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[Article]

Spatial and Temporal Variability in Size at Maturity of Walleye Pollock in the Eastern Bering Sea

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Abstract.—Size at maturity is incorporated into stock assessments of walleye pollock *Theragra chalcogramma*. For eastern Bering Sea walleye pollock, however, this important biological variable has not been examined since 1976 and possible interannual and geographic variations have never been evaluated. Maturity condition and fish length data were collected from 10,197 walleye pollock aboard factory trawlers during winter 2002 and 2003. We also analyzed a smaller, previously unanalyzed data set on maturity collected annually by National Marine Fisheries Service scientists during eight echo integration–trawl surveys over 1989–2002. Length at 50% maturity (L_{50}) was estimated by year and area by logistic regression using maximum likelihood methods. Spatial (within subareas) and temporal (interannual) variability were found. For instance, fish matured at the smallest lengths north of the Pribilof Islands and in the years 1989, 1991, and 1995 and at the largest lengths in the southeastern Bering Sea and in the years 2001 and 2002. We found evidence that the variability in size at maturity was related to biological mechanisms. Length at 50% maturity appeared to be directly related to growth as measured by length at age. Moreover, an inverse relationship between walleye pollock biomass and L_{50} suggests that growth is density dependent. This spatiotemporal variability in size at maturity has implications for estimates of spawning stock biomass and should be incorporated into the annual stock assessments for setting annual catch specifications.

The goal of this study was to estimate the spatial and temporal variability in the size of maturity of walleye pollock *Theragra chalcogramma* in the eastern Bering Sea. Until now, published maturity schedules for this important commercial species have come from a single year (1976) of observations pooled over a large area of the eastern Bering Sea shelf (Bakkala and Smith 1978). Although some data were collected over a limited portion of the eastern Bering Sea during echo integration–trawl surveys during 1989–2002, these data have not yet been analyzed for potential geographic or interannual shifts in size at maturity.

Walleye pollock are a subarctic species ranging from the northwest Pacific Ocean, including the Sea of Japan, the Okhotsk Sea, and the Commander Islands, north through the Bering and Chukchi seas and south into the Gulf of Alaska to Puget Sound (and rarely as far south as central California) (Mecklenburg et al. 2002). Population structure remains somewhat unresolved within the eastern Bering Sea. Recent studies of allozymes, microsatellites, and mitochondrial DNA and analyses of DNA sequence data from the pantophysin locus indicate weak structuring over large geographical distances, conforming to an isolation-by-distance pattern of neutral divergence. This suggests either that gene flow is high or that the genetic drift since separation has been insufficient for significant levels of differentiation to accumulate (Olsen et al. 2002; O'Reilly et al. 2004; Canino et al. 2005). Morphometrics and life history characteristics imply that there are three to five stocks in the eastern Bering Sea (Hinckley 1987; Dawson 1994), and length at age (Hinckley 1987), juvenile otolith composition (Mulligan et al. 1992), and size composition and growth (Lynde et al. 1986; Shuck 2000) differ among one or more subareas. For fishery management purposes, walleye pollock from the U.S. portion of the Bering Sea are assessed and managed as three separate stocks: the eastern Bering Sea shelf from Unimak Pass to the U.S.–Russia Convention line, the Aleutian Islands shelf region (170°W to the U.S.–Russia Convention line), and the central Bering Sea–Bogoslof Island region (includes the Aleutian Basin) (Ianelli et al. 2005).

Our study focuses on walleye pollock collected during National Marine Fisheries Service (NMFS) fishery-independent surveys and from commercial fisheries targeting the eastern Bering Sea shelf stock. Because our spatial analyses subsequently revealed that some samples were actually collected off the continental shelf in basin waters, we also examined our results with respect to stock delineation, as these results could have broader implications for fishery stock assessment and management.

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TABLE 1.—Classification of walleye pollock ovarian maturity condition based on macroscopic observation; criteria were derived from the National Marine Fisheries Service five-stage scale.

Maturity code	Condition	Macroscopic examination
1	Immature	Ovary transparent with no eggs visible; gonad small and tucked inside body cavity.
2	Developing	Ovaries translucent to opaque, occupying about one-half the body cavity; spawn within the following year.
3	Pre-spawning	Ovaries orange and reddish, occupying about two-thirds of the body cavity; eggs discernible and opaque.
4	Spawning	Roe runs with slight pressure; most eggs hydrated (translucent), with few opaque eggs.
5	Spent	Ovaries empty and flaccid.

There are two fishing seasons for the shelf stock of walleye pollock in the eastern Bering Sea. In the "A" season, the fishery is concentrated along the 100-m depth contour between the Pribilof Islands and Unimak Island. The fishery targets prespawning fish for their valuable roe but also produces fillets, whole (headed and gutted) fish, and surimi. The season opens on January 20 and extends as late as June 10, but the total allowable catch (TAC) is usually taken within 4–6 weeks (Ianelli et al. 2005). In the postspawning "B" season, the same seafood products are produced except for roe. The B season fishery runs from June 10 to November 1 but is usually concentrated in August–October and occurs slightly northwest of the range during the A season (Ianelli et al. 2005).

The North Pacific Fishery Management Council sets catch specifications based on biological reference points derived from spawning biomass estimates (Ianelli et al. 2005). Fishing limits are based on the fishing mortality rate that produces the maximum sustainable yield, which is assumed to be the rate associated with a reduction in the spawning biomass to 35% of that of the unfished population ($F_{35\%}$). The acceptable biological catch (ABC) is conservatively set at $F_{40\%}$, and the TAC is set at or below the ABC. This strategy requires accurate estimates of spawning biomass and therefore of size at maturity.

Female spawning stock biomass (B_t) is calculated for a given year from the equation

$$B_t = \sum w_a \cdot \phi_a \cdot N_{at}, \qquad (1)$$

where w_a is mean fish weight at age a, ϕ_a is the proportion of mature females at age a, and N_{at} is the number of fish of age a in year t (Ianelli et al. 2005). The numbers of fish are estimated by statistical age-structured assessment models that incorporate data collected during bottom trawl and echo integration–trawl (EIT) surveys, from observers aboard commercial fishing vessels, and via a catch accounting system (Ianelli et al. 2005). The assessments use maturity-at-age estimates fitted by Smith (1981) to data collected in 1976 by Bakkala and Smith (1978). In years when the fishery harvests a large proportion of immature fish, small shifts in the maturity curve may alter the actual harvest rates significantly; as a result, it is useful to determine whether ϕ_a varies by year or area within the range of the stock. Thus, a reexamination of walleye pollock maturity schedules and consideration of possible spatial and temporal variability among them are long overdue for this commercially and ecologically important resource.

Methods

Data Collection

Maturity data were collected aboard vessels belonging to members of the Pollock Conservation Cooperative (PCC) during the A fishing season from late January to the beginning of April in 2002 and 2003 throughout the geographic area fished in the eastern Bering Sea. Twelve PCC vessels participated in data collection in 2002 and 15 in 2003. Ten female fish were sampled over a range of lengths from one randomly chosen haul per day. The following information was collected from each fish: fork length (cm), body weight (g), ovary weight (g), and maturity stage (the latter based on macroscopic visual observation following criteria adapted from an NMFS five-stage scale; Table 1). From other fish, NMFS observers aboard PCC vessels collected otoliths that were aged to determine length at age. A subsample of these otoliths was aged at the Age and Growth Laboratory of NMFS, Alaska Fisheries Science Center (AFSC), using the break and burn methods of Chilton and Beamish (1982). The aging methods used at the AFSC have been corroborated (Kimura et al. 2006) and validated for walleye pollock up to age 8 using a method based on the disequilibrium of lead-210 and radium-226 (Kastelle and Kimura 2006). The mean percent agreement among two experienced age readers at AFSC was 72.4% over all ages and 79.1% over ages 3–8 (Kimura and Lyons 1991).

Fishery-independent maturity data were available from EIT stock assessment surveys conducted annually (1989–2002) by NMFS on the eastern Bering Sea shelf from January to April. These surveys are intended to

collect information on the off-bottom component of the walleye pollock stock. The EIT assessment is primarily conducted by hydroacoustics, but occasional trawl tows are made to characterize the fish comprising the schools. The data collected include fork length, ovary and body weight, and macroscopic maturity stages (the latter based on a five-stage scale before 1996 and an eight-stage scale since 1996). Despite the collection of these observations before our study, these maturity-at-length data were not previously analyzed or incorporated into annual stock assessments. Finally, for comparison with the fixed maturity schedule currently used to estimate spawning stock biomass in annual stock assessments, we also reanalyzed length and maturity stages (based on the five-stage scale) for 3,585 walleye pollock collected by demersal trawl surveys from April through August 1976 (Bakkala and Smith 1978).

Analytical Methods

Size at maturity.—The following logistic regression model was used to estimate the proportion of mature walleye pollock by length:

$$P = 1/[1 + e^{-a(L-b)}], \quad (2)$$

where P is the predicted proportion of mature fish at a particular fork length (cm) L and a and b are estimated parameters (McCullagh and Nelder 1989), a describing the shape of the curve and b being the inflection point where 50% of fish for that length are mature, L_{50}. The negative log likelihood ($-\log_e L$) was calculated as

$$-\log_e L = -[M \log_e(P + 0.0001) + \{I \log_e[1 - (P + 0.0001)]\}], \quad (3)$$

where M is the number of mature and I the number of immature walleye pollock. Excel Solver was used to minimize $-\log_e L$ while estimating parameters a and b.

Logistic regression was initially performed using three different interpretations of the PCC maturity data. To estimate maturity curves and L_{50}, mature fish that will spawn during the year of sampling must be distinguished from immature fish that will not spawn until the following year. Histological examination of a subsample of fish ovaries collected by one of us (J.P.S.) aboard a PCC vessel in 2003 revealed that 16% of the ovaries macroscopically classified as developing (stage 2) would not spawn until the following year, whereas 84% would spawn after the A fishing season in 2003 (Stahl and Kruse 2008). This conclusion was based on the presence of yolked oocytes in the ovaries of specimens collected during the A season and the finding that development from primary yolk oocyte stage to spawning is 4 months in Funka Bay, Japan (Y. Sakurai, Hokkaido University, personal communication). Because of the uncertainty in the true fate of the walleye pollock ovaries macroscopically staged as developing, we conducted separate statistical analyses based on three alternative interpretations of the fish with developing ovaries. In the first interpretation, we considered them as immature (developing [D] = immature [I]). In the second, we considered them as mature (D = mature [M]). The third interpretation was based on the gonadosomatic index (GSI; [ovary weight/body weight] × 100). Values of the GSI were plotted against length for 158 histological samples; a gap in these values occurred at 3.8–6.9 across all length-classes (Figure 1; Stahl and Kruse 2008). Fish with GSI values below the gap included all of the fish classified as immature by histology plus 26% of those classified as mature. All fish with GSI values above the gap were classified as mature (Stahl and Kruse 2008). Consequently, fish classified macroscopically as developing with GSI values greater than 6.94 (the smallest GSI value of mature fish above the gap) were considered to be mature in our third interpretation (D = GSI); fish classified macroscopically as developing with GSI values less than 6.94 were assumed to be immature. Because the D = GSI model uses the most information on the maturity condition of developing fish, we considered this model to be the best. To facilitate comparisons with current practice, however, we retained the $D = I$ and $D = M$ approaches to estimate L_{50} for the combined 2002–2003 data set. For simplicity, the D = GSI approach alone was used in other analyses (see Stahl 2004 for detailed analyses with the other models).

Spatial and temporal differences in maturity.—Although the walleye pollock population of the entire shelf of the eastern Bering Sea is treated as one stock for management purposes, there are differences in life history characteristics, length at age (Hinckley 1987), and growth (Lynde et al. 1986) within this stock. To explore whether there are also geographic differences in maturity schedules, we subdivided the eastern Bering Sea shelf into three areas based on bathymetry and natural breaks in walleye pollock distribution, as evidenced by the fishery data. The PCC data were separated into those pertaining to the area north of the Pribilof Islands, those pertaining to the area south of the Pribilof Islands, and those pertaining to the Aleutian Basin (Figure 2). The areas south and north of the Pribilof Islands were distinguished by a break in the PCC data between longitudes −169.2 and −169.9; both of these areas are located on the continental shelf at depths less than 150 m. All waters in the Aleutian basin are at least 150 m deep and include both the basin and the continental slope. In addition to these three

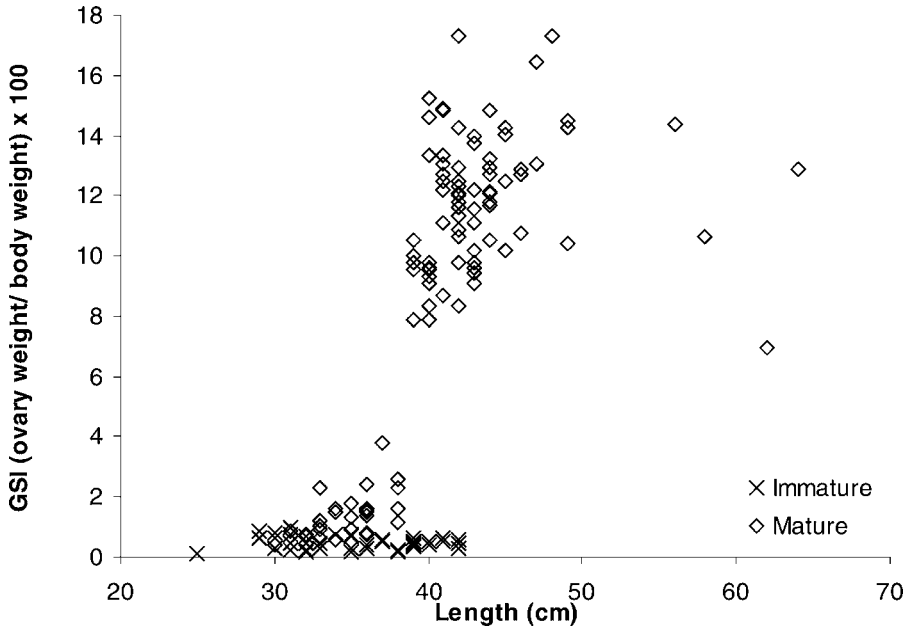

FIGURE 1.—Plot of the gonadosomatic index (GSI) versus fork length for histological samples of walleye pollock collected in the eastern Bering Sea in 2003 showing a gap in GSI values from 3.8 to 6.9 across all length-classes; only mature fish had values above 6.9 (from Stahl and Kruse 2008).

large areas, the area south of the Pribilof Islands was subdivided into central and southern subareas by a line perpendicular to the 100-m isobath intersecting the 50-m contour at coordinates −163.0, 57.3 and the 150-m contour at −166.7, 54.98. The basin was subdivided into central and southern basin subareas by a break in PCC data between latitudes 54.8 and 55.2 (Figure 2).

Maturity curves were estimated by area for the PCC data in 2002 and 2003 separately and combined, and likelihood ratio tests were performed to determine whether the shapes of the maturity curves and the L_{50} parameters were statistically different by area. Statistical significance between two or more maturity curves was determined by

$$\chi^2 = 2[(-\log_e L_R) - (-\log_e L_F)], \qquad (4)$$

where L_R is the $-\log_e L$ for the reduced model and L_F is the $-\log_e L$ for the full model (Quinn and Deriso 1999). To calculate the $-\log_e L_R$, one set of parameters was estimated for all data sets, whereas for $-\log_e L_F$, parameters were estimated for each separate data set. The $-\log_e L$ for each separate data set was summed to derive $-\log_e L_F$. Statistical significance was set at 0.05, and the degrees of freedom was the difference between the number of parameters in the full and reduced models. A χ^2 value was calculated and compared with the critical value to determine whether there was a statistically significant difference in the shape of the maturity curves (parameter a). If so, the same test was performed to determine whether b (L_{50}) was also statistically different. In the latter case, $-\log_e L$ was minimized while reestimating parameter b alone; parameter a was held constant at the value estimated in the reduced model.

Temporal differences in size at maturity were explored. To examine potential within-season differences among PCC data collected during 2002 and 2003, the A fishing season was subdivided into early (January 20–February 24) and late (February 25–April 2) periods. Maturity data from the EIT surveys were subdivided into those for the same three areas as the PCC data. Sample sizes for GSI in EIT surveys were sufficient for analysis in the following areas and years: south of the Pribilofs for 1989, 1991–1993, 1995, and 2000–2002 and the basin for 1991, 1993, and 2001–2002. Statistical differences in a and b among years by area or among early and late periods within the A fishing season were estimated by likelihood ratio tests identical to those used to test for differences among areas (equation 4).

Biological factors affecting maturity.—We explored the possibility that the observed differences in size at maturity could be attributed to biological factors, including length at age and density dependence. We used NMFS observer samples to estimate length at age

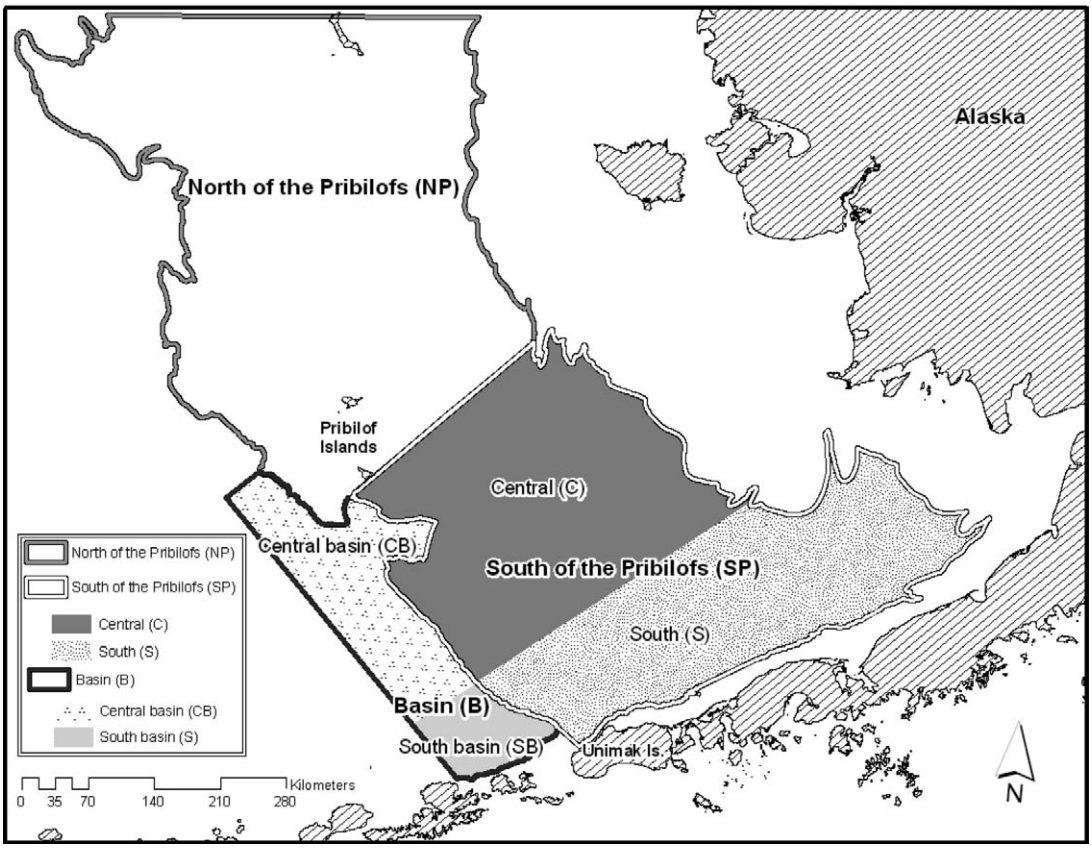

FIGURE 2.—Geographical areas by which walleye pollock maturity data in the eastern Bering Sea collected by Pollock Conservation Cooperative members in 2002–2003 were separated for spatial analysis.

by area in 2002 and 2003 and the von Bertalanffy growth model to estimate growth parameters by area, that is,

$$L_t = L_{\text{inf}}[1 - e^{-K(t-t_0)}], \tag{5}$$

where L_t is length at age t and the parameters to be estimated are L_{inf} (the mean maximum body size), K (the growth rate coefficient), and t_0 (the hypothetical age at length 0) (Quinn and Deriso 1999). To test for statistically significant differences between growth parameters, an analysis of the residual sum of squares (RSS) was performed (Quinn and Deriso 1999). The RSS and degrees of freedom were estimated and summed for each curve to calculate Σ RSS and Σ df. Data for all curves were pooled to derive RSS_p and df_p. Then, an F-statistic was calculated as follows:

$$F = \frac{\text{RSS}_p - \sum \text{RSS}}{\text{df}_p - \sum \text{df}} \times \frac{\sum \text{df}}{\sum \text{RSS}}. \tag{6}$$

The degrees freedom were computed as $3(K-1)$ and $(N-3)(K)$, where K is the number of curves being compared and N is the sum of the number of ages in each curve's data set. Statistical significance was set at 0.05.

We also considered whether L_{50} might be affected by length at age for large year-classes. Length at age for females was estimated by NMFS by year from their summer bottom trawl survey data (G. E. Walters, NMFS, personal communication), and a mean length for each age was determined by averaging the survey data from 1983 to 2003. The size of a year-class estimated by NMFS with statistical age-structured assessment models (Ianelli et al. 2005) and its mean length at age for a particular age and year were both considered as potential explanatory variables for changes in L_{50}.

To explore potential density-dependent effects, variations in walleye pollock abundance and biomass were examined as additional explanatory variables for spatial and temporal differences in L_{50}. Values of L_{50} were linearly regressed on annual estimates of the biomass of fish age 1 and older (hereafter, age-1+ fish;

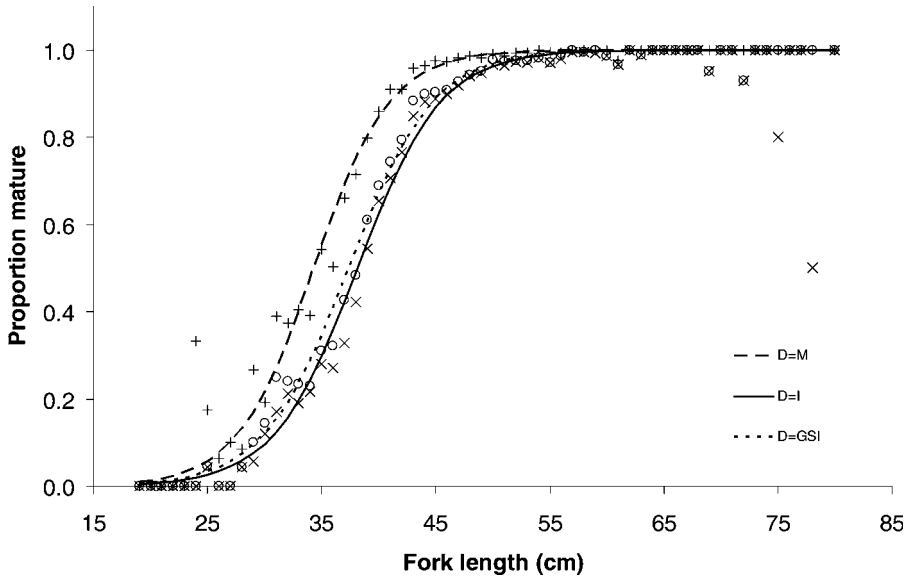

FIGURE 3.—Maturity curves for walleye pollock in the eastern Bering Sea estimated by fitting logistic regression models to the observed proportion mature by length. The models are based on three different assumptions with respect to developing fish: (1) that all such fish are mature (the $D = M$ model; plus signs), (2) that all such fish are immature (the $D = I$ model; times signs), and (3) that developing fish with gonadosomatic index (GSI) values higher than 6.94 are mature and those with lower values are immature (the $D =$ GSI model; circles).

Ianelli et al. 2003), the biomass of age-3+ fish, and the number of age-3+ fish (T. W. Buckley, NMFS, personal communication) from summer bottom trawl surveys. Relationships between L_{50} and the biomass and number of age-3+ fish were explored by area. The areas over which NMFS disaggregated their biomass data differed slightly from our area designations. The NMFS designated a northwest area that extends north to about 61.0 latitude and a southeastern area that extends south to Unimak (Alaska Peninsula), which are separated by diagonal line bisecting the two Pribilof Islands (Acuna et al. 2003). We divided our areas north and south of the Pribilofs with a line just south of the Pribilofs. Because there are few maturity observations between the two lines and virtually all of the walleye pollock biomass occurs either south or north of the Pribilofs (and not between the islands), we related maturity data for the areas north and south of the Pribilof Islands to the abundance and biomass data for NMFS northwestern and southeastern areas, as well as for all areas combined.

Results

Size at Maturity and Population Parameters

Maturity data were collected from 4,964 walleye pollock in 2002 and from 5,098 in 2003; these data were pooled to produce maturity curves for all models (Figure 3). The L_{50} was estimated to be 38.14 cm for the $D = I$ model, 34.31 cm for the $D = M$ model, and 37.36 cm for the $D =$ GSI model. A maturity curve fits the observed data well for all models except for a few large lengths for the $D = I$ and $D =$ GSI models and a few small lengths for the $D = M$ model. Large immature walleye pollock were removed in a sensitivity test for the $D = I$ model in which L_{50} was changed from 38.14 cm to 38.15 cm. The proportion mature at age increased with age, based on the $D =$ GSI model. Age at 50% maturity was estimated to be about age 4 for 2002 and 2003 (Stahl 2004).

Spatial and Temporal Analysis

Spatial analysis revealed geographic variability in maturity curves in 2002 and 2003; L_{50} ranged between 34.93 and 40.82 cm (Table 2). For all data sets, the more southerly areas had the largest L_{50} values, namely, the area south of the Pribilof Islands (central and southern subareas combined) and the southern portion of the Aleutian basin, depending on the year. The smallest L_{50} values occurred for the northerly areas, that is, the area north of the Pribilofs and the central Aleutian basin, depending on the year.

Likelihood ratio tests showed that maturity curves were significantly ($P < 0.05$) different between the areas north and south of the Pribilof Islands in 2003 and 2002–2003 combined; however, there were no significant differences between these areas in 2002

TABLE 2.—Length (cm) at 50% maturity of walleye pollock estimated by area (see Figure 2) from data collected by the Pollock Conservation Cooperative in the eastern Bering Sea, 2002 and 2003.

Area	2002	2003	Both years combined
North of Pribilof Islands	36.04	34.93	35.10
South of Pribilof Islands	37.46	40.42	38.56
Central	36.33	39.27	37.41
Southern	37.88	40.82	38.94
Aleutian Basin	36.21	37.93	37.52
Central	35.81	37.96	37.53
Southern	37.60	[a]	37.60

[a] Sample size too small to estimate length at 50% maturity.

(Table 3). Some significant differences occurred between areas in all years, depending on the year(s) and area tested (Table 3). For all areas combined, there was no significant difference between the maturity curves for 2002 (36.96 cm) and 2003 (37.66 cm).

Within-year analysis revealed significant differences in the early and late portions of the season, most likely because of the spatial distribution of the fishery (Figure 4). The distribution of observations collected aboard all participating PCC vessels in the 2002 and 2003 A fishing season was highly concentrated north of Unimak Island and followed the 100-m depth contour past the Pribilof Islands (Figure 4). In 2002 the fishery mainly operated south of the Pribilof Islands during the early part of the season and spread both north and south of the Pribilof Islands during the latter part of the season. During 2003, the fishery had a distribution similar to that in 2002 early in the season, but unlike in 2002, the late-season fishery occurred mainly north of the Pribilof Islands with a small concentration south in the Aleutian Basin. Likelihood ratio tests revealed statistically significant differences in L_{50} between the early and late periods for 2003 and 2002–2003 combined, but not for 2002.

Consistent with the fishery-derived samples, the fishery-independent collections also showed variability in maturity; interannual variation in maturity was evident in the maturity curves estimated for the samples collected in NMFS winter EIT surveys during 1989, 1991–1993, 1995, and 2000–2002 (Figure 5). The L_{50} values ranged from 34.10 to 43.58 cm for the area south of the Pribilof Islands and from 40.50 to 46.18 cm for the Aleutian Basin area (Table 4). The limited geographic distributions of these surveys prevented analysis of the size of maturity north of the Pribilof Islands. There were statistically significant differences in the maturity curves between years for each area; at least one year was statistically different from all of the other years tested. South of the Pribilof Islands, similar maturity curves with large L_{50} values occurred for 1992, 2000, and 2001; the 2002 maturity curve was similar for fish with small lengths but shifted for fish with large lengths. Smaller L_{50} values occurred for 1989, 1991, 1993, and 1995; however, the maturity curves for these years were incomplete because of insufficient sample sizes, particularly at small lengths. For the Aleutian basin, the largest L_{50} values occurred for 2001.

Biological Factors Affecting Maturity

The possibility that spatial and temporal differences are attributable to differences in walleye pollock growth rates was explored by fitting the von Bertalanffy growth equation to length-at-age data by area and year for the eastern Bering Sea. Due to small

TABLE 3.—Results of likelihood ratio tests between areas or subareas (see Figure 2) testing maturity curves for walleye pollock for statistical differences between shape and fork length at 50% maturity (L_{50}). Results were considered significant at $\alpha = 0.05$, where * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.01$, and ns = not significant. Likelihood ratio tests were not performed when data did not allow or for L_{50} values for which there was a nonsignificant difference between maturity curves.

	2002		2003		Both years	
Areas compared[a]	Shape	L_{50}	Shape	L_{50}	Shape	L_{50}
NP versus SP	ns		***	***	***	***
NP versus B			***	ns	***	ns
NP versus B versus CSP versus SSP	***	***	***	***	***	***
(NP, B) versus (CSP, SSP)			***	***		
(NP, B) versus CSP					**	**
(NP, B) versus SSP					***	***
NP versus (CSP, B)	**	ns				
(NP, CSP, B) versus SSP	***	***				
CSP versus SSP			*	ns	***	***
CSP versus B	ns					
CB versus SB					ns	

[a] Areas include those north of the Pribilof Islands (NP); south of the Prilof Islands (SP) and its central (CSP) and southern (SSP) subareas; and the Aleutian Basin (B) and its central (CB) and southern (SB) subareas.

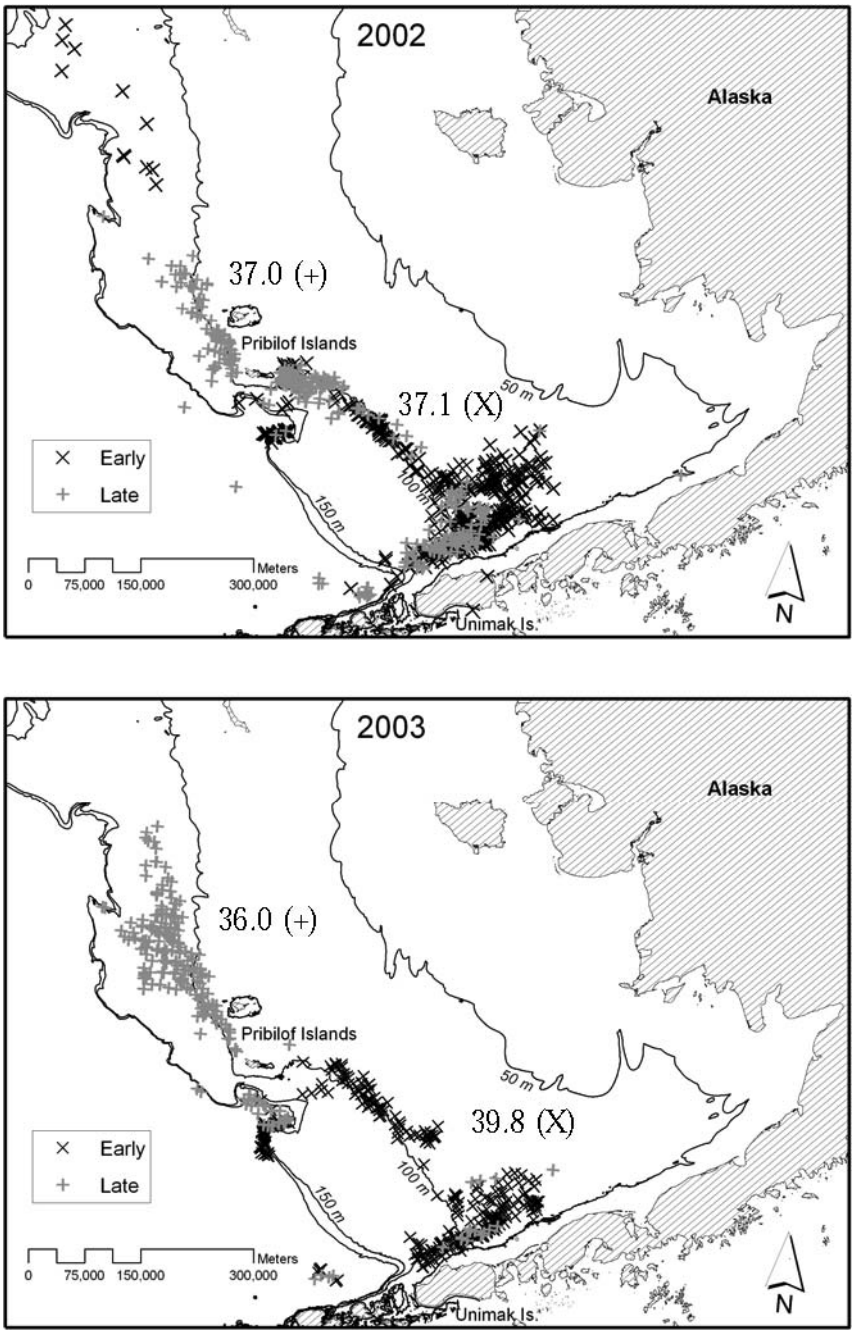

FIGURE 4.—Distribution of walleye pollock maturity samples collected during the early (January 20 to February 24) and late (February 25 to April 2) portions of the 2002 and 2003 commercial fishing seasons in the eastern Bering Sea. This fishery was concentrated south of the Pribilof Islands during the early portion of the fishing season and more to the north late in the season, especially in 2003. Estimates of the length (cm) at which 50% of the fish were mature (numbers above the clusters of data points) differed significantly between the early and late periods in 2003 but not in 2002.

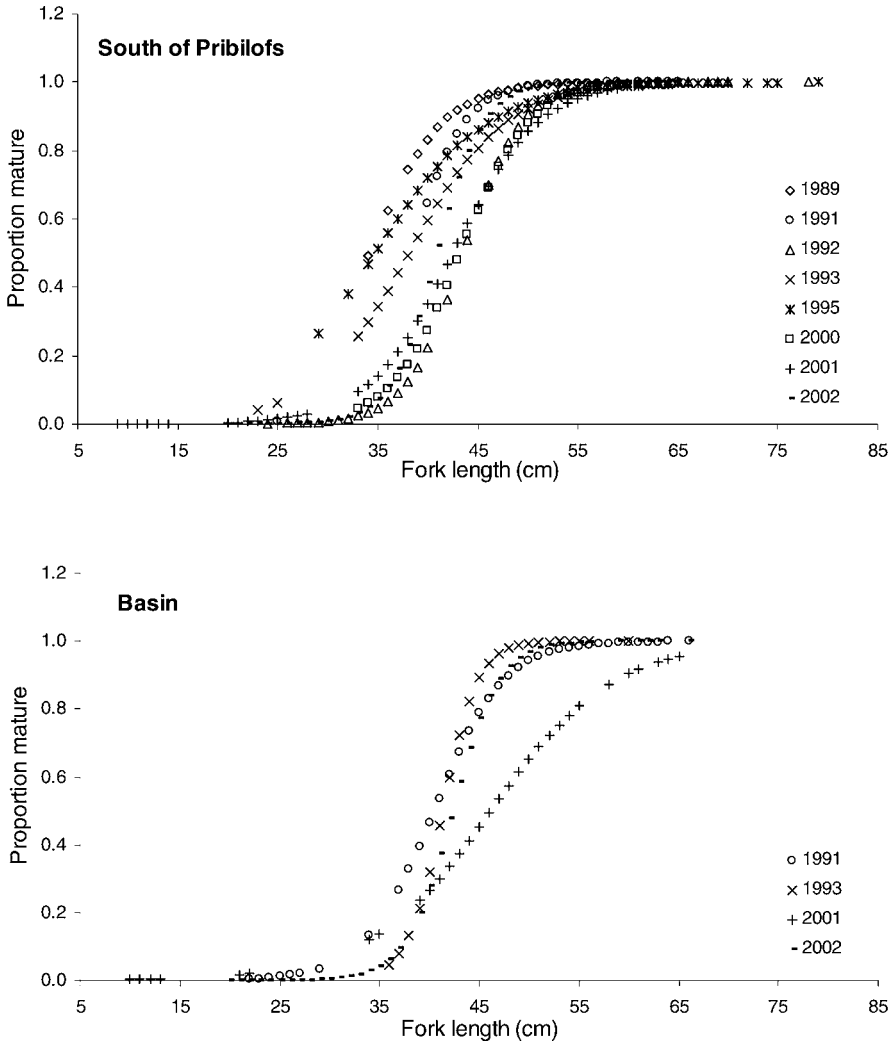

FIGURE 5.—Maturity curves of walleye pollock estimated from samples collected during the National Marine Fisheries Service (NMFS) winter echo-integration–trawl surveys in the eastern Bering Sea. Data are presented by year for the area south of the Pribilof Islands and the Aleutian basin (data provided by N. Williamson, NMFS).

samples sizes (<50 fish) for some area–year combinations, the tests for differences in growth parameters were limited to (1) the central versus the southern subarea in 2002 and (2) the northern versus the southern subarea in 2003. There were significant differences in the growth parameters for 2003 between the north, central, and south subareas ($P = 0.03$) and the north and south subareas ($P = 0.04$). Age-3–11 fish were larger in the southern subarea than in the area north of the Pribilof Islands.

We investigated large walleye pollock year-classes to determine whether length at age was driving the interannual trends in the maturity schedule. For each NMFS survey year, we identified any year-class comprising more than 25% of the abundance, as estimated by a combination of EIT trawl and bottom trawl surveys along with fishery data (Ianelli et al. 2003; Table 5), which we compared with shifts in L_{50} (Table 4; Figure 5). The length at age for a particular age and year was compared with the average length at age from 1983 to 2003 and considered below or above average if it was less than or greater than 5% of the mean, respectively (Table 6). Below-average lengths at age occurred for the 1988 year-class at age 3, which accounted for 28% of age-3+ fish in 1991 (note that below-average growth for this year-class in 1991

TABLE 4.—Fork lengths at 50% maturity (L_{50}) for walleye pollock in the eastern Bering Sea by National Marine Fisheries Service winter echo integration–trawl survey year and area (see Figure 2).

Survey year	L_{50} (cm)
South of Pribilof Islands	
1989	34.10
1991	38.42
1992	43.58
1993	38.13
1995	34.69
2000	43.27
2001	42.53
2002	40.79
Aleutian basin	
1991	40.50
1993	41.31
2001	46.18
2002	42.20

corresponds to a small L_{50} in that year; Table 4); the 1992 year-class at age 3, which accounted for 53% of age-3+ fish in 1995; and the 1998 year-class at age 3, which accounted for 27% of age-3+ fish in 2001. Above-average lengths at age occurred for the 1989 year-class at age 3, which accounted for 72% of age-3+ fish in 1992; the 1989 year-class at age 4, which accounted for 50% of age-3+ fish in 1993; the 1990 year-class at age 3, which accounted for 35% of age-3+ fish in 1993; and the 1999 year-class at age 3, which accounted for 36% of age-3+ fish in 2002. An average length at age occurred for the 1996 year-class at age 4, which accounted for 38% of the age-3+ fish in 2000; the 1996 year-class at age 5, which accounted for 28% of age-3+ fish in 2001; and the 1984 year-class at age 5, which accounted for 30% of age-3+ fish in 1989.

Two findings bear upon consideration of the density-dependent effects on size of maturity. First, bottom trawl survey catches of age-3+ walleye pollock were lower in the southeastern than in the northwestern Bering Sea in 2002 (1,544 versus 4,747) and 2003 (3,783 versus 6,144), consistent with the reduction in L_{50} with latitude. Second, there is a statistically significant ($P = 0.013$) negative relationship between L_{50} and the biomass of age-1+ walleye pollock in the eastern Bering Sea (Figure 6). However, relationships between the number ($P = 0.057$) and biomass ($P = 0.274$) of age-3+ fish and L_{50} in the Bering Sea were not significant.

Discussion

Ours is the first study to demonstrate spatial and temporal patterns in the size at maturity of walleye pollock in the eastern Bering Sea. With regard to geographic trends, we found two possibly related trends; that is, both L_{50} and length at age tend to decrease with increasing latitude on the eastern Bering Sea shelf. These results are consistent with higher growth rates (Lynde et al. 1986) and the larger length at age of young walleye pollock in the southern Bering Sea shelf (Shuck 2000). Samples from the Aleutian Basin were similar to those on the shelf north of the Pribilof Islands with respect to size at maturity (Table 2), possibly because walleye pollock from these areas are composed of the same predominant year-classes. For instance, the 1996 year-class was strong both in the Aleutian Basin (Ianelli et al. 2003) and on the

TABLE 5.—Number (millions) of eastern Bering Sea walleye pollock at age estimated from the stock assessment model using a combination of bottom trawl survey, echo integration–trawl (EIT) survey, and fishery data (Ianelli et al. 2003). Length at age was examined for the possible effects of strong year-classes on the lengths at 50% maturity estimated from the EIT data. Bold italics indicate ages accounting for more than 25% of the abundance estimate for an EIT survey year.

	Age								
Year	3	4	5	6	7	8	9	10+	Total
1989	2,005	2,458	***4,585***	1,111	2,966	536	598	894	15,153
1990	1,199	1,444	1,684	3,002	698	1,775	322	906	11,030
1991	***2,522***	857	975	1,022	1,734	375	980	684	9,149
1992	***14,429***	1,797	574	581	577	907	202	893	19,960
1993	***6,978***	***10,088***	1,147	308	289	256	418	514	19,998
1994	5,607	5,083	6,587	634	142	144	136	531	18,864
1995	***14,181***	4,103	3,438	3,954	334	79	84	411	26,584
1996	3,862	10,409	2,837	2,171	2,259	199	49	319	22,105
1997	3,010	2,826	7,405	1,935	1,313	1,241	113	219	18,062
1998	7,062	2,204	2,015	5,071	1,182	732	711	197	19,174
1999	11,120	5,178	1,577	1,390	3,157	678	430	541	24,071
2000	4,967	***8,137***	3,647	1,056	886	1,920	410	618	21,641
2001	***5,305***	3,628	***5,688***	2,403	657	523	1,127	641	19,972
2002	***7,433***	3,869	2,520	3,700	1,469	379	299	1,074	20,743
2003	8,022	5,414	2,687	1,625	2,206	840	214	832	21,840

TABLE 6.—Average length at age (mm) of female walleye pollock from the eastern Bering Sea estimated from National Marine Fisheries Service bottom trawl surveys, 1983–2003. For selected year-classes, the length at age for a particular age and year was compared with the average length at age and considered below (–) or above (+) the average if it differed from the average by more than 5%, average (0) if it differed by 5% or less.

Year	Age 3	Age 4	Age 5
1983	336	389	436
1984	352	391	436
1985	352	412	439
1986	314	396	421
1987	348	386	417
1988	361	390	429
1989	298	400	424(0)
1990	308	394	434
1991	291(–)	408	429
1992	361(+)	400	447
1993	375(+)	422(+)	438
1994	334	429	460
1995	293(–)	395	432
1996	290	387	438
1997	302	353	414
1998	295	383	431
1999	330	388	414
2000	336	397(0)	425
2001	309(–)	396	442(0)
2002	348(+)	402	445
2003	383	417	458
1983–2003	329	397	434

northwest shelf in 2002 and 2003 (T. W. Buckley, NMFS, personal communication). Moreover, the growth rates in the Aleutian Basin appear to be similar to those on the northern shelf and slope (Lynde et al. 1986).

It is somewhat ironic that some fish were harvested off the continental shelf, seemingly from the central Bering Sea (or Aleutian Basin) stock, during the fishery on the eastern Bering Sea shelf in 2002 and 2003 (e.g., Figure 4). Despite the separate stock assessments for the eastern Bering Sea shelf, Aleutian shelf, and central Bering Sea, it appears that these fisheries are not geographically well defined. Interactions among "stocks" have been recognized in annual stock assessments (Barbeaux et al. 2005; Ianelli et al. 2005). For example, a clear distinction between Aleutian Islands walleye pollock and those further east was not tenable in stock assessments conducted in the late 1990s because of a continuous distribution of catches and a preponderance of catch at the eastern boundary of the region. Moreover, in some years significant harvests from the Aleutian Islands were taken from deep waters; perhaps these fish would be best assigned to the central Bering Sea stock. The 2003 stock assessment confirmed such an offshore distribution of walleye pollock in the Aleutian region (Barbeaux et al. 2005). Such fuzzy boundaries between

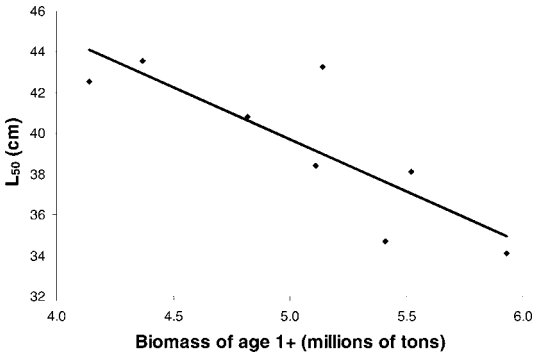

FIGURE 6.—Relationship between annual estimates of the length at which 50% of eastern Bering Sea walleye pollock were mature (L_{50}; estimated from fish collected during National Marine Fisheries Service [NMFS] winter echo integration–trawl surveys [Table 4]) and age-1+ fish biomass (estimated from NMFS bottom trawl surveys; Ianelli et al. 2003); the relationship is significant ($P = 0.013$).

fishery management units make it particularly important to conduct spatially explicit analyses of biological variables, such as in our study.

In-season temporal patterns in maturity were equivocal in 2002 and 2003 because of spatial shifts in the fishery from the southeastern Bering Sea at the beginning of the A season to the northwest as the season progressed (Figure 4). Significant differences in maturity schedules between early- and late-season samples from 2003 and 2002–2003 combined resulted from the general movement of the fishery from the south, near Unimak Island, to north of the Pribilof Islands along the 100-m contour. Thus, the larger values of L_{50} early in the season are most likely explained by the existence of a southeast–northwest cline in size of maturity. Changes in the in-season spatial distribution of the fishery were less pronounced in 2002; correspondingly, there was no significant difference in L_{50} values that year.

On the other hand, the interannual variability of the maturity curves is clearly apparent during 1989–2002 (Figure 5) and may be the result of annual changes in growth rates with a fixed maturity-at-age schedule and (or) age at 50% maturity (A_{50}) with a fixed length-at-age schedule. Temporal variation in percent maturity at age occurs in haddock *Melanogrammus aeglefinus*, another gadid species (Overholtz 1987). Unfortunately, the walleye pollock age data collected during the NMFS surveys were insufficient to estimate the interannual variation in $A_{50.}$ However, we found evidence that the interannual variation in L_{50} was caused by both differential growth rates by year-class and the variable contribution of each year-class to the annual abundance estimates (Tables 3, 4). For example,

the average and above-average lengths at age for the large year-classes of 1989 and 1996 may explain the comparatively large L_{50} and similar maturity curves south of the Pribilof Islands for NMFS surveys in 1992, 2000, and 2001 (Figure 5). The 2001 maturity curve had a large L_{50} in spite of the below-average length at age 3 for the 1998 year-class, which appears to shift the curve left at small lengths. Likewise, an above-average length at age also occurred for the 1999 year-class and may explain the large predicted proportion mature in the same area for 2002. Conversely, the below-average length at age of the 1988 and 1992 year-classes may explain the comparatively small L_{50} and similar maturity curves estimated for 1991 and 1995. However, the small L_{50} value for 1993 cannot be explained by the length at age of its predominant year-classes. Interannual variation in length at age was also observed in Aleutian Basin fish (Nishimura et al. 2001), and we found interannual variability in L_{50} in the basin with the limited data available to us.

We found both indirect and direct evidence that spatial and interannual variability in maturity results from density-dependent mechanisms. Indirectly, the increase in the number of age-3+ walleye pollock and the corresponding decrease in L_{50} from south to north of the Pribilof Islands in both 2002 and 2003 are consistent with density-dependent effects. A significant inverse relationship between annual estimates of the biomass of age-1+ fish and L_{50} for the EIT survey years provides direct evidence for density-dependent effects (Figure 6). The lack of a significant relationship between the abundance and biomass of age-3+ fish and L_{50} may mean that density dependence is strongest at ages 1 or 2 when cohort abundance is greatest. The fact that trajectories for early (small) or late (large) maturity are generally established when fish are less than 30 cm long (Figures 3, 5) is consistent with this interpretation. Also, fish less than 30 cm do not participate in seasonal spawning and feeding migrations (Kotwicki et al. 2005), so perhaps their relatively small movements make them more prone to prey depletion. The consequences of increased density may be increased competition for prey, a commensurate reduction in growth, and delay in maturation.

Density-dependent effects on growth and maturity are consistent with the results of studies of related species and other walleye pollock stocks. Interannual variation in percent mature at age in haddock and age at maturity in Atlantic cod *Gadus morhua* were both related to variation in abundance; a decrease in abundance resulted in an increase in the percent mature at age 2 in haddock (Overholtz 1987) and a decrease in age at maturity in Atlantic cod (Junquera and Saborido-Rey 1996). Interannual variation in the size at maturity in Gulf of Alaska walleye pollock (Megrey 1988) and the length at age of those in the Aleutian Basin (Nishimura et al. 2001) was related to the variation in stock abundance; the relationships between density and maturity and length at age both suggest that density-dependent growth occurred (Megrey 1988; Nishimura et al. 2001). For instance, the lower densities of walleye pollock in the Gulf of Alaska than in the eastern Bering Sea (Dorn et al. 2002; Ianelli et al. 2005) may reduce the competition for food, leading to greater growth (Megrey 1988) and the larger L_{50} (41.5 cm) among Gulf of Alaska (Dorn et al. 2002) fish than indicated by our L_{50} estimates (37.4 cm) for the eastern Bering Sea fish.

The potential for sampling bias should be considered in any field study. Bias can occur for a number of reasons, including selective behavior of the fishery, gear selectivity, and spatial segregation of different components of the fish stock. Because it behooves the commercial walleye pollock fishery during the A season to maximize their catches of prespawning schools with high-quality roe, immature fish might not be well represented in our fishery samples, especially if there is spatial segregation in the distribution of mature and immature fish. Although this source of bias cannot be fully discounted, a number of factors lead us to conclude that it is probably not a major concern in our study. First, our fishery samples were collected over a very broad geographic range (spanning the continental shelf over a period of several months), and this should minimize the likelihood of missing spatially or temporally separated aggregations of fish of a particular ovarian maturity status (e.g., immature, spent, and hydrated). Second, there are differences in the vertical distribution of walleye pollock of different ages; young fish tend to have more of an off-bottom distribution than do adults, which at age 6 fully recruit to the bottom trawl survey (Ianelli et al. 2005). Thus, the young fish, including those more likely to be immature, are distributed in the water column fished by this midwater trawl fishery. Indeed, gear selectivity (probably due to mesh size) is apparent because the fishery catches few age-1 and age-2 fish (Ianelli et al. 2005), the vast majority of which are immature; therefore, their underrepresentation in our samples should have minimal effects on the estimated maturity curves. Third, concerns about maturity-selective fishery behavior would not seem to apply to the summer hydroacoustic survey data, which were also included in our analysis. Yet, the descending limb of the maturity curves for the fishery samples for 2002 and 2003 (Figure 3) were better defined than some maturity curves derived from the EIT survey

(Figure 5) because of the larger sample sizes in the fishery-derived samples. Finally, in 2002 and 2003, the L_{50} was estimated to be about age 4. In these same years, the fishery caught larger proportions of age-4 fish than were estimated to be in the population by the age-structured assessment (Ianelli et al. 2005), along with proportions of age-3 fish comparable to those estimated to be in the population.

Our findings lead us to offer some advice for further research as well as fishery management. Size at maturity should be estimated with the GSI-based model. If GSI values are not available, the $D = I$ model should be used for management because it results in more precautionary estimates of spawning biomass. Using this model, size of maturity may be overestimated if some immature or developing walleye pollock actually spawn later in the season. Our histological results and the schedule of development in Funka Bay, Japan (Y. Sakurai, Hokkaido University, personal communication), suggest that developing fish spawn in the same year as data collection, but the time from development (stage 2) to spawning is unknown in the eastern Bering Sea. Consequently, resolving the schedule of ovarian development for walleye pollock in the eastern Bering Sea is a pressing need.

Spatial and interannual variability in size at maturity should be incorporated into management of the eastern Bering Sea stock. Use of maturity data collected only in the southeastern Bering Sea would tend to overestimate L_{50} and underestimate the proportion of mature fish to the northwest. Use of a fixed maturity schedule would overestimate or underestimate L_{50}, depending on the year. For instance, our results for 2002–2003 combined show a statistically significant difference in size at maturity since 1976, when our PCC-collected data are trimmed to exclude areas not sampled in 1976 by Bakkala and Smith (1978). The estimated values of parameters a and L_{50} in equation (2) were 0.27 and 35.15 cm for 1976, versus 0.26 and 37.46 cm for 2002–2003. To approximate the implications of these differences for stock assessment, we first used mean size at age to convert the proportion mature at length to the proportion mature at age. Then we multiplied the proportion mature at age by the number at age and weight at age to estimate the spawning stock biomass. This calculation indicated that use of the 1976 maturity resulted in a 1.8% underestimate of spawning biomass in 2002 and a 9.7% underestimate in 2003. However, we caution against relying too heavily on this result because these biomass estimates do not consider the effects of variations in length at age.

Although it may not be practical or advisable to adjust maturity schedules to account for random year-to-year variability, significant trends toward smaller or larger values of L_{50} in response to interrelated changes in climate and fish density and distribution may lead to systematic bias in the estimation of spawning biomass for annual catch specifications. Thus, it is advisable to reevaluate critical stock assessment variables, such as size at maturity, more often than is currently being done. Ideally, NMFS annual winter sampling should be performed both north and south of the Pribilof Islands at fixed locations each year to collect otolith, length, and maturity information so that interannual changes in population variables and maturity can be detected and included in annual stock assessments, as appropriate.

Significant latitudinal differences in walleye pollock size at maturity lead us to recommend consideration of a spatially explicit management plan for the eastern Bering Sea shelf stock that might separate walleye pollock north of the Pribilof Islands from those in the south near Unimak Island. Without such spatially explicit accounting of harvests, north–south shifts in the fishery due to climate change or other factors could result in significant changes in realized harvest rates of spawning biomass, as influenced by differences in size at maturity between areas. We do not advocate splitting the eastern Bering Sea shelf stock into two stocks. Instead, because the northern and southern areas occupied by this stock have differing levels of productivity as indexed by growth (Lynde et al. 1986; Shuck 2000) and size at maturity, we recommend adopting area-specific harvest rates. More research should be conducted to determine the location of the dividing line between these two potential management areas because we found that the central area was sometimes significantly different from the areas north and south of the Pribilof Islands (Table 3).

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