests (0.8%) deviated from expected Hardy-Weinberg proportions (at the $P<0.05$ level) in the four samples. The Attu Island sample had an excess of heterozygotes for *ADA** ($P=0.013$).

When the four samples were pooled and tested as one population, none of the 30 tests of polymorphic loci deviated from expected Hardy-Weinberg proportions.

Average heterozygosity ranged from 0.135 to 0.142 (unweighted mean=0.136, Table 7) Percentage of polymorphic loci at the $P_{0.95}$ level ranged from 32.4% to 35.1%, and the mean number of alleles per locus ranged from 2.2 to 2.4. Seventeen unique, rare (frequency ≤0.01) alleles were identified; two each in Umnak Island and Attu Island, four in Kiska Island, and nine in Seguam Pass. Correlation of these alleles with sample size was 0.99.

Allele frequencies were similar for all samples for all polymorphic loci. The largest pair-wise allele frequency difference was 11.7% between Umnak Island (n=59) and Seguam Pass (n=96) for *ADA**100 (Table 3).[5] Only one of the 14 chi-square contingency tests for the $P_{0.95}$ loci was statistically significant (*AH-2**, P=0.004). The total chi-square was not statistically significant (P=0.08). Nei's unbiased genetic distance values ranged from 0.0000 to 0.00017 for the four samples. The mean F_{ST} for the 30 polymorphic loci was 0.004.

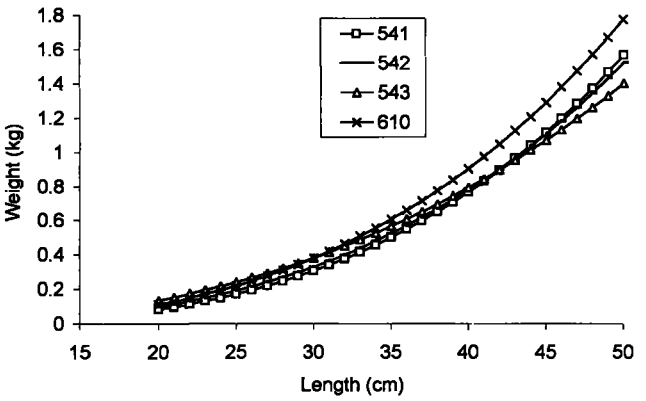

Figure 5

Estimated weight-length curves for Atka mackerel by fishery management area (541=eastern Aleutian, 542=central Aleutian, 543=western Aleutian Islands, and 610=western Gulf of Alaska) based on data collected from resource assessment surveys of the Aleutian Islands and Gulf of Alaska during 1993 and 1994, respectively.

Discussion

Growth and electrophoretic analyses

Analysis of variance showed that length-at-age and weight-at-age data were statistically different among the four management areas tested. In order to illustrate these differences, the age-length data were fitted to the commonly

[5] The power of this single locus pair-wise comparison is fairly high. For example, the probability of detecting a frequency difference of 0.15 between P_2 =0.40 and P_2 = 0.55 is 80% for samples consisting of 93 individuals each—similar to these samples sizes (Sokal and Rohlf, 1981). To be 90% certain of detecting such a difference, a sample of 122 individuals is needed.

Table 3

Parameter estimates from the von Bertalanffy growth equation (L_∞, K, t_0), and length-weight relationship (a, b), standard errors of the parameter estimates, mean square errors (MSE), and sample sizes (n) for the western Gulf of Alaska, eastern Aleutian, Central Aleutian, and Western Aleutian Islands.

	Gulf of Alaska		Eastern Aleutian Islands		Central Aleutian Islands		Western Aleutian Islands	
	Estimate	Standard error	Estimate	Standard error	Estimate	Standard error	Estimate	Standard Error
von Bertalanffy model								
L_∞	46.63	0.911	47.25	1.219	44.02	0.735	40.93	0.618
K	0.869	0.173	0.39	0.064	0.404	0.037	0.461	0.053
t_0	0.965	0.182	–0.041	0.389	–0.094	0.183	–0.05	0.247
MSE	5.98		5.36		3.44		6.52	
n	95		94		163		158	
Length-weight model								
a	0.859E-05	0.452E-05	0.237E-03	1.103E-04	0.878E-04	0.316E-04	0.652E-04	0.190E-04
b	3.132	0.137	2.212	0.123	2.46	0.098	2.55	0.08
MSE	0.01		0.01		0.01		0.01	
n	95		94		163		158	

Table 4

Two-way factorial analysis of variance of Atka mackerel length-at-age data collected from the 1993 and 1994 trawl surveys of the Gulf of Alaska and Aleutian Islands, respectively. The model contains the factors age and area, and an interaction term of age × area. SS = sum of squares.

Source	df	SS	Mean square	*F*-value	*P*>*F*
Age	11	14,576.45	1325.13	275.00	<0.0001
Area	3	5380.33	1793.44	372.19	<0.0001
Age × area	20	260.09	13.00	2.70	<0.0001
Error	477	2298.51	4.82		

Table 5

Two-way factorial analysis of variance of Atka mackerel length-weight data collected from the 1993 and 1994 trawl surveys of the Gulf of Alaska and Aleutian Islands, respectively. The model contains the factors length and area, and an interaction term of length × area. SS = sum of squares.

Source	df	SS	Mean square	*F*-value	*P*>*F*
Length	28	59.73	2.13	278.13	<0.0001
Area	3	1.21	0.40	52.77	<0.0001
Length × area	56	1.65	0.10	3.85	<0.0001
Error	425	3.26	0.01		

Table 6

Allele frequencies for 22 loci in Atka mackerel. "No." represents the number of successfully screened fish. Rare variation is described for 7 alleles[1] and 8 additional loci.[2] Seven loci were monomorphic: *AK**, *CK**, *bGALA**, *bGLUA**, *mMDH-2**, *sMDH-2**, and *PEPB-2**.

Locus, sample size and alleles	Sample location: Umnak Island	Seguam Pass	Kiska Island	Attu Island
*AAT-1**				
No.	39	100	73	74
*-100	1.000	0.995	0.993	0.993
*-63	0.000	0.005	0.007	0.007
*AAT-2**				
No.	62	100	80	73
*100	0.815	0.860	0.875	0.829
*60	0.185	0.135	0.112	0.164
*115	0.000	0.000	0.006	0.007
*82	0.000	0.005	0.006	0.000
*AAT-3**				
No.	70	89	76	73
*100	0.900	0.916	0.888	0.925
*110	0.100	0.084	0.112	0.075
*ADA**				
No.	59	96	78	72
*100	0.534	0.417	0.449	0.444
*75	0.280	0.292	0.269	0.285
*89	0.025	0.036	0.026	0.021
*110	0.008	0.031	0.064	0.049
*115	0.000	0.010	0.026	0.000
*120	0.110	0.172	0.135	0.174
*130	0.034	0.016	0.032	0.014
*140	0.000	0.010	0.000	0.000
*155	0.008	0.016	0.000	0.014
*ADH**				
No.	69	100	76	67
*-100	0.870	0.875	0.908	0.836
*-183	0.094	0.100	0.086	0.149
*-250	0.022	0.025	0.007	0.015
*-25	0.014	0.000	0.000	0.000

Locus, sample size and alleles	Sample location: Umnak Island	Seguam Pass	Kiska Island	Attu Island
*AH-2**[3]				
No.	56	96	80	71
*100	0.536	0.521	0.613	0.514
*115[a]	0.384	0.354	0.300	0.366
*120	0.054	0.063	0.044	0.070
*117	0.009	0.000	0.019	0.014
*94	0.009	0.005	0.000	0.014
*84	0.009	0.057	0.025	0.021
*ALAT**				
No.	63	92	78	73
*100	0.563	0.533	0.564	0.555
*70	0.413	0.457	0.436	0.425
*120	0.024	0.011	0.000	0.021
*EST**				
No.	62	74	73	61
*100	0.645	0.608	0.541	0.648
*90	0.290	0.345	0.390	0.303
*110	0.040	0.041	0.062	0.033
*85	0.024	0.007	0.007	0.016
*G3PDH-1**				
No.	74	94	80	74
*-100	0.993	0.995	0.981	1.000
*-70	0.007	0.005	0.019	0.000
*G3PDH-2**[1]				
No.	72	98	67	74
*100	0.993	0.964	0.985	1.000
*125	0.007	0.031	0.015	0.000
*GPI-1**				
No.	73	100	80	74
*100	0.904	0.880	0.881	0.926
*25	0.096	0.120	0.119	0.074

continued

Table 6 (continued)

Locus, sample size and alleles	Sample location: Umnak Island	Seguam Pass	Kiska Island	Attu Island
IDDH[1]*				
No.	63	86	76	74
*100	0.984	0.948	0.954	0.973
*165	0.016	0.006	0.007	0.007
*25	0.000	0.041	0.039	0.020
*IDHP-1**				
No.	100	80	74	
*100	1.000	1.000	0.988	0.980
*65	0.000	0.000	0.000	0.007
*140	0.000	0.000	0.000	0.014
*MPI**				
*100	0.971	0.969	0.994	0.993
*110	0.014	0.020	0.006	0.007
*116	0.014	0.000	0.000	0.000
*90	0.000	0.010	0.000	0.000
PEPB-1[1]*				
n	74	90	80	74
*100	0.993	0.994	1.000	0.993
*90	0.007	0.000	0.000	0.007
No.	73	99	80	74
*100	0.562	0.576	0.544	0.500
*110	0.397	0.394	0.387	0.439
*118	0.007	0.005	0.019	0.034
*90	0.000	0.005	0.000	0.007
*113	0.034	0.020	0.050	0.020
*PEPD**				
No.	63	93	80	74
*100	0.738	0.742	0.794	0.804
*110	0.222	0.226	0.175	0.182
*120	0.024	0.011	0.025	0.014
*92	0.016	0.022	0.006	0.000
PGDH[1]*				
No.	69	99	79	72
*100	0.819	0.818	0.816	0.771
*80	0.152	0.152	0.152	0.153
*115	0.022	0.030	0.032	0.076
PGK-1[1]*				
No.	72	100	79	74
*100	0.785	0.765	0.829	0.770
*71	0.097	0.115	0.082	0.122
*45	0.097	0.090	0.082	0.101
*15	0.014	0.030	0.006	0.007
PGM[1]*				
No.	74	99	80	74
*100	0.926	0.960	0.944	0.953
*80	0.074	0.040	0.050	0.047
*SOD**				
No.	75	96	80	74
*100	0.993	0.964	0.981	0.993
*190	0.007	0.036	0.019	0.007
*TPI**				
No.	74	100	80	74
*-100	1.000	1.000	0.994	0.986
*-500	0.000	0.000	0.006	0.014

[1] Variation at alleles not listed above where the frequency of the allele is < 0.010: *G3PDH-2*90* and *IDDH*40* in Seguam Pass; *IDHP-1*90* and **50* in Kiska Island; *PEPB1*115* in Seguam Pass; *PGDH*70* and *PGK-1*55* in Gulf of Alaska; and *PGM*115* in Kiska Island.

[2] Variation at 8 loci not listed above where the frequency of the alternate allele is < 0.010: *AH-1*118* in Attu Island; *ENO*-180* in Seguam Pass; *FH*77*, and *GPI-2*93* , and **105* in Kiska Island; *IDHP-2*73* in Seguam Pass; *LDH*155* in Attu Island; *MDH-1*150* (*n*=100) and *PK*-350* in Seguam Pass.

[3] A seventh allele (**110*) could not be reliably distinguished from the **115* allele and therefore was pooled with the latter allele.

used von Bertalanffy curve, and the length-weight data were fitted to an allometric length-weight relationship. The *F*-tests on the growth curves determined that there was significant variability in the data among areas that was explained by separate growth curves rather than a single growth curve for all areas combined. Although the Gulf of Alaska and eastern Aleutian Islands data sets were small, data fits to the separate von Bertalanffy models were good, and an *F*-test indicated that separate growth curves were appropriate. There were low numbers of fish greater than five years in the Gulf of Alaska; however, the data set still allowed for fairly precise estimation of the asymptotic length (CV=0.02), the parameter most likely to be affected by the lack of older ages.

Morphological and meristic evidence and growth patterns suggest that Atka mackerel may have some degree of stock separation, at least by broad geographic areas (the eastern Bering Sea, Aleutian Islands, and Gulf of Alaska[1,2,3]; Lee, 1985; Kimura and Ronholt, 1988). The present study is the first genetic

Table 7

Within-sample genetic variability over 37 loci.

Location	Average heterozygosity	Percent of loci $P_{0.95}$	Average number of alleles/locus
Umnak Island	0.135	35.1	2.2
Seguam Pass	0.142	32.4	2.4
Kiska Island	0.135	35.1	2.3
Attu Island	0.137	32.4	2.2

survey of Atka mackerel intended to help understand the level and pattern of reproductive isolation among areas thought to be reflected in the areal growth differences. Samples of Atka mackerel were collected during the spawning season when groups of this species are locally aggregated, presumably providing the best separation of potentially reproductively isolated groups.

Our results show that Atka mackerel have above-average levels of genetic variation for a marine fish. The average heterozygosity per locus for Atka mackerel is 0.137, well above the average reported by Ward et al. (1994) for 57 species of marine fish (0.064 ± 0.004). Assuming that the majority of the allozyme variation is selectively neutral (Kimura, 1968), we believe that large levels of genetic variation are most parsimoniously explained by large, historically stable populations. An alternative explanation is that large levels of variability reflect a response to inhabiting a heterogeneous habitat (Avise, 1994). Nonetheless, 30 polymorphic loci provide substantial statistical power to assess the level of between-sample differentiation.

Between-sample variation was extremely low among the four samples of Atka mackerel. In a study where electrophoretic data for marine, freshwater, and anadromous fishes were compared, Ward et al. (1994) calculated an average G_{ST} (roughly equivalent to F_{ST}) of 0.062 for 57 species of marine fish (compared with 0.22 for freshwater species of fish). The F_{ST} for Atka mackerel (0.004) is far smaller than this average, providing evidence that a large amount of gene flow is occurring throughout the range represented by these samples. Very low genetic distance values between samples were observed; the largest distance value between two samples was 0.00017, indicating little or no stock differentiation. Furthermore, the nonsignificant Hardy-Weinberg test of the four samples pooled together did not indicate any between-sample heterogeneity. In light of these two genetic results, we can not reject the null hypothesis that our samples came from a single genetically homogenous population of Atka mackerel. There was also no apparent gradual differentiation throughout the Aleutian Archipelago corresponding to the clinal geographic variation seen in the growth data. Stock delineations based on the age-length and weight-length relationships were not supported by the allozyme data.

Concordance of electrophoretic and growth data sets

A lack of congruence between genetic and life history characteristics was also found for Pacific ocean perch by Seeb and Gunderson (1988). They analyzed data from the Washington coast to the Bering Sea. Stock delineations based on age structure, age-length relationships, and ages at maturity were not supported by the allozyme data. Although they did not find clear genetic stock differentiation, they did find a cline of gene frequencies within the Gulf of Alaska and significant allele frequency differences between the extremes of the geographic range for some loci.

There are at least three possible explanations for the lack of genetic stock differentiation for Atka mackerel in the Aleutian Islands. First, the genetic technique surveyed invariant gene loci when in fact genetic differences may exist among the sampled stocks. As in any genetic study, the absence of genetic differentiation does not preclude the possibility that true genetic differences exist, and other genetic techniques may be employed to further examine this possibility (Avise, 1994). Second, the species could perform a major spawning migration encompassing the entire population, with mixing and spawning in one area. Third, separate spawning locations are used but gene flow occurs among locations through the dispersal of pelagic larvae and juveniles. We consider the third explanation most likely given the growth differences seen in adult Atka mackerel.

The Aleutian Archipelago encompasses several wide and deep straits that could form barriers to significant movement across the island chain for adult demersal fish residing over the continental shelf. The pelagic behavior of larval and juvenile fish and their presumed distribution in the open ocean habitat, however, would make them susceptible to wide dispersal by currents, thus accounting for the genetic homogeneity among samples. A schematic diagram of the basic surface currents in the north Pacific is shown in Figure 6 (McAlister and Favorite, 1977). The Alaska stream flows westward throughout the Aleutian Archipelago, with significant northward flow to the Bering Sea through Amukta, Amchitka, and Buldir passes. The North Aleutian current flows eastward to Umnak Island providing a thorough mixing mechanism across the Aleutian Island chain. The currents could thus provide the mechanism for sufficient gene flow through the Aleutian chain to actually prevent genetic differentiation. It is presumed that adults do not undertake large-scale migrations and assume a fairly localized existence, which might thus account for the differences in length, age, and weight comparisons of the adults. Observed spawning areas in the Aleutian, Shumagin, and Commander Islands, which have been historically referenced in the literature (Turner, 1886; Rutenberg, 1962), are thus presumed to attract nearby resident schools that migrate inshore.

Although there are no major currents flowing eastward from the Aleutian Islands to the Gulf of Alaska,

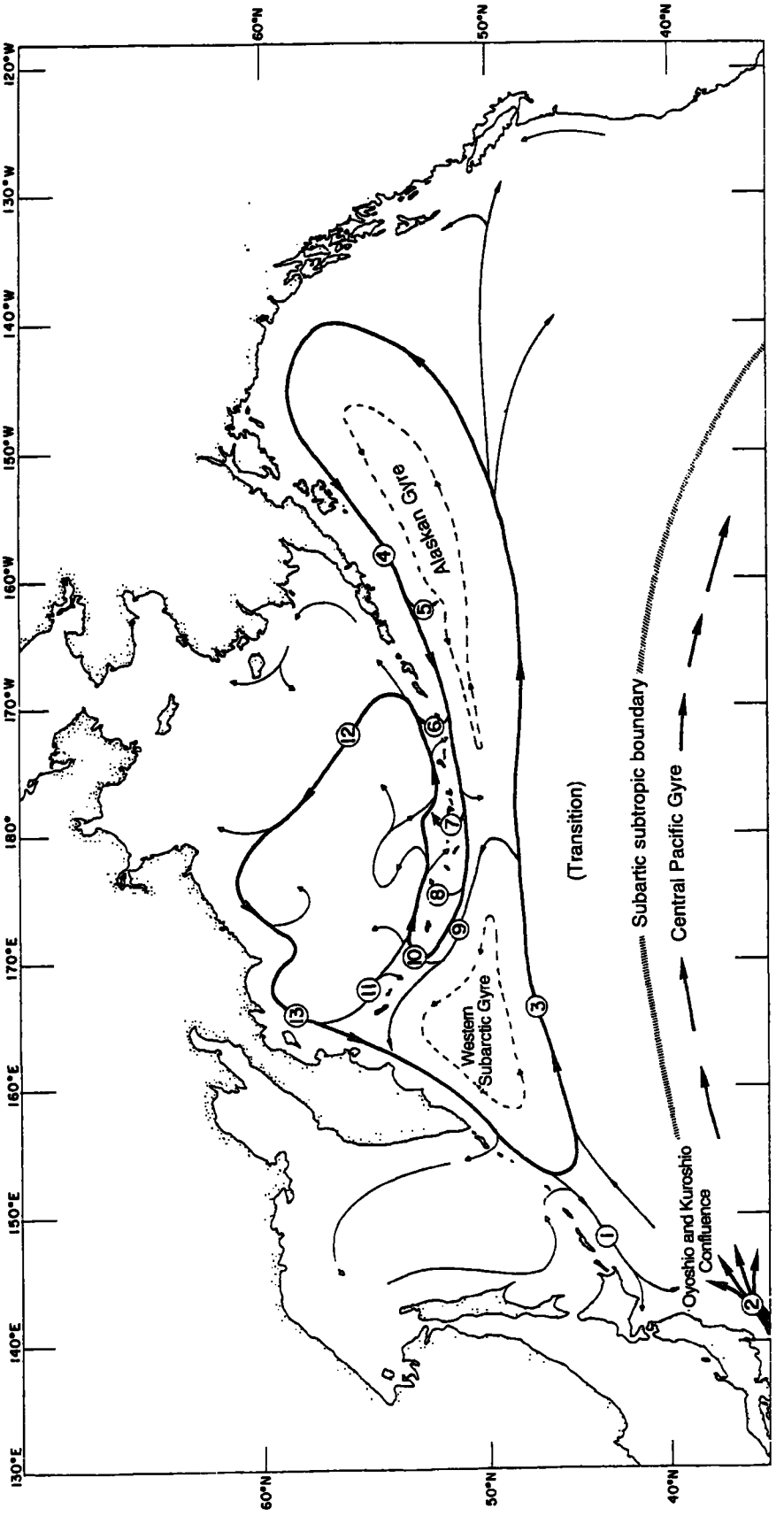

Figure 6

Subarctic Pacific region showing the western subarctic gyre and the Alaskan gyre within the subarctic gyre and associated currents. Numbers refer to currents: 1 = Oyashio; 2 = Kuroshio; 3 = subarctic; 4 = Alaskan Stream; 5 = Aleutian; 6 = Amukta; 7 = Amchitka; 8 = Buldir; 9 = west subarctic; 10 = Near; 11 = Commander; 12 = Transverse; and 13 = East Kamchatka (as presented by McAlister and Favorite, 1977).

the western Gulf of Alaska portion of the population may be the result of juvenile or adult migration (or both) or habitat expansion. Kimura and Ronholt (1988) postulated that Gulf of Alaska Atka mackerel are at the extreme limit of their geographic range (the extreme limit of which is populated only during periods of favorable environmental conditions).

Zolotov (1984) found that Atka mackerel spawning habitat in Russian waters extended from the Kamchatka Peninisula through the Kurile Islands almost without breaks. Continuous distribution of Atka mackerel spawning habitat and dispersal of larvae into the open ocean pointed to an absence of mechanisms that would result in reproductively isolated stocks in Russian waters. Zolotov (1984) thus concluded that Atka mackerel did not form ecological groupings along the Kamchatka Peninsula and Kurile Islands but made up a single population. Although we cannot rule out that there are unknown mechanisms or processes which might result in reproductive isolation of groupings of Aleutian Island Atka mackerel, life history information suggests that a process for extensive mixing occurs during the early life stages. We currently do not have any observations to support the necessary processes (e.g. larval retention, natal homing, genetic imprinting), that would result in reproductive isolated populations in the Aleutian Islands.

We interpret the areal growth differences exhibited by Atka mackerel as indications of localized assemblages made up of groupings from a single mixing stock that aggregates during the adult portion of its life history. We suggest that the local specific growth variability seen in adults is a reflection of environmental effects. It is unknown which environmental characteristics might be most influential on growth of Atka mackerel; however, temperature and salinity are noted to be the most important hydrological factors affecting the distribution of hexagrammids, and food, predators, and parasites the most important biological factors (Rutenberg, 1962). Seeb and Gunderson (1988) noted that local growth and age-at-maturity differences could also reflect historical influences and fishing pressure. A large and sustained Atka mackerel fishery has been conducted throughout the Aleutian Islands since the early 1970s. Catches have fluctuated with the demise of the foreign fishery and the development of the domestic fishery, and in recent years the fishery has been concentrated in the eastern Aleutian Islands where the largest fish reside. The fish in the western Aleutian Islands were not heavily exploited from 1980 to 1994, but they have historically been the smallest fish. The geographic size cline noted in the growth data seems to run counter to what we might expect given the differential fishing pressure.

Stock assessment and management implications

The stock structure of Atka mackerel has stock assessment and fishery management implications. From a stock assessment perspective, we are interested in elucidating the underlying population processes that would result in stock separation, or lack of, and in evaluating the impacts of the fishery on the genetic stock(s), particularly on the spawning concentrations. From a fishery management perspective, the practical recognition of fishery-targeted assemblages (not necessarily genetically distinct) and the spatial and temporal affects of harvesting these assemblages are of interest.

Historically, small-scale Alaskan subsistence fisheries targeted spawning concentrations of Atka mackerel, but the very shallow and presumably rough habitat of the spawning grounds are not accessible to the current large-scale commercial fisheries. Analysis of commercial fishery data indicates that bottom trawling is probably not disturbing the nesting sites.[6] Thus, the unique reproductive life history features of Atka mackerel may provide for some protection of the spawning stock.

Booke (1981) distinguished between inherited (genetic) versus "acquired" or "environmentally induced" characters; the latter including morphological and phenotypic characteristics. Because acquired phenotypic markers by definition are appropriated through contact with the environment, they may not reflect the population genetic characteristics (Avise, 1994). However, acquired markers can serve an important role in population analysis because they can reveal where individuals have spent various portions of their lives (Avise, 1994). From both a stock assessment and fishery management perspective, the localized aggregations of adult Atka mackerel, although not genetically distinct, are important to our understanding of the population dynamics of this species and the impact of the fishery.

Indications of localized populations of Atka mackerel raise the issue of potential localized depletion by the fishery. Another fundamental fishery management and assessment question has been the relation of Gulf of Alaska Atka mackerel to Aleutian Islands Atka mackerel. Atka mackerel are currently managed by two major areas, the Gulf of Alaska and the Aleutian Islands, and by three subareas within the Aleutian Islands. For management purposes, there are at least two catch quotas that must be set given the management area boundary at 170°W which divides the Gulf of Alaska and the Aleutian Islands. Any further subdivisions of the quota are generally based on stock separation rationale or the desire to spread out fishing effort over large geographic areas (or both). The Gulf of Alaska Atka mackerel are assessed separately from Aleutian Islands Atka mackerel, mainly because of the different sources of data (two different survey time series), and to a lesser extent on the presumption that Gulf of Alaska Atka mackerel showed some level of separation from Aleutian Islands Atka mackerel. The results of this study show no evidence of Atka mackerel genetic stock separation between the western Gulf of Alaska and throughout the Aleutian Islands chain. However, because adults show evidence of localized aggregations, it seems appropriate to set at least two separate quotas in Alaskan waters (Gulf of Alaska and Aleutian Islands), with further subdivisions to distribute fishing effort.

The North Pacific Fishery Management Council (NPFMC) implemented Amendment 28 to the "Fishery Management Plan for the Groundfish of the Bering Sea and Aleutian Islands," creating three subareas within the large Aleutian Islands management area (Fig. 1). The impetus for the implementa-

[6] Fritz, L. W., and S. A. Lowe. 1997. Seasonal distributions of Atka mackerel (*Pleurogrammus monopterygius*) in commercially-fished areas of the Aleutian Islands and Gulf of Alaska. NMFS. Alaska Fisheries Science Center, 7600 Sand Point Way NE, Seattle, WA 98115-0070. Unpubl. manuscript.

tion of additional management areas was the possibility of localized depletion of Atka mackerel by the fishery given the presumed localized distribution of this species and the localized, highly concentrated fishery effort. This study shows that genetically distinct populations of Atka mackerel do not exist in this area, and therefore a significant amount of gene flow may occur among locales within this species. However, gene flow is presumably occurring during the early life stages (larval, juvenile) and is dependent on dispersal by currents. The potential for localized depletion by the fishery at the adult stage is still a concern. Until we have a better understanding of the dispersal and distribution mechanisms affecting Atka mackerel early life stages, management strategies should strive to spread out fishing effort to help reduce the potential for localized depletion. We conclude that despite the genetic homogenization, the phenotypic variation in adult Atka mackerel warrants consideration by fishery managers.

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