

**Abstract**—Length at age, length at maturity, and age at maturity of yellowfin sole, *Pleuronectes asper*, in the eastern Bering Sea, are influenced by area of sampling and bottom depth. Yellowfin sole sampled during spring and summer bottom trawl surveys (1982–94) grew faster in the northwest area compared with the southeast area. Mean lengths at age were generally more than 2 cm greater than those for southeast fish at ages greater than 10 years. Length at 50% maturity in females during 1993 and 1994 was respectively 2.3 cm and 0.94 cm larger in the northwest area than in the southeast area. In contrast, there was no apparent difference in age at 50% maturity between areas.

Spring-summer patterns in bathymetric habitation of yellowfin sole differ for immature and mature individuals and cause a potential bias in estimates of growth and maturity. There is a clear relation between length and depth for immature fish, with older, immature fish inhabiting deeper water. In contrast, mature fish distribute similarly by size across a wide range of bottom depths. As a result, estimates of length and age at 50% maturity ( $L_{50}$ ,  $A_{50}$ ) tended to increase with increasing bottom depth. Because current resource assessment surveys do not sample the shallowest areas of the summer distribution of yellowfin sole, estimates of  $L_{50}$  and  $A_{50}$  are inherently biased high.

## Effects of geography and bathymetry on growth and maturity of yellowfin sole, *Pleuronectes asper*, in the eastern Bering Sea

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Yellowfin sole, *Pleuronectes asper*, inhabit the nearshore shelf areas of the eastern Bering Sea, from Bristol Bay to north of Nunivak Island (60°N lat.) (Fig. 1), during spring and summer months. Adult individuals overwinter near the shelf-slope break at approximately 200 m. Two main eastern Bering Sea overwintering groups, composed mainly of sexually mature adults (Krivobok and Tarkovskaya, 1964) have been identified: a southern complex near Unimak Island and a central complex located west of the Pribilof Islands (Fadeev, 1970; Bakkala, 1981; Wakabayashi, 1989). During spring, as the edge of the shelf ice recedes toward the coast, yellowfin sole migrate across the shelf to nearshore spawning areas in Bristol Bay and off Nunivak Island (Bakkala, 1981). Yellowfin sole generally spawn at bottom depths less than 50 m (Wilderbuer et al., 1992); most spawning activity, however, occurs at depths less than 30 m, May through August (Nichol, 1995). Juvenile yellowfin sole probably do not undergo the long cross-shelf migration. At least some juveniles (<6 years) are known to overwinter nearshore (Fadeev, 1970; Wilderbuer et al., 1992), whereas relatively few juveniles overwinter offshore (Krivobok and Tarkovskaya, 1964; Fadeev, 1970).

Bottom trawl surveys for groundfish resource assessment are conducted annually in the eastern Bering Sea to obtain abundance estimates of commercially important fish and invertebrate species. Differences in fish distributions and oceanographic factors have prompted scientists who analyze survey results to stratify the eastern Bering Sea into discrete northwest and southeast areas, and three different depth regimes (Walters and McPhail, 1982; Walters, 1983; Wakabayashi, 1989; Bakkala, 1993). Thus, both geographic and bathymetric factors affect fish distribution and abundance in the eastern Bering Sea. In this paper I describe regional differences in growth of yellowfin sole (*P. asper*) from the eastern Bering Sea and effects of geographic area and bottom depth on estimates of length and age at maturity.

Commercial catch records (Norris et al.<sup>1</sup>) indicate that yellowfin sole occur in substantial numbers in waters shallower than 30 m, where

<sup>1</sup> Norris, J. G., J. D. Berger, and K. T. Black. 1991. Fisherman's guide to catch per unit effort and bycatch data from the National Marine Fisheries Service Observer Program: Bering Sea/Aleutian Island yellowfin sole trawl fishery. AFSC Proc. Rep. NOAA-NMFS 91-07, 200 p. Alaska Fisheries Science Center, Natl. Mar. Fish. Serv., NOAA, 7600 Sand Point Way NE, Seattle, WA 98115-0070.

research surveys are not routinely carried out. Thus, current survey biomass estimates underestimate population abundance of the species; exclusion of juveniles in shallow water, as well as sexually mature yellowfin sole that inhabit these nearshore spawning areas during the survey period (June–August), may introduce a sampling bias into estimates of growth and estimates of size at maturation. To determine the extent of this potential problem, I considered the effects of bottom depth on fish size.

## Materials and methods

### Survey area

Resource assessment surveys were conducted in the eastern Bering Sea (Bakkala, 1993; Wakabayashi et al., 1985), from June to mid-August. Standard survey stations were based on a 20 by 20 nautical mile grid that covered the area from inner Bristol Bay west to the continental slope edge and from the Alaska Peninsula north to approximately latitude 61°N (Fig. 1). Bottom trawl tows of approximately 1.5 nautical miles and of 30-min duration were made at each station. Surveys began in inner Bristol Bay and generally followed north- and south-directed transects, proceeding westward with each finished transect.

### Data

Yellowfin sole otoliths were collected from 3,891 males and 5,209 females during AFSC surveys, 1982–94 (Table 1). Fish were measured to the nearest centimeter total length (TL) and sagittal otoliths were removed and stored in 50% ethanol for subsequent age determination. Ages were determined by using the break-and-burn technique (Chilton and Beamish, 1982).

Female maturity data were collected during 1992–94 surveys (Table 2). Maturity codes were based on macroscopic gonadal appearance (Nichol, 1995). For the purpose of this study, codes were simplified to either mature or immature. Females were consid-

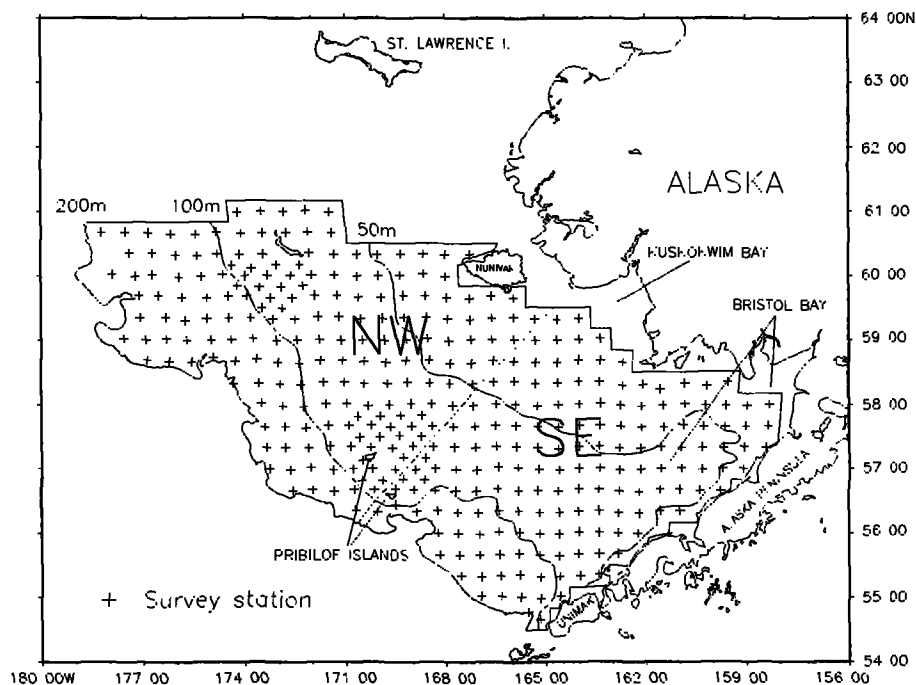


Figure 1

Map of the survey stations where yellowfin sole were sampled by the eastern Bering Sea crab-groundfish bottom trawl survey of the Alaska Fisheries Science Center from 1982 to 1994. Northwest (NW) and southeast (SE) areas are delineated by the strata boundary line extending from north of Kuskokwim Bay, southeast through the Pribilof Islands.

ered mature if ovaries contained yolked or hydrated oocytes, or were recently spent. Immature ovaries contained no visible oocytes. Data collected during 1993 (Table 2) were best for examining spatial differences in female length at maturity because samples were collected at nearly all survey stations within the 50-m contour line, and maturity code assignments were verified by histological examination (Nichol, 1995).

### Analysis

The total survey area was subdivided into northwest and southeast areas (Wakabayashi, 1989; Bakkala, 1993) extending from north of Kuskokwim Bay southeast through the Pribilof Islands (Fig. 1).

**Length at age** Factorial analysis of variance (ANOVA) models (Reish et al., 1985) was constructed independently for males and females to examine the variance in length at each age due to geographic area (northwest or southeast) and to bottom depth. For ANOVA, bottom depths were grouped into three levels (<30 m, 30–49 m, and ≥50 m; Table 1). A model, which included interaction terms and which was pooled across years, was analyzed for both males and

females. Preferred models were estimated by a least-squares backward stepwise procedure that sequentially removed the highest-order nonsignificant factor until only significant terms remained. Nonsignificant ( $P \geq 0.05$ ) main effects were retained if they were included in one or more significant interaction terms. Residual plots were examined to test assumptions of homoscedasticity and normality of error terms. Least squares estimates of model coefficients were obtained by means of the Statistical Analysis System procedure GLM (SAS Institute, 1989).

**Length at maturity** Logistic regression was used to assess the effects of area and bottom depth on the

probability that an individual of a given length (cm) was mature or immature. The following equation was fitted independently to 1992, 1993, and 1994 female yellowfin sole length-maturity data by using the Statistical Analysis System maximum likelihood procedure LOGISTIC (SAS Institute, 1989):

$$MAT = \frac{1}{1 + e^{-(\mu + \beta \cdot L + \alpha \cdot \text{area} + \delta \cdot D + \Delta \cdot L \cdot D)}} \quad (1)$$

where  $MAT$  = mature proportion of female yellowfin sole given its length ( $L$ ), area, and bottom depth ( $D$ ) of capture.

Area was treated as a factor indicating either northwest or southeast areas. Depth was treated as a continuous variable. Length, area, and depth coefficients were represented by  $\beta$ ,  $\alpha$ , and  $\delta$ , respectively, and  $\mu$  denoted the intercept (on the logit scale). A length  $\times$  depth interaction term ( $L \cdot D$ ; Eq. 1) with coefficient  $\Delta$  was also tested for significance. Nonsignificant ( $P \geq 0.05$ ) highest order terms were removed from the model.

Length at 50% maturity ( $L_{50}$ ) was calculated by substituting 0.5 for  $MAT$  in Equation 1 and solving for  $L$  as follows:

$$L_{50} = - \left( \frac{\mu + \alpha \cdot \text{area} + \delta \cdot D + \Delta \cdot L \cdot D}{\beta} \right) \quad (2)$$

Due to sample-size inequalities (Table 2), length at maturity comparisons between northwest and southeast areas were limited to females sampled in 1993 and 1994.

**Table 1**

Number of male and female yellowfin sole sampled for age and length by the Alaska Fisheries Science Center during resource assessment surveys conducted in northwest and southeast areas of the eastern Bering Sea from 1982 to 1994.

Year	Bottom depth (m)					
	Northwest			Southeast		
	<30	30-49	$\geq 50$	<30	30-49	$\geq 50$
<b>Males</b>						
1982	26	58	26	65	97	45
1983	0	52	85	56	87	27
1984	14	102	31	31	109	42
1985	28	99	36	26	65	84
1986	0	100	42	39	74	66
1987	133	30	13	38	111	31
1988	44	33	13	27	28	98
1989	29	35	39	23	105	87
1990	49	58	48	36	74	92
1991	82	64	26	0	65	97
1992	32	0	25	73	79	39
1993	31	50	18	47	0	46
1994	24	64	21	72	13	37
Total	492	745	423	533	907	791
<b>Females</b>						
1982	15	110	49	65	97	83
1983	0	80	129	57	102	41
1984	0	143	71	33	137	83
1985	41	154	40	43	57	129
1986	0	113	97	48	57	103
1987	152	67	24	36	112	51
1988	58	38	46	47	31	100
1989	0	82	113	39	92	96
1990	47	81	86	54	38	129
1991	85	73	35	0	69	146
1992	35	0	91	86	79	67
1993	28	67	100	61	0	101
1994	29	55	49	61	20	76
Total	490	1,063	930	630	891	1,205

**Table 2**

Summary of female yellowfin sole length-maturity collections during the 1992-94 Alaska Fisheries Science Center eastern Bering Sea groundfish bottom trawl surveys. A = Age, length, and maturity data collected by sex-cm interval; L = Length and maturity (random measurements); O = Ovaries, lengths, and maturity data collected by size category,  $\geq 25$  cm TL. Ages were determined for 53 of these specimens.

Year	Sample type	Number of samples	
		Northwest	Southeast
1992	A	107	218
	L	0	1,260
1993	A	98	162
	O	256	512
1994	A	133	158

**Age at maturity** Analysis of female age at maturity was treated in the same manner as with length at maturity, substituting age ( $A$ ) in years for length ( $L$ ). Owing to smaller sample sizes (Table 2), data for years 1992–94 were pooled.

## Results

### Length at age

The general effects of area and bottom depth on length at age were highly significant for both males and females (Table 3). Mean length-at-age plots for both male and female yellowfin sole indicated greater

sizes at age in the northwest than in the southeast area of the eastern Bering Sea shelf (Fig. 2). Male and female yellowfin sole were on average 1.22 and 1.02 cm larger at age, respectively, in the northwest area than in the southeast area. Average length-at-age differences between areas (northwest-southeast) increased with increasing age to more than 2 cm for both males and females (Fig. 3). Total lengths were generally greater at age in deeper ( $\geq 50$  m) waters than in shallow waters ( $< 50$  m) for males and females less than 8 and 9 years of age, respectively (Fig. 3).

### Length at maturity

Female yellowfin sole lengths corresponding to 50% maturity ( $L_{50}$ ) were greater in the northwest than in the southeast area, and  $L_{50}$  increased with increasing bottom depth (Fig. 4). Area accounted for a 2.3 cm female length-at-maturity difference ( $P=0.0001$ ) in 1993 and a 0.91 cm difference ( $P=0.049$ ) in 1994 (Fig. 4; Table 4). Female  $L_{50}$  increased with increasing bottom depth ( $P \leq 0.013$ ), varying by as much as 4 cm between shallow and deeper waters (Fig. 4; Table 4). Annual variation (1992–94) in  $L_{50}$  appeared to be approximately 1 cm (Fig. 4).

### Age at maturity

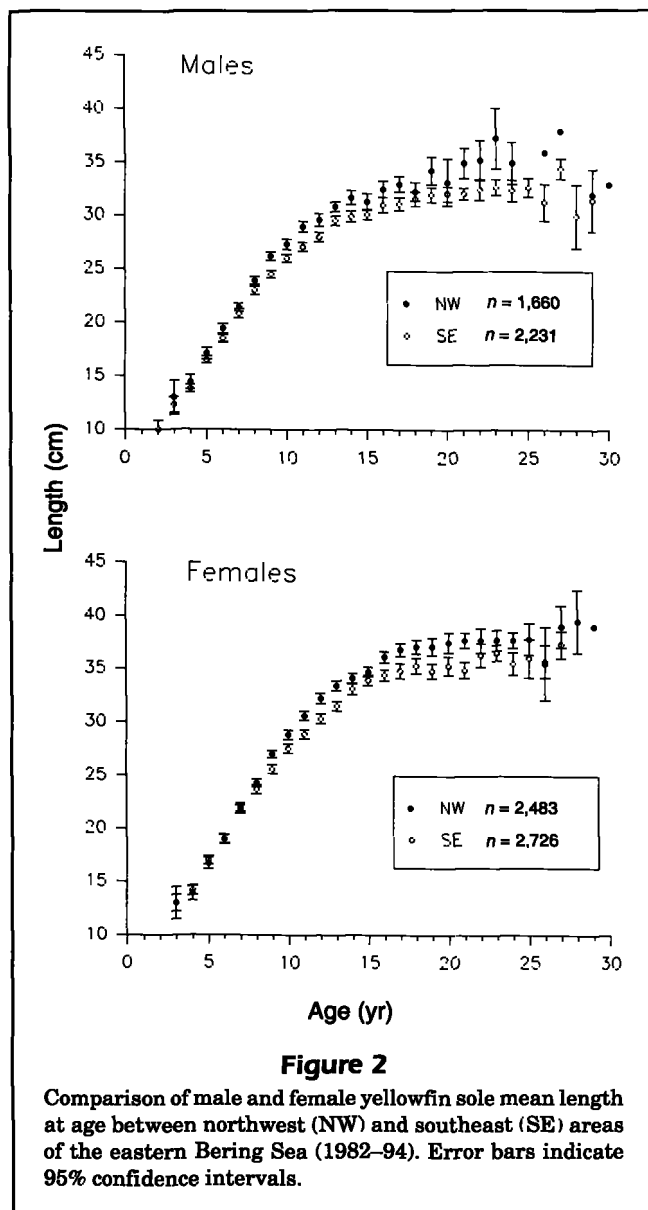
In contrast to length-at-maturity results, no significant age-at-maturity difference ( $P=0.080$ ) was found for females between the two areas (Fig. 5; Table 5). A similar increase in female age at maturity, however, did occur with increasing bottom depth ( $P=0.0001$ ), with age at 50% maturity increasing by 3 years from shallow to deeper waters (Fig. 5).

## Discussion

Larger northwest fish lengths corresponding to a particular age or percent maturity, combined with no apparent age-at-maturity difference between areas, indicate faster yellowfin sole growth in the northwest area than in the southeast area. Bottom depth effects on length-at-age, length-at-maturity, and age-at-maturity estimates, however, were more the result of sampling uneven fish distributions, as discussed below.

### Area effects

The length-at-age and length-at-maturity differences found between areas support the hypothesis that northwest and southeast complexes are functionally allopatric during the summer spawning period. Tag-



ging studies (Wakabayashi, 1989) indicated only limited movements of yellowfin sole between northwest and southeast areas as they migrate inshore, and Kashkina (1965) supported a two-stock concept, cit-

ing differences in egg-stage advancement and abundance between northern and southern regions of the eastern Bering Sea. Despite the lack of genetic evidence supporting the coexistence of two independent

**Table 3**

Factorial analysis of variance of male and female yellowfin sole length (cm) at age (years), by area (northwest and southeast) and bottom depth (<30, 30–49, and ≥50 m), pooled across years 1982–94. Note that nonsignificant ( $P \geq 0.05$ ) main effects were retained because they were included in one or more significant interaction terms. SS = sum of squares.

Source	df	SS	Mean square	F-value	P > F
<b>Males</b>					
Age	29	68,007.6	2,345.1	360.0	0.0001
Area	1	295.5	295.5	45.4	0.0001
Depth	2	5.7	2.8	0.4	0.6457
Age × depth	49	1,906.9	38.9	6.0	0.0001
Age × area	24	160.4	6.7	1.0	0.4268
Area × depth	2	51.8	25.9	4.0	0.0188
Age × area × depth	34	366.9	10.8	1.7	0.0098
Error	3,749	24,421.2	6.5		
<b>Females</b>					
Age	29	152,746.0	5,267.1	667.9	0.0001
Area	1	408.1	408.1	51.8	0.0001
Depth	2	2.1	1.1	0.1	0.8738
Age × depth	49	3,219.2	65.7	8.3	0.0001
Age × area	24	411.2	17.1	2.2	0.0008
Area × depth	2	44.7	22.3	2.8	0.0589
Age × area × depth	44	593.1	13.5	1.7	0.0025
Error	5,057	39,880.8	7.9		

**Table 4**

Logistic regression coefficients for the equation  $MAT = 1 / (1 + e^{-\mu + \beta \cdot L + \alpha \cdot \text{area} + \delta \cdot D + \Delta \cdot L \cdot D})$  relating female yellowfin maturity status to fish length ( $L$ ), binary variable area (northwest or southeast), and continuous variable depth ( $D$ ).  $L \times D$  denotes the interaction between length and depth. SE = standard error of the estimate.  $L \times D$  coefficients were considered nonsignificant ( $P \geq 0.05$ ) and were therefore removed from the model. Remaining coefficients and estimates result from model runs with  $L \times D$  removed (underlined values).

Year	n	Variable	Symbol	Coefficient		P > chi-square
				Estimate	SE	
1992 <sup>1</sup>	1,478	Length	$\beta$	-0.82	0.047	0.0001
		Depth	$\delta$	0.046	0.0048	0.0001
		L × D	$\Delta$	0.0046	0.0024	<u>0.057</u>
		Intercept	$\mu$	22.22	1.36	0.0001
1993	1,028	Length	$\beta$	-0.83	0.063	0.0001
		Area	$\alpha$	2.29	0.30	0.0001
		Depth	$\delta$	0.042	0.0078	0.0001
		L × D	$\Delta$	-0.0065	0.0035	<u>0.063</u>
		Intercept	$\mu$	21.70	1.81	0.0001
1994	291	Length	$\beta$	-0.69	0.085	0.0001
		Area	$\alpha$	0.91	0.46	0.049
		Depth	$\delta$	0.042	0.012	0.0004
		L × D	$\Delta$	0.0046	0.0048	<u>0.34</u>
		Intercept	$\mu$	17.92	2.52	0.0001

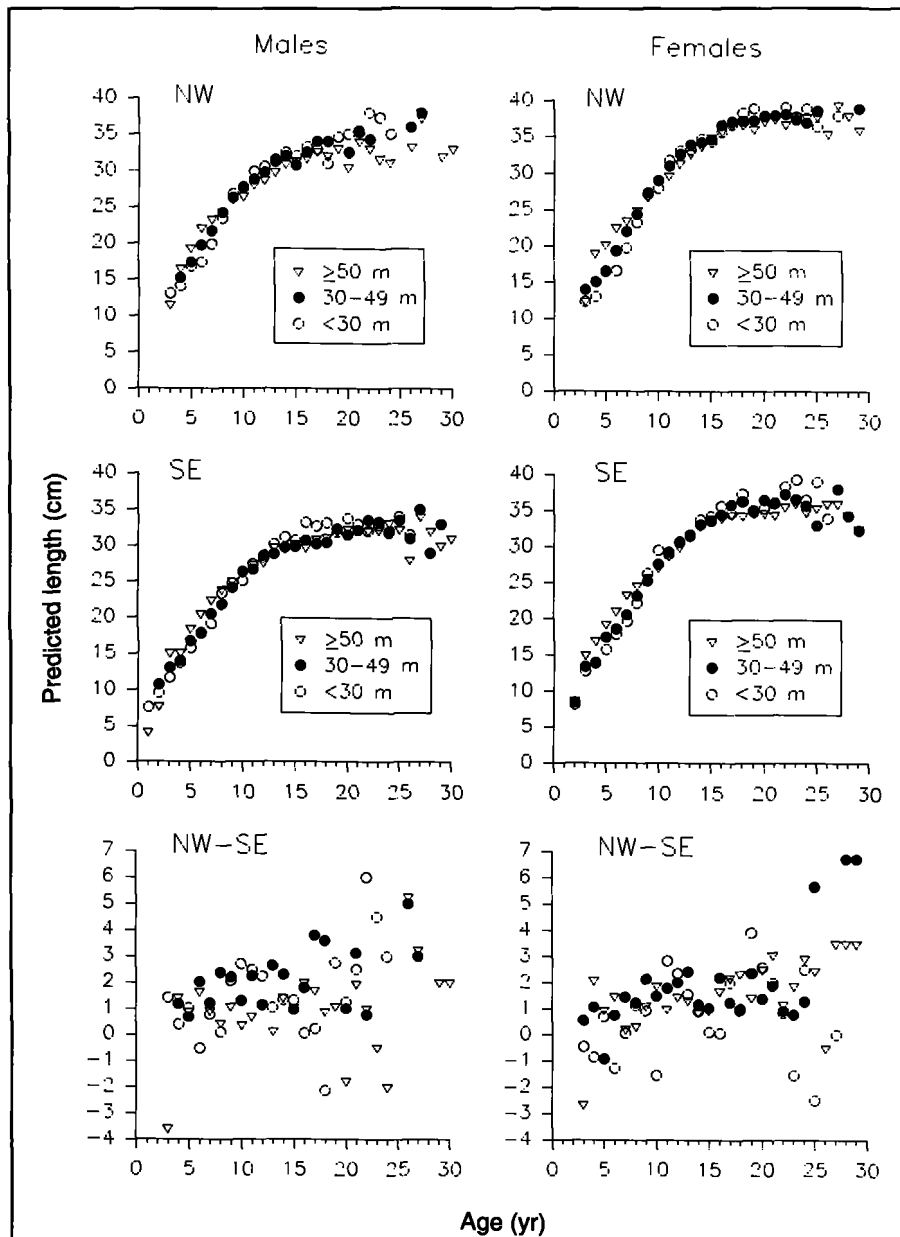
<sup>1</sup> Southeast area only. Small sample size in the northwest area (n=107) limited a comparison by area.

stocks (Grant et al., 1983), the persistence of area-based differences suggests that mixing of adults between northwest and southeast complexes may be minimal.

Growth-rate differences may be associated with geographic differences in yellowfin sole density or bottom temperature (or both). Yellowfin sole mean density (1982–94; author, unpubl. data), measured in catch per unit of effort (kg/hectare) during spring-

summer, has been consistently higher in the southeast area (88.9 kg/ha) than in the northwest area (27.8 kg/ha). Spring-summer bottom temperatures have also been consistently higher in the southeast area than in the northwest area (Fig. 6). The higher yellowfin sole growth rate in the northwest areas is consistent with density-dependent hypotheses (Beverton and Holt, 1957; Cushing, 1975; Rijnsdorp, 1994) that suggest a negative correlation between fish growth and fish density. Reasons why fish growth appears faster in cooler northwest waters are less clear.

Age-composition data used in stock assessments for yellowfin sole in the eastern Bering Sea (Wakabayashi et al., 1985) have been based upon age-length keys generated from annual age-length collections (Armistead and Nichol, 1993). Although independent age (otolith) collections have been made for the southeast and northwest areas, age-length keys are currently pooled across areas. The resulting estimates of growth are considered accurate because Alaska Fisheries Science Center age-structure collections have been spread fairly evenly between areas. However, given the spatial patterns described here, separate northwest-southeast age-length keys might improve the precision of these estimates.

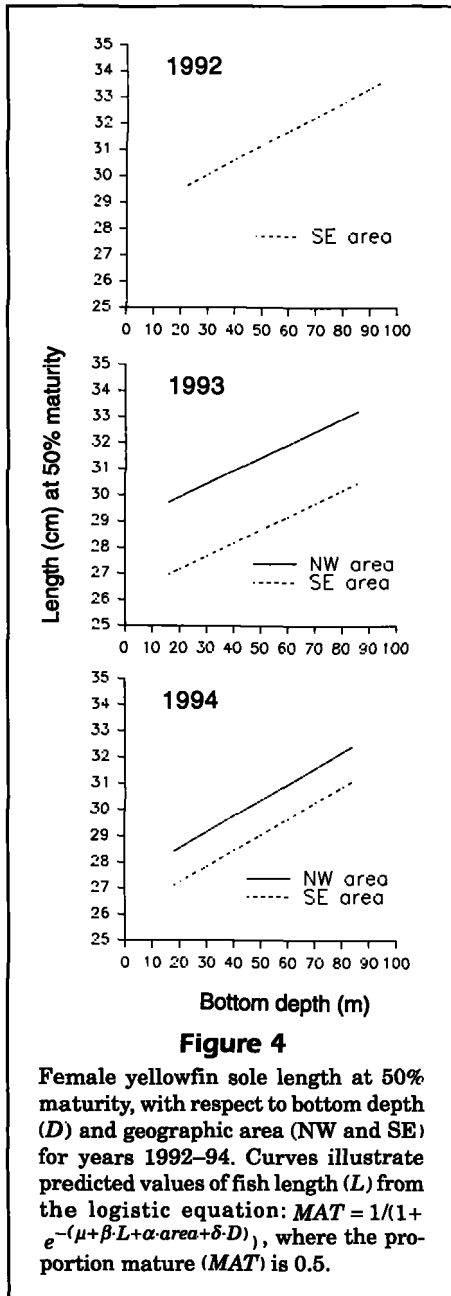


**Figure 3**

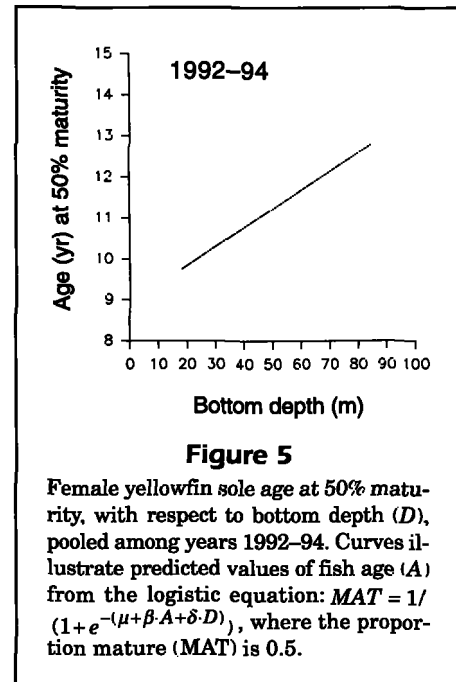
Factorial length at age model results comparing length at age of male and female yellowfin sole across bottom depths (m) in both northwest (NW) and southeast (SE) areas of the eastern Bering Sea. Age  $\times$  Area  $\times$  Depth interactions are included with data pooled across 1982–94 age-length collections.

### Implications of depth-related sampling biases

Immature yellowfin sole, like many other fish species (Hunter et al., 1990; Macpherson and Duarte, 1991; Jacobson and Hunter, 1993), undergo an ontogenetic migration, distributing themselves along a size-depth continuum where smaller individuals inhabit shallow waters and larger individuals inhabit deeper waters. A single cohort can also distribute itself along this size-depth continuum. In doing so, faster-growing individuals can be found at



deeper depths than can slower-growing individuals. Length-at-age estimates for immature yellowfin sole (<8 years of age) from shallower waters, therefore, are biased low in comparison with those from deeper waters (Fig. 3). The cessation of this depth effect with increasing bottom depth after 8 years of age (Fig. 3) may indicate the approximate age at which immature yellowfin sole leave the size-depth continuum and become migratory (i.e. to shelf-slope waters in winter and back to nearshore waters in spring-summer). The timing of first maturity may very well coincide with the initiation of a “spawning” migration.



The increase in female length and age at maturity with increasing bottom depth was largely due to the variation of immature female length distributions as depth increased. In spring-summer, when yellowfin sole have migrated nearshore for spawning, distributions of mature migratory individuals and immature “ontogenetically driven” individuals overlap. The differences between these two migration patterns act to separate immature and mature fish of similar lengths (and ages) along a bottom depth gradient. Immature females were distributed unevenly by size across depth; larger sizes (25–32 cm TL) were more common at deeper depths (Fig. 7). In contrast, mature females were distributed similarly by length between shallow (<30 m) and deeper (≥30 m) bottom depths (Fig. 7).

The absence of these larger immature females in shallow water resulted in lower values of length at maturity for shallow waters and higher values for deeper waters (Fig. 7). Trippel and Harvey (1991) demonstrated how age at maturity of white suckers (*Catostomus commersoni*) could be affected if year classes falling within the progression from immaturity to maturity are missing. Missing length classes, similarly, affect estimates of length at maturity. Sampling of female yellowfin sole in shallow waters (<30 m) misses critical length and age classes of immature individuals on the verge of maturity.

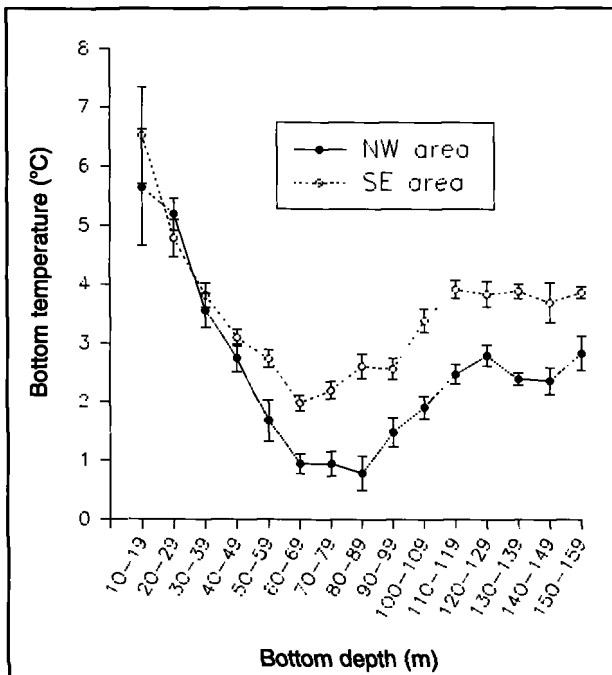
Length or age at maturity, as with growth relations, are often measured simultaneously across multiple cohorts and are therefore approximations

**Table 5**

Logistic regression coefficients for the equation  $MAT=1/(1 + e^{-\mu + \beta \cdot A + \alpha \cdot \text{area} + \delta \cdot D + \Delta \cdot A \cdot D})$  relating female yellowfin maturity status to fish age (*A*), binary variable area (northwest or southeast), and continuous variable depth (*D*). *A* × *D* denotes the interaction between age and depth. SE= standard error of the estimate. *A* × *D* and age coefficients were considered nonsignificant ( $P \geq 0.05$ ) and were therefore removed from the model. Remaining coefficients and estimates result from model runs with *A* × *D* and age removed (underlined values).

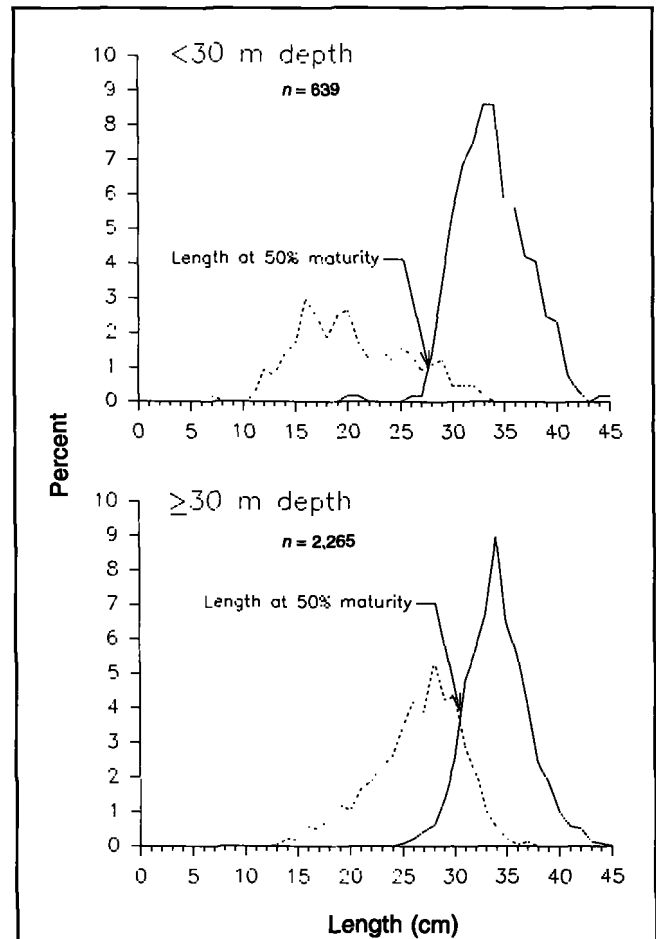
Year <sup>1</sup>	n	Variable	Symbol	Coefficient		
				Estimate	SE	P > chi-square
1992-94	929	Age	$\beta$	-0.70	0.048	0.0001
		Area	$\alpha$	0.38	0.21	<u>0.080</u>
		Depth	$\delta$	0.032	0.0056	0.0001
		A × D	$\Delta$	-0.0040	0.0021	<u>0.054</u>
		Intercept	$\mu$	6.25	0.50	0.0001

<sup>1</sup> Data were pooled among years 1992-94.



**Figure 6**

Mean bottom temperatures of the southeast and northwest areas of the eastern Bering Sea shelf, averaged across years 1982-94 at 10 m bottom depth intervals. Error bars indicate 95% confidence intervals.



**Figure 7**

Length distribution of mature (solid line) and immature (dashed line) female yellowfin sole at bottom depths less than 30 m and greater than 30 m, 1992-94 data combined.

of individual growth and length or age at maturity. This estimation assumes that there is no between year-class growth or maturity differences with respect to a given age and that samples within each age class are random with respect to the population



(Ricker, 1975). Obtaining representative samples from each age class becomes difficult when fish size and age vary with bottom depth. Considering also that during spring-summer, yellowfin sole abundance increases with decreasing bottom depth (Nichol, 1995), population estimates of yellowfin sole growth and length or age at maturity should be weighted accordingly. Because groundfish assessment surveys in the eastern Bering Sea do not cover the shallowest areas of yellowfin sole distribution during spring-summer, current estimates of yellowfin sole growth, as well as size and age at maturity, are inherently biased high. Given that most demersal fish distribute themselves along a size-depth continuum (Macpherson and Duarte, 1991), the potential for similar depth-related sampling biases in other demersal fish species appears probable.

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