

Abstract—This study investigates the temporal stability of length- and age-at-maturity estimates for female Pacific cod (*Gadus macrocephalus*) in the Gulf of Alaska and eastern Bering Sea. Females reached 50% maturity (A_{50}) at 4.4 years in the Gulf of Alaska and at 4.9 years in the eastern Bering Sea. Total body length at 50% maturity (LT_{50}) was significantly smaller (503 mm) in the Gulf of Alaska than in the eastern Bering Sea (580 mm). The estimated length- and age-at-maturity did not differ significantly between winter and spring in either the Gulf of Alaska (1999) or Bering Sea (2003) areas. The results of this study raised the spawning biomass estimate of female Alaskan Pacific cod from 298×10^3 t for 2005 to 499×10^3 t for 2006. The increased spawning biomass estimate resulted in an increased over-fishing limit for Pacific cod.

Geographic and seasonal variations in maturation and growth of female Pacific cod (*Gadus macrocephalus*) in the Gulf of Alaska and Bering Sea

James W. Stark

Email address: jim.stark@noaa.gov

Resource Assessment and Conservation Engineering Division
Alaska Fisheries Science Center
NOAA/National Marine Fisheries Service
7600 Sand Point Way NE
Seattle, Washington 98115

Pacific cod (*Gadus macrocephalus*) was the fourth most important commercial species landed in the United States during 2003 by volume, and catches totaled 27×10^4 metric tons (t) and had a value of \$160 million. The Pacific cod stocks in Alaska were not considered to be overfished in 2005 (Thompson and Dorn, 2005; Thompson et al., 2005). Pacific cod range from California, around the North Pacific Rim, to the Sea of Japan (Hart, 1973). In Alaska, this species is found along the continental shelf and upper slope, primarily at depths <300 m (Matarese et al., 2003). The objectives of this study were to determine the length- and age-at-maturity, as well as growth of female Pacific cod, in order to provide for significantly improved stock management in the Gulf of Alaska, eastern Bering Sea, and Aleutian Islands. Previous estimates of Pacific cod length-at-maturity were based on visual (macroscopic) observations of ovaries taken during the spawning season (Welch and Foucher, 1988; Thompson et al., 2005), or on a gonadosomatic index (*IG*) (Teshima, 1985; Hattori et al., 1992).

The macroscopic observation and *IG* methods can introduce sampling bias through misclassifications of the stage of oocyte maturity (Hunter et al., 1992). The macroscopic method of maturity classification is contingent upon differentiating between ova that contain yolk (mature ova) which can appear transparent to the naked eye, and opaque ova that do not con-

tain yolk. The change in opacity is the result of yolk sequestering within the ova, resulting in distension and transparency of the chorion (external covering of the ova). Opacity is more difficult to discern in the small ova that are produced by smaller fish. Therefore, the macroscopic method of classification can result in a bias against smaller fish.

With macroscopic classification, there is also a bias against specimens in early vitellogenesis, because during this period only a small quantity of yolk has been sequestered within the ova, resulting in an opaque chorion that is not distended. With macroscopic observation methods, an ovary containing only postovulatory follicles and opaque ova would be classified as immature; postovulatory follicles can be detected only through the use of histological methods.

Macroscopic observations also have the disadvantage of generally being conducted under less than ideal lighting and weather conditions. Maturity classifications based on histological examination are not subject to these biases because the maturity classifications are based on a comprehensive microscopic assessment of ova and associated structures, such as postovulatory follicles, under controlled laboratory conditions. Histological methods provide a high probability that yolk sequestered within ova will be detected because ova are sectioned and stained with eosin that renders yolk pink.

Manuscript submitted 20 September 2006 to the Scientific Editor's Office.

Manuscript approved for publication 23 March 2007 by the Scientific Editor.
Fish. Bull. 105:396–407 (2007).

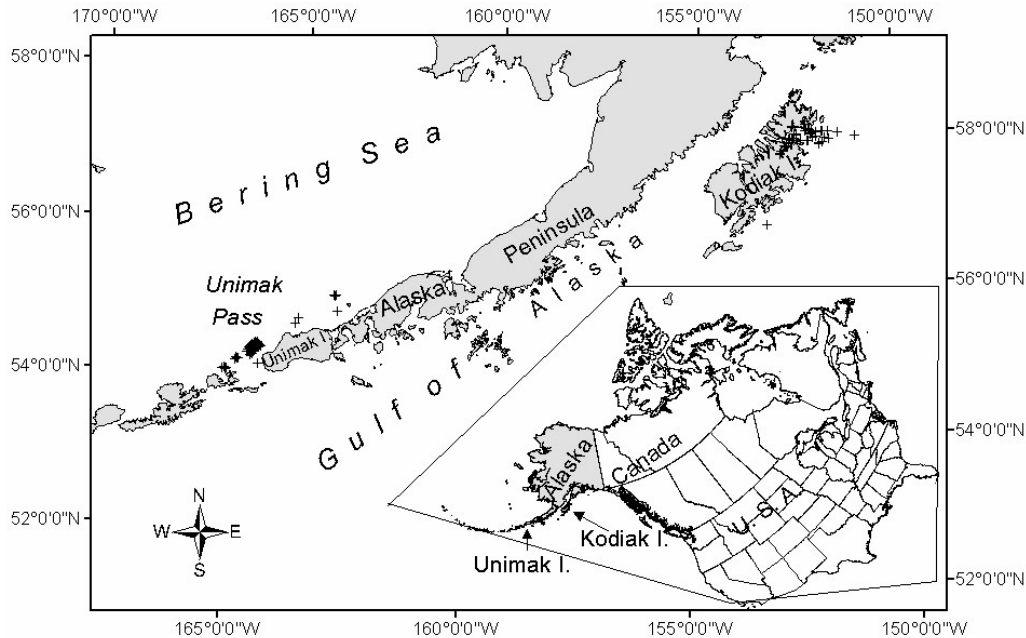


Figure 1

Locations (+) sampled during Alaska Fisheries Science Center survey cruises from October 1988 through January 2004 for assessment of the maturity stages of Pacific cod (*Gadus macrocephalus*).

Materials and methods

Ovaries and otoliths were collected from Pacific cod in two geographic areas, the Gulf of Alaska and eastern Bering Sea (Fig. 1). Seasonal sampling was used to estimate the time of spawning, rate of ovary development, and length- and age-at-maturity for female Pacific cod. The first area, located in the central Gulf of Alaska, was sampled during October 1998, January 1999, and April 1999 (Table 1) during a cooperative seasonal maturity study conducted by the Alaska Department of Fish and Game (ADFG) and the National Oceanic and Atmospheric Administration Alaska Fisheries Science Center (NOAA/AFSC). The area was sampled with bottom trawl gear again in June 1999 during the annual ADFG crab survey and during the commercial fishery in January 2004. Seawater temperature, and depth data were collected with a calibrated trawl-mounted microbathythermograph. The second area, within Unimak Pass and the adjacent southeastern Bering Sea, was sampled during the January, February, and March 2003 AFSC Pacific cod pot study. Growth was determined by using the cod length- and geographic area-stratified otolith collections from the 2003 AFSC area wide surveys in the Gulf of Alaska and eastern Bering Sea (Table 1). Otoliths were aged by using the methods developed during 2002 for Pacific cod (Roberson et al., 2005; Thompson and Dorn, 2005) by personnel of the AFSC Age and Growth Program.

In both the Gulf of Alaska and Bering Sea collections, ovaries were removed and placed in individu-

ally labeled cloth bags and stored in a solution of 4% buffered formaldehyde. The ovary samples for the Gulf of Alaska consisted of whole ovaries and samples from the Bering Sea area were excised ovarian cross-sections (minimum of two 16.4-mm-diameter samples per individual). For each whole ovary sample, a section was taken from the posterior region of the ovary. From 50 of these specimens, two additional sections were taken from the anterior and median regions.

Oocytes within each ovary were classified into five histological stages based on criteria used by Hunter et al. (1992) and Stark and Somerton (2002). The five stages were perinucleus, cortical alveoli, vitellogenesis, hydrated oocytes, and postovulatory follicles. Individual ovaries were classified according to the most advanced stage of oocytes present in the histological sections. Individuals classified as spawners were those with ovaries containing either hydrated oocytes or post-ovulatory follicles. Mature individuals were defined by using two different classification criteria in order to compare results from each method. One method classified mature specimens as those with ovary stages ranging from vitellogenesis through postovulatory follicles. The other method included the additional stage of cortical alveoli ovaries in the mature category.

Ovarian development was compared across months, by tabulating the proportion of fish classified within each of the five histological stages only for females that had reached the minimum total body length (LT) at maturity, as determined by a length-at-maturity analysis. A selection of samples from the entire length range of

Table 1

Summary of data on samples collected by the National Oceanic and Atmospheric Administration Alaska Fisheries Science Center used to estimate maturity and growth of Pacific cod (*Gadus macrocephalus*). Categories include date of sample collections, location of sample collections, sources of sample collections, types and numbers (*n*) of specimen samples. The ovaries and otoliths used to estimate length- and age-at-maturity and timing of the reproductive cycle were taken from specimens collected in the Gulf of Alaska (GOA) and Bering Sea (BS). The GOA sampling was conducted during surveys extending from October 1998 to June 1999, and additional specimens were collected from a seafood processing plant (referred to as "Plant" in table) during 2004. The BS ovary and otolith specimens were collected during the 2003 Pacific cod surveys. The length data and the otoliths (of both sexes) used to estimate growth were collected during the 2003 bottom trawl surveys conducted in the GOA and BS.

Period of sample collections	Location of sample collections	Source of sample collections	No. of specimens sampled for histological examination of ovaries	No. of specimens aged
For maturity estimates				
October 1998	GOA	Survey	59	58
January 1999	GOA	Survey	107	104
April 1999	GOA	Survey	60	57
June 1999	GOA	Survey	66	48
January 2004	GOA	Plant	50	50
	GOA	Total	342	317
January 2003	BS	Survey	30	29
February 2003	BS	Survey	133	129
March 2003	BS	Survey	96	92
	BS	Total	259	250
	GOA and BS	Total	601	567
For growth estimates				
May–July 2003	GOA	Survey females		375
May–July 2003	GOA	Survey males		336
June–July 2003	BS	Survey females		676
June–July 2003	BS	Survey males		684
	GOA and BS	Total		2071

mature females allowed the investigation of the full seasonal progression of ovary development. The proportion of females in spawning condition was estimated for each month by dividing the sum of the fish classified as spawning by the sum of the fish classified as mature. The length- and age-at-maturity estimates that were chosen as representing the standard for each area were based on specimens collected during the prespawning or initial yearly spawning period, January 1999 and 2004 and February 2003. By January and February, all specimens that would mature that year had matured according to the results of seasonal sampling from this study. The data from January of 1999 and 2004 were combined to obtain length- and age-at-maturity estimates with the lowest variance. The monthly length and age composition of females in mature condition were estimated by using standard length- and age-at-maturity analysis.

Maturity as a function of length was estimated by fitting a logistic function to the maturity data with generalized linear modeling (Venables, 1997); for this procedure, S-Plus software (vers. 2000 Professional release 3, Math-

Soft Inc., Cambridge, MA) was used. The significance of between-area, between-month, and between-classification methods differences were tested by fitting the model of maturity as a function of L_T with a term distinguishing area, month, and method and by recalculating without each term. Significance of the area, month, and method terms were determined by using analysis of deviance (Venables, 1997). Length at 50% maturity was also estimated by evaluating the fitted model at 50% maturity and algebraically solving for length. The variance of $L_{T_{50}}$ was estimated for each area, month, and method by using bootstrapping (Efron and Tibshirani, 1993) based on 200 resamplings, with replacement, of the maturity and length data. Between-area, between-month, and between-method differences in $L_{T_{50}}$ were then tested with a *z*-test (Sokal, 1969). With these same procedures, maturity was described as a function of age, and spawning was estimated as a function of L_T , age, month, and ambient water temperature.

With the use of S-Plus software, length-at-age was described by the von Bertalanffy growth function, which incorporated nonlinear least-squares fitted to

L_T and age data (Venables, 1997). Between-sex and between-area differences in growth were tested by first fitting the von Bertalanffy model with a term distinguishing sex and area and again tested for the combined sexes and areas. The likelihood ratio of the two models was then determined for each category (Kimura, 1980). Significance of the likelihood ratio was tested to determine if growth differed by sex or area.

The gonadosomatic index (I_G) was calculated from the specimens sampled for maturity as the ratio of gonad weight (W_G) to body weight (W) with the gonads removed ($IG=100 W_G/W$). The body weight portion of the data included food contents for the Gulf of Alaska specimens, whereas stomachs were emptied for all 250 Bering Sea specimens that were weighed. However, weight of the stomach contents represented less than 1% of the total body weight for the Bering Sea specimens. A z -test (Sokal, 1969) was performed with S-Plus software to determine if there were between-area and between-month differences in I_G .

Results

The results provided information on the relationship between ovary growth and maturation for Pacific cod in the Gulf of Alaska and Bering Sea. The I_G data were available for 95% of the Gulf of Alaska specimens and 99% of the Bering Sea specimens sampled for maturity. For both areas, the I_G cycled according to the season (Fig. 2). The observed I_G was highest during the winter months (Jan=4.24 I_G and February=8.48 I_G), declined through the spring (March=6.37 I_G and April=3.50 I_G), and reached the lowest levels in early summer (June=1.02 I_G). Maturation of the population of oocytes to be spawned the following year occurred at a slow rate through October (1.74 I_G).

Similarly linked to the Pacific cod spawning cycle, was the development of oocytes within the ovaries (Fig. 3), which was consistent in all quadrants of each ovary. By January, over 70% of the sampled ovaries were in the vitellogenesis stage of development in preparation for spawning, in both the Gulf of Alaska and Bering Sea Pacific cod. Females that had vitellogenesis-stage oocytes during the spring were expected to develop and spawn those oocytes that year. By June, all stocks of vitellogenesis-stage oocytes had been exhausted. In the Gulf of Alaska, over half of the female Pacific cod spawned during April and June. Pacific cod spawning began during February in the Bering Sea area, and

Table 2

Length-at-maturity results based on samples of ovaries (n) collected between the late prespawning and initial spawning period for female Pacific cod (*Gadus macrocephalus*) in the Gulf of Alaska (GOA) and Bering Sea (BS) areas, by date of collection. The parameters of the logistic equation that were used to fit the data are given: B (slope of the line) and A (Y intercept), variance (the square of the standard deviation of B and A), covariance (the product of the standard deviations of B and A and the coefficient of correlation between them), length (mm) at which 50% of females were expected to reach sexual maturity (L_{T50}), and variance of L_{T50} .

Sampling statistics	Gulf of Alaska	Bering Sea
	January 1999 and 2004	February 2003
n	157	133
B	0.0222	0.0132
A	-11.1425	-7.6248
Variance (B)	2.0649	1.3807
Variance (A)	6.5528	3.2433
Covariance (B,A)	-0.0002	0.0001
L_{T50} (mm)	502.5543	579.9599
Variance (L_{T50})	212.5733	309.3380

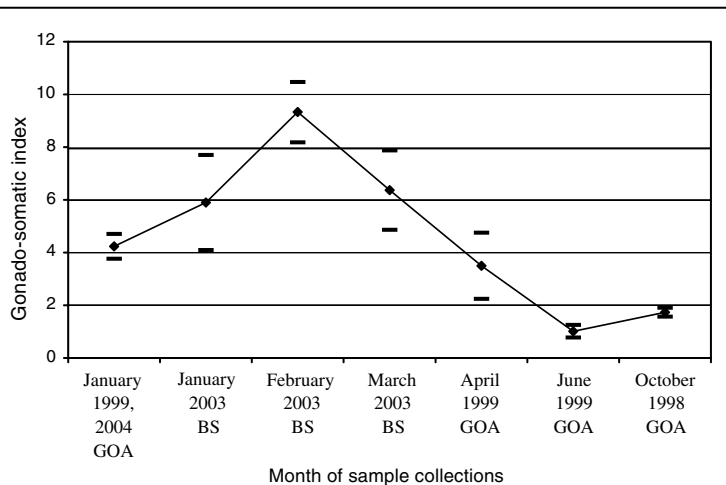


Figure 2

Mean gonadosomatic index of female Pacific cod (*Gadus macrocephalus*). Sample sites were located in the Gulf of Alaska (GOA) during January 1999 and 2004, April and June 1999, and October 1998 (total $n=327$), and the Bering Sea (BS) during January, February, and March 2003 (total $n=261$). The 95% confidence intervals are represented by bars located adjacent to each data point.

approximately 10% of the fish population participated. During October, 5% of female Pacific cod had vitellogenesis-stage ovaries, whereas 95% of Gulf of Alaska cod were in earlier stages of maturation. The likelihood of female Pacific cod spawning was significantly

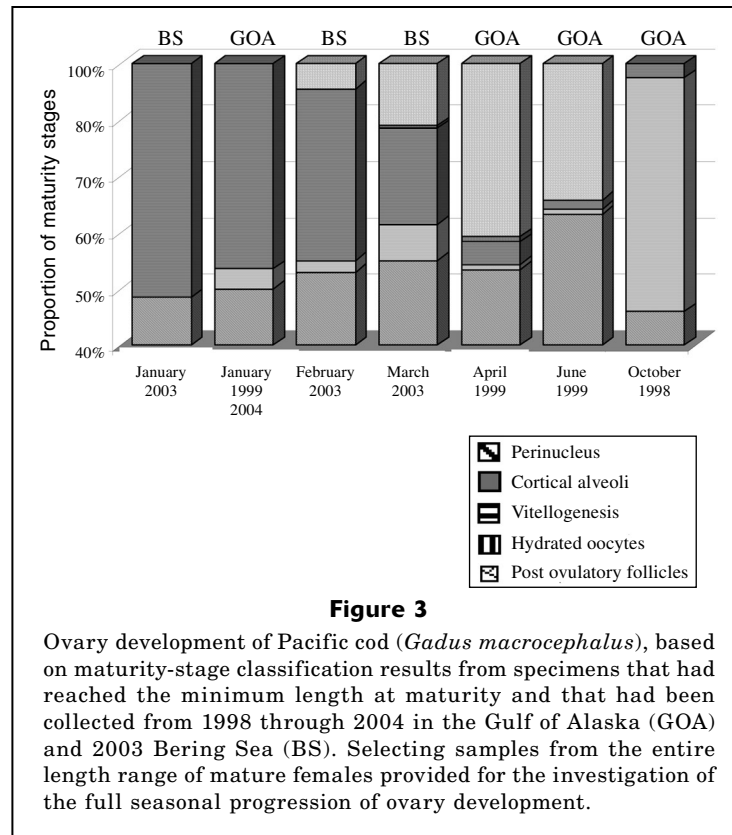


Figure 3

Ovary development of Pacific cod (*Gadus macrocephalus*), based on maturity-stage classification results from specimens that had reached the minimum length at maturity and that had been collected from 1998 through 2004 in the Gulf of Alaska (GOA) and 2003 Bering Sea (BS). Selecting samples from the entire length range of mature females provided for the investigation of the full seasonal progression of ovary development.

($P < 0.001$) associated with the time of month and not significantly associated with L_T ($P = 0.06$), age ($P = 0.06$), or ambient water temperature ($P = 0.21$). However, by April and June in the Gulf of Alaska, L_T was slightly ($P = 0.01$) associated with the likelihood of spawning. Spawners ranged in L_T from 420 mm to 1060 mm. The age-at-spawning ranged from 4 year olds up to the oldest females taken, at 10 years of age. Spawning female Pacific cod were found in all areas, including bays and offshore gullies, sampled during April and June 1999 in the Gulf of Alaska. Ambient seawater temperatures were similar in 1999 during January and April (2.21°C to 6.10°C), and increased only slightly in June (3.7°C to 7.01°C).

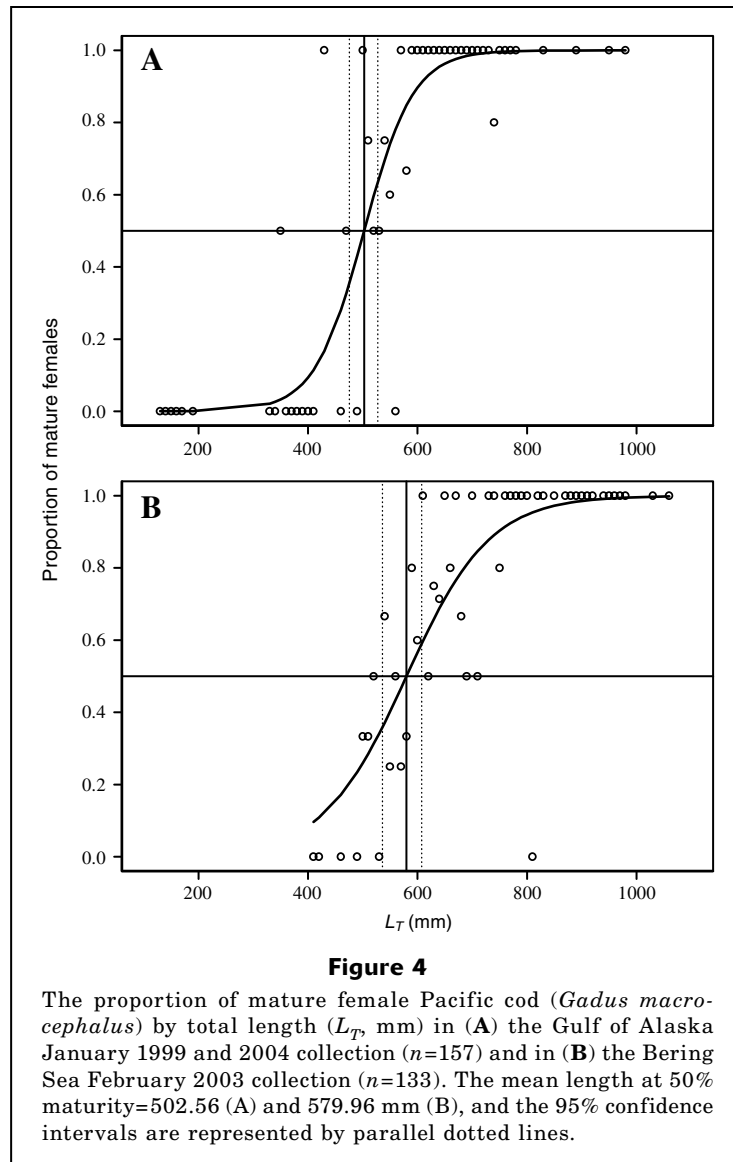
The estimates of L_{T50} did not differ significantly between the two histology-based methods used to define mature females, except for a slight difference ($P = 0.02$) with January Gulf of Alaska estimates, which used the combined data from 1999 and 2004. The January L_{T50} estimates were 503 mm based on a mature classification that did not include cortical alveoli (CA) stage ovaries, and 437 mm when CA-stage ovaries were included as part of the mature category.

However, there was a significant area difference ($P < 0.001$, Fig. 4, Table 2) between the January 1999, 2004 Gulf of Alaska L_{T50} (503 mm) and the February 2003 Bering Sea L_{T50} (580 mm). In both areas, the estimates of length-at-maturity did not differ significantly between months, with the exception of a slight differ-

ence ($P = 0.03$) between January (496 mm) and June (601 mm) 1999. In the present study the expected L_T range of mature female P. cod was adequately assessed from a sample L_T distribution that extended to 130 mm L_T in the Gulf of Alaska and 350 mm L_T in the Bering Sea (Table 3) and on the documentation of only a single specimen smaller than 420 mm L_T .

The estimated age at which 50% of the females reached maturity (A_{50}) did not differ significantly between the two histological methods for assigning maturity. With either method, the A_{50} differed slightly ($P = 0.02$) between the Gulf of Alaska (4.4 years) and Bering Sea (4.9 years, Table 4, Fig. 5). However, within each area, the estimated ages at maturity did not differ significantly between months ($P > 0.16$). Similarly, the January 1999 and 2004 Gulf of Alaska female cod ages at maturity did not differ significantly ($P = 0.19$).

The otoliths taken during the 2003 AFSC bottom trawl surveys of the Gulf of Alaska ($n = 711$) and eastern Bering Sea ($n = 1360$) provide the largest and most comprehensive collection of age data available for female and male Pacific cod. The otolith specimens were selected by region, sex, and L_T . Pacific cod had wide variations in age at length (Fig. 6, Table 5). Based on these collections, the von Bertalanffy growth function differed significantly ($P < 0.001$) between the Gulf of Alaska and Bering Sea for both males and females (Table 5). Female Pacific cod length at age was smaller in the Gulf of Alaska than in the Bering Sea. The Gulf



of Alaska female Pacific cod growth differed significantly ($P < 0.001$) from the growth of males. The rate of growth declined more with age for males than for females in the Gulf of Alaska (Fig. 6). However, in the Bering Sea, male growth was nearly as rapid ($P = 0.015$) as that of females. Males were estimated to reach a slightly smaller maximum theoretical L_∞ of 1044 mm in the Gulf of Alaska than in the Bering Sea (1101 mm).

Discussion

This study provides the most extensive and representative estimates of female Pacific cod length- and age-at-maturity and growth available. This is the first Pacific cod study to rely on histological methods to assess ovary maturity, and the first to make temporal comparisons of maturity. It is the first northeast Pacific Ocean study

to assess Pacific cod age-at-maturity. Before this study, managers of the Alaska Pacific cod fishery (Thompson and Dorn, 2005; Thompson et al., 2005) used a female L_{T50} estimate of 670 mm from macroscopic maturity classifications made by commercial fishery observers on specimens collected after March in 1993 and 1994. However, the macroscopic maturity classification method can introduce sampling bias and misclassifications. In contrast, in this study, it was determined that the most representative method for estimating L_{T50} relied on making histological maturity assessments of large numbers of ovary samples from a wide L_T range of specimens collected before the late spawning period.

The results from this study are similar to the results from studies conducted in other areas. The estimated female Pacific cod A_{50} differed only slightly between the Gulf of Alaska and Bering Sea study areas and were similar to the ages estimated for Sea

Table 3

Total length (mm) and age (years) composition of female Pacific cod (*Gadus macrocephalus*) specimens collected in the Gulf of Alaska (GOA) during January 1999 and 2004 and in the Bering Sea (BS) during February 2003 to estimate the length and age at which 50% reached sexual maturity. The objective was to collect a minimum of five specimens per length class, subject to availability. n = number of fish in the sample.

Length (mm)	GOA n	BS n	Length (mm)	GOA n	BS n	Age (years)	GOA n	BS n
130	1		660	4	5	1	6	
140	1		670	4	2	2	3	
150	1		680	8	6	3	20	3
160	1		690	5	2	4	16	16
170	1		700	4	2	5	32	32
190	1		710	6	6	6	42	22
330	1		720	8		7	26	30
340	1		730	8	1	8	6	18
350	2		740	5	5	9	2	6
360	3		750	2	5	10	1	2
370	5		760	5	3			
380	7		770	2	1			
390	3		780	1	2			
400	3		790		3			
410	4	1	800		4			
420		2	810		1			
430	1		820		3			
460	1	3	830	1	2			
470	2		850		1			
490	1	1	870		1			
500	1	3	880		3			
510	4	3	890	1	2			
520	4	2	900		1			
530	4	1	910		1			
540	4	3	920		1			
550	5	4	940		1			
560	1	2	950	1	1			
570	2	4	960		1			
580	3	3	970		1			
590	3	5	980	1	1			
600	4	5	1030		1			
610	4	2	1060		1			
620	2	4						
630	5	2						
640	4	3						
650	1	4						

of Okhotsk (5 years of age, Rovnina et al., 1997) and Sea of Japan (4 years of age, Hattori et al., 1992) female Pacific cod. Results from previous studies support the between-area differences in female Pacific cod length-at-maturity found during the present study. Like Gulf of Alaska Pacific cod, female Pacific cod from Canadian waters were estimated to mature at a smaller L_{T50} (median 450 mm during the 1970s and 550 mm during the 1960s; Welch and Foucher, 1988) than Bering Sea Pacific cod. The Bering Sea estimate of L_{T50} was within the range estimated for

the Sea of Okhotsk female Pacific cod (550 mm L_T to 600 mm L_T ; Rovnina et al., 1997). In the present study, no significant differences were found in female Pacific cod L_{T50} or A_{50} for any of the months sampled, within either the Gulf of Alaska or Bering Sea areas. The temporal agreement for female Pacific cod A_{50} and L_{T50} estimates indicates they are reliable. Results were also similar between the two histology-based methods of classifying mature female Pacific cod, indicating that either method could be used to define A_{50} or L_{T50} .

Table 4

Age-at-maturity results based on ovary samples (n) collected between the late prespawning and initial spawning periods for female Pacific cod (*Gadus macrocephalus*) in the Gulf of Alaska (GOA) and Bering Sea (BS) areas, by date of collection. The parameters of the logistic equation that were used to fit the data are given: B (slope of the line) and A (Y intercept), variance (the square of the standard deviation of B and A), covariance (the product of the standard deviations of B and A and the coefficient of correlation between them), age (years) at which 50% of females were expected to reach sexual maturity (A_{50}), and variance of A_{50} .

Sampling statistics	Gulf of Alaska	Bering Sea
	January 2003 and 2004	February 2003
n	154	129
B	1.9632	0.9654
A	-8.5395	-4.7143
Variance (B)	0.0145	0.0065
Variance (A)	2.1246	1.3680
Covariance (B,A)	0.0059	0.0013
A_{50}	4.3499	4.8832
Variance (A_{50})	0.0224	0.0663

Spawning participants sampled during this study, included female Pacific cod as small as 420 mm L_T in the Gulf of Alaska and 460 mm in the Bering Sea area. In comparison, cod (*Gadus morhua*) from the northwest Atlantic Ocean initiated spawning in 1995 at 400 mm—a decline from 500 mm in 1992 (Saborido-Rey and Junquera, 1998).

Spawning is an annual occurrence for female Pacific cod according to the results of seasonal ovary development, the I_G cycle, and the wide range in age and body length composition of the spawning population each month. This conclusion was consistent with that from Teshima's (1985) study, which found that the Bering Sea Pacific cod gonadosomatic index increased in November and December because of maturation and that spawning was not expected to occur until the following year. Similarly, Atlantic cod individuals have an annual reproductive cycle (Norberg et al., 2004) and spawn despite being raised in captivity under conditions of starvation (Kjesbu et al., 1991).

Based on results from this study, the spawning activity for female Pacific cod is believed to begin during late winter and peak during the spring. This estimated period of peak spawning, based on results summarizing ovarian maturities by month of collection, is validated by larval abundance estimates from the Gulf of Alaska and Bering Sea ichthyoplankton surveys conducted since 1980 by the AFSC (Matarese et al., 2003). Similarly, the Sea of Okhotsk population is estimated to have a peak spawning period that includes the months of March and May, based on a 1995 study (Rovnina et al., 1997). Spawning probably ends in early summer in the Gulf of Alaska, as indicated by

the lack of any specimens in June with vitellogenesis-stage ovaries.

The likelihood of female Pacific cod spawning was strongly associated ($P < 0.001$) with the time of month, and later in the spawning season, spawning was associated ($P = 0.01$) with LT . There were no associations with spawning and age, or ambient water temperature; consequently these factors probably do not regulate the timing of spawning for Pacific cod. Similarly, seawater temperature was not the most important environmental cue regulating the maturation and spawning of Atlantic cod and other commercially cultured Atlantic Ocean fish species, including rainbow trout (*Oncorhynchus mykiss*), Atlantic halibut (*Hippoglossus hippoglossus*) and sole (*Solea solea*) (Norberg et al., 2004). For these cultured Atlantic species, photoperiod is the most important regulator of the reproductive cycle. Pacific cod maturation and spawning was significantly associated with time of month, as determined by this study, which would indicate that photoperiod may regulate the reproductive cycle in this species. Photoperiod should be similar for both the Gulf of Alaska and Bering Sea study areas sampled by this survey, given their similar latitudes (Fig. 1), and could account for the similarity in the timing of spawning within the Gulf of Alaska and Bering Sea waters found during this study and during the ichthyoplankton surveys.

Regardless of where spawning occurs, the reproductive effort by the fish represents a substantial investment, based on ovary weight that represents up to 30% of the total female Pacific cod body weight and Atlantic cod body weight (Lambert and Dutil, 2000). Pacific cod have among the highest fecundities of any tele-

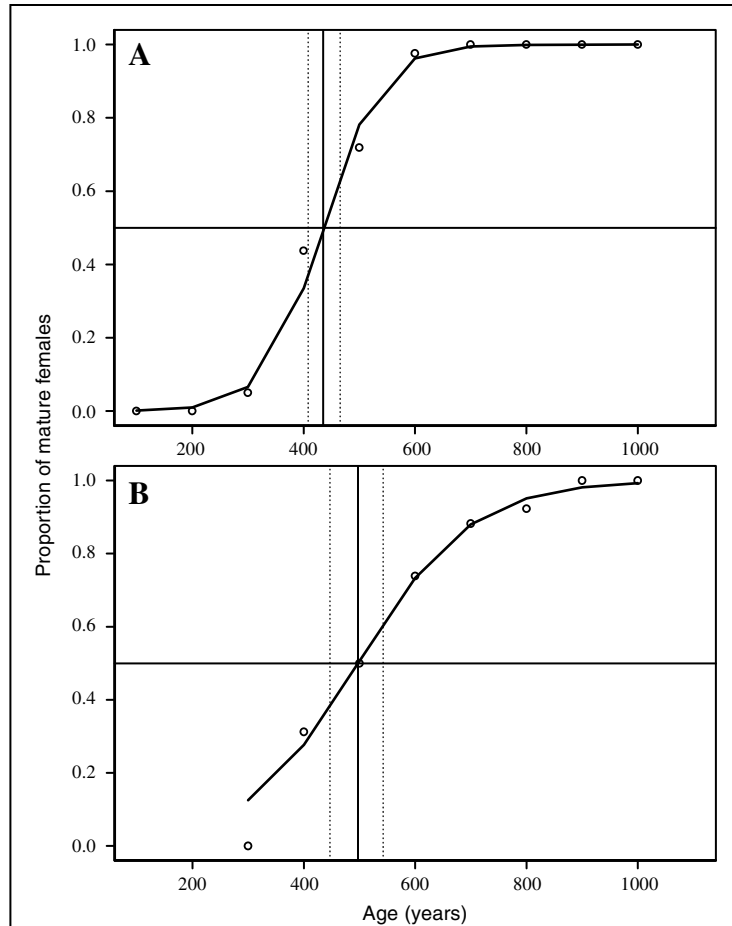


Figure 5

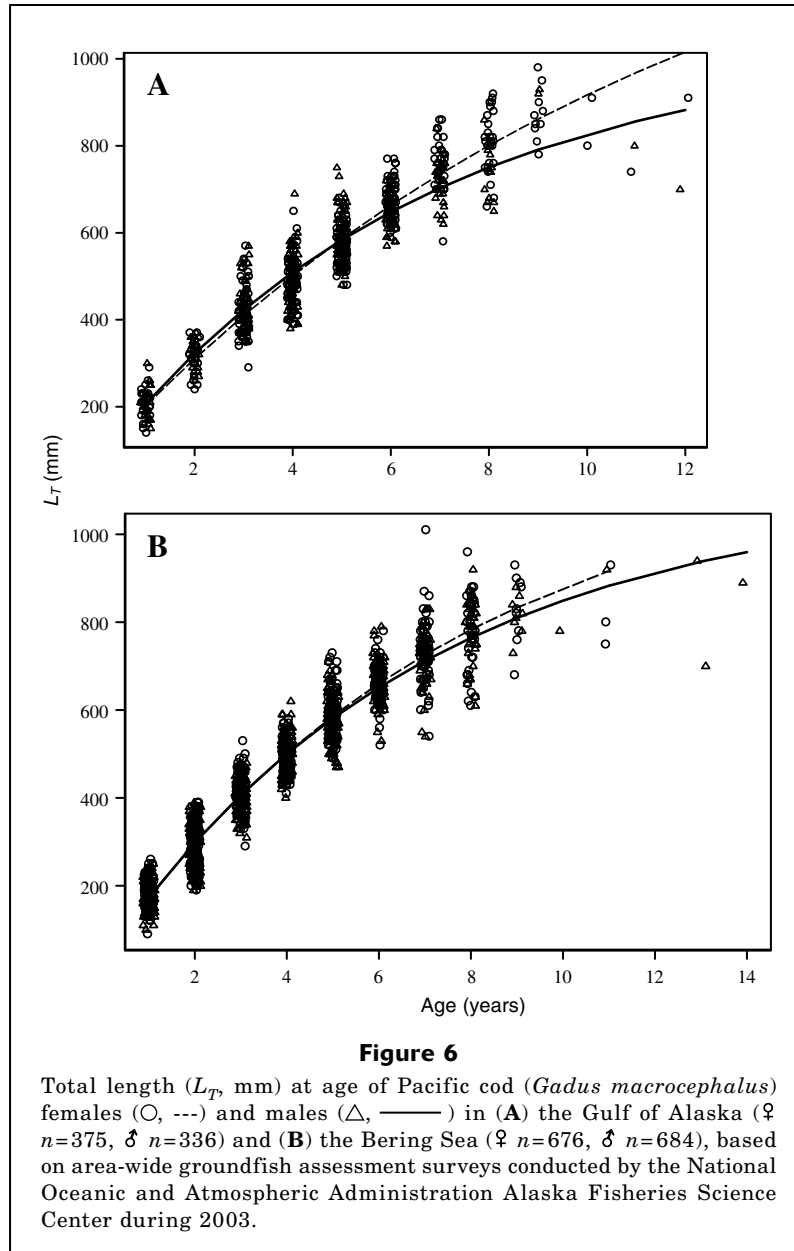
The proportion of mature female Pacific cod (*Gadus macrocephalus*) by age in (A) the Gulf of Alaska, based on the January 1999 and 2004 ($n=154$) collection and in (B) the Bering Sea, based on the February 2003 ($n=129$) collection. The mean age at 50% maturity=4.4 (A) and 4.9 years (B), and the 95% confidence intervals are represented by the parallel dotted lines.

ost (Waiwood, 1982; Foucher and Tyler, 1990) and can produce up to 5.7 million ova each year. However, it appears that the metabolic costs of spawning do not diminish female Pacific cod growth.

Female Pacific cod growth does not significantly decline upon reaching A_{50} in either the Gulf of Alaska or Bering Sea. Males in the Gulf of Alaska area reach a smaller maximum length than females. Similarly, in the eastern Sea of Okhotsk, male Pacific cod reach a smaller total length than females (Rovnina et al., 1997). In contrast male Pacific cod in the Bering Sea area reach a maximum length similar to that of females, and female Pacific cod grow significantly faster in the Bering Sea than in the Gulf of Alaska. The growth results support the maturity-at-length results in the present study that indicate a much larger L_{T50} for the Bering Sea females. Longevity, however, is similar for Gulf of Alaska and Bering Sea Pacific cod and does not differ between sexes. Pacific cod growth probably

occurs primarily during the summer and fall, as does growth in Atlantic cod (Norberg et al., 2004), and not during the winter through early summer months, the period used by the present study to assess length- and age-at-maturity.

With the estimates of A_{50} and L_{T50} from this study, the spawning stock biomass of female Pacific cod for the Gulf of Alaska and eastern Bering Sea increased from the 2005 estimate of 300×10^3 t that was based on a previous study, to an 2006 estimate of 500×10^3 t (Thompson and Dorn, 2005; Thompson et al., 2005). The spawning biomass estimates are of critical importance for stock management models from which are determined the allowable commercial catch quotas of Pacific cod in the northeast Pacific Ocean and Bering Sea (Thompson and Dorn, 2005; Thompson et al., 2005). The increased spawning stock biomass estimates of female Pacific cod resulting from this study support the establishment of higher over-fishing limits for Pacific



cod than would have otherwise occurred. As a result, the revised 2006 management plan increased the estimated spawning stock biomass by 80% in the Gulf of Alaska and by 10% in the eastern Bering Sea and Aleutian Islands, over the 2005 plan estimates. These increases offset declines in the estimated biomass of Pacific cod over 2 years of age for the Gulf of Alaska (4%) and for the eastern Bering Sea and Aleutian Islands (19%) during the same period. Consequently, the recommended over-fishing limit increased 51% in the Gulf of Alaska and declined only 18% in the Bering Sea and Aleutian Islands.

Although temporal stability was found for Pacific cod A_{50} and L_{T50} estimates in the present study, maturity

assessments should be conducted on a periodic basis in the future to ensure that managers continue to receive representative estimates of Pacific cod A_{50} and L_{50} and timing of spawning, which are essential for rational stock management. Maturity assessments would be particularly important during periods of significant change in climate or habitat.

Acknowledgments

Thanks to the following Alaska Fisheries Science Center personnel for their contributions: D. Somerton, G. Stauffer, R. Nelson, A. Hollowed, D. Nichol,

Table 5

Length-at-age described by the von Bertalanffy growth equation for male and female Pacific cod (*Gadus macrocephalus*) in the Gulf of Alaska (GOA) and Bering Sea (BS). Also provided are sample size (n) and parameters L_{∞} (length at maximum age in mm), k (estimated growth increment), t_0 (theoretical age when fish length is 0). Numbers in parentheses represent the number of fish in the sample.

	Gulf of Alaska		Bering Sea	
	Males	Females	Males	Females
n	347	389	684	676
L_{∞} (mm)	1043.7900	1567.2000	1100.630	1203.9400
var (L_{∞})	3564.9736	24716.8707	1281.3393	2641.7441
k	0.1498	0.0825	0.1449	0.1277
var (k)	0.0003	0.0002	0.0001	0.0001
t_0	-0.4670	-0.6712	-0.1814	-0.2233
var (t_0)	0.0182	0.0246	0.0032	0.0042
cov (L_{∞}, k)	-0.9892	-2.0091	-0.3052	-0.4808
cov (L_{∞}, t_0)	-6.1381	-20.3573	-1.4960	-2.5903
cov (k, t_0)	0.0020	0.0018	0.0004	0.0005

E. Acuna, R. MacIntosh, C. Armistead, J. Haaga, M. Wilkins, S. Neidetcher, L. Logerwell, P. Munro, C. Johnston, M. Nelson, G. Duker, and J. Lee. Thanks to the following Alaska Department of Fish and Game staff for sample collections: J. Blackburn, D. Urban, D. Pengilly, K. Phillips, T. Dinnocenzo, I. MacIntosh, M. Ruccio, D. Jackson, the Captain R. Kutchick, and crew of the RV *Resolution*. K. MacIntosh from the Alaska Groundfish Databank collected the plant samples.

Literature cited

- Efron, B., and R. J. Tibshirani.
1993. An introduction to the bootstrap, 436 p. Chapman and Hall, New York, NY.
- Foucher, R. P., and A. V. Tyler
1990. Estimation of the fecundity of Pacific cod *Gadus macrocephalus*. Can. Man. Rep. Fish. Aquat. Sci. 2088, 49 p.
- Hart, L.
1973. Pacific fishes of Canada. Fish. Res. Board Can. Bull. 180,740 p.
- Hattori, T., Y. Kasurai, and K. Shimazaki.
1992. Maturation and reproductive-cycle of female Pacific cod in waters adjacent to the southern coast of Hokkaido, Japan. Nihon. Suisan. Gakkai-Shi 58:2245-2252.
- Hunter, J. R., B. J. Macewicz, N. C. H. Lo, and C. A. Kimbrell.
1992. Fecundity, spawning, and maturity of female Dover sole, *Microstomus pacificus*, with an evaluation of assumptions and precision. Fish. Bull. 90:101-128.
- Kimura, D. K.
1980. Likelihood methods for the von Bertalanffy growth curve. Fish. Bull. 77:765-776.
- Kjesbu, O. S., J. Klungsoyr, H. Kryvi, P. R. Witthames, and M. Greer-Walker.
1991. Fecundity, atresia, and egg size of captive Atlantic cod (*Gadus morhua*) in relation to proximate body composition. Can. J. Fish. Aquat. Sci. 48:2333-2343.
- Lambert, Y., and J. D. Dutil.
2000. Energetic consequences of reproduction in Atlantic cod *Gadus morhua* in relation to spawning level of somatic energy reserves. Can. J. Fish. Aquat. Sci. 57:815-825.
- Matarese, A. C., D. M. Blood, S. J. Picquelle, and J. L. Benson.
2003. Atlas of abundance and distribution patterns of ichthyoplankton from the Northeast Pacific Ocean and Bering Sea ecosystems based on research conducted by the Alaska Fisheries Science Center 1972-1996. U.S. Dep. Commer. NOAA Prof. Pap. NMFS 1, 281 p.
- Norberg, B., C. L. Brown, O. Halldorsson, K. Stensland, and B. T. Bjornsson.
2004. Photoperiod regulates the timing of sexual maturation, spawning, sex steroid and thyroid hormone profiles in the Atlantic cod *Gadus morhua*. Aquaculture 229:451-467.
- Roberson, N. E., D. K. Kimura, D. R. Gunderson, and A. M. Shimada.
2005. Indirect validation of the age-reading method for Pacific cod (*Gadus macrocephalus*) using otoliths from marked and recaptured fish. Fish. Bull. 103:153-160.
- Rovnina, O. A., N. V. Klovach, A. I. Glubokov, and A. P. Selyutin.
1997. On the biology of Pacific cod *Gadus macrocephalus* in the eastern part of the Sea of Okhotsk. J. Ichthyol. 37:21-26. Translated from Russian [1997 Voprosy Ikhtologii 37:27-32] by Interperiodica Publishing, Russia.
- Saborido-Rey, F., and S. Junquera.
1998. Histological assessment of variations in sexual maturity of cod (*Gadus morhua* L.) at the Flemish Cap (north-west Atlantic). ICES J. Mar. Sci. 55:515-521.
- Sokal, R. R.
1969. Biometry, 776 p. W.H. Freeman and Company, San Francisco, CA.
- Stark, J. W., and D. A. Somerton.
2002. Maturation, spawning and growth of rock soles off Kodiak Island in the Gulf of Alaska. J. Fish Biol. 61:417-431.
- Teshima, K.
1985. Maturation of Pacific cod in the eastern Bering Sea. Bull. Jap. Soc. Sci. Fish. 51:21-31.

- Thompson, G. G., and M. W. Dorn.
2005. Stock assessment and fishery evaluation: Bering Sea and Aleutian Island cod, 90 p. North Pacific Fishery Management Council. Anchorage, AK.
- Thompson, G. G., H. H. Zenger, and M. W. Dorn.
2005. Stock assessment and fishery evaluation: Gulf of Alaska Cod, 112 p. North Pacific Fishery Management Council. Anchorage, AK.
- Venables, W. N.
1997. Modern applied statistics with S-Plus, 548 p. Springer-Verlag, New York, NY.
- Waiwood, K. G.
1982. Growth history and reproduction in Atlantic cod (*Gadus morhua*). In Proceedings of the international symposium on reproductive physiology of fish (C. J. J. Richter, and H. J. Th. Goos, eds.), 256 p. Pudoc Press, Wageningen, The Netherlands.
- Welch, D. W., and R. P. Foucher.
1988. A maximum-likelihood methodology for estimating length-at-maturity with application to Pacific cod (*Gadus macrocephalus*) population dynamics. Can. J. Fish. Aquat. Sci. 45(2):333-343.

Corrigendum

Fishery Bulletin 105(3), p. 404.

Stark, James W.

Geographic and seasonal variations in maturation and growth of female Pacific cod (*Gadus macrocephalus*) in the Gulf of Alaska and Bering Sea

Page 404. The x-axis scale in Figure 5 should read as follows:

