Reproductive biology, spawning season, and growth of female rex sole (*Glyptocephalus zachirus*) in the Gulf of Alaska

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Abstract—Rex sole (*Glyptocephalus zachirus*) have a wide distribution throughout the North Pacific, ranging from central Baja California to the western Bering Sea. Although rex sole are an important species in the commercial trawl fisheries off the U.S. West Coast, knowledge of their reproductive biology is limited to one study off the Oregon coast where ovaries were analyzed with gross anatomical methods. This study was initiated to determine reproductive and growth parameters specific to rex sole in the Gulf of Alaska (GOA) stock. Female rex sole (n=594) ranging in total length from 166 to 552 mm were collected opportunistically around Kodiak Island, Alaska, from February 2000 to October 2001. All ovaries were analyzed by using standard histological criteria to determine the maturity stage. Year-round sampling of rex sole ovaries confirmed that rex sole are batch spawners and have a protracted spawning season in the GOA that lasts at least eight months, from October to May; the duration of the spawning season and the months of spawning activity are different from those previously estimated.

Female rex sole in the GOA had an estimated length at 50% maturity (ML_{50}) of 352 mm, which is greater than the previously estimated ML_{50} at southern latitudes. The maximum age of collected female rex sole was 29 years, and the estimated age at 50% maturity (MA_{50}) in the GOA was 5.1 years. The von Bertalanffy growth model for rex sole in the GOA was significantly different from the previously estimated model for rex sole off the Oregon coast. This study indicated that there are higher growth rates for rex sole in the GOA than off the Oregon coast and that there are differences in length at maturity and similarity in age at maturity between the two regions.

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Rex sole (*Glyptocephalus zachirus*) have a wide distribution throughout the North Pacific, ranging from central Baja California to the western Bering Sea (Mecklenburg et al., 2002). The rex sole population is made up of several stocks that are managed as four separate units: the U.S. West Coast stock which includes waters off the coasts of California, Oregon, and Washington; the British Columbia stock which is managed separately by the Canadian government; the Gulf of Alaska (GOA) stock; and the Bering Sea stock (Turnock[1]). The U.S. West Coast stock of rex sole provided a steady and stable commercial fishery in California between 1970 and 1989, but landings began to decline in the 1990s (Quirollo and Dewees[2]). Rex sole are managed as part of the "other flatfish" category for both the West Coast stock (Quirollo and Dewees[2]) and the Bering Sea stock (Spencer et al.[3]).

Throughout its range, the largest commercial harvest of rex sole occurs in the GOA where rex sole are one of the major commercial flatfish species. Since 1988, the commercial trawl fishery for flatfish in the GOA has concentrated in the central Gulf on the continental shelf and slope east of Kodiak Island (DiCosimo and Kimball[4]). Development of a management plan for the rex sole fishery in the GOA has undergone several phases. Prior to 1990, all flatfishes in the GOA with the exception of Pacific halibut (*Hippoglossus stenolepis*) were managed as one assemblage. In 1990, four flatfish categories were created for stock assessment: shallow-water complex, deep-water complex (rex sole included), flathead sole (*Hippoglossoides elassodon*), and arrowtooth flounder (*Atheresthes stomias*). In 1993, rex sole were removed from the deep-water complex and managed as a separate species.

In 2003, biomass estimates for rex sole in the Gulf of Alaska totaled 99,950 metric tons (t), and the acceptable biological catch (ABC) was 9466 t (Turnock et al.[5]). Annual commercial landings for GOA rex sole averaged about 3000 t during 1999–2003, approximately 35% of the ABC (Turnock et al.[5]). The low harvest level may be due, in part, to constraints placed on

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[1] Turnock, B. J. 2004. Personal commun. Alaska Fisheries Science Center, National Marine Fisheries Service, 7600 Sand Point Way NE, Seattle, WA 98115.

[2] Quirollo, L. F., and C. M. Dewees. 2001. California's living marine resources: a status report. California Department of Fish and Game. Website: http://www.dfg.ca.gov/mrd/status/rex_sole.pdf [accessed on 9 September 2004].

[3] Spencer, P. D., G. E. Walters, and T. K. Wilderbuer. 2001. Stock assessment and fishery evaluation: Bering Sea other flatfish. Website: http://www.afsc.noaa.gov/refm/docs/2001/BSoflats.pdf [accessed on 13 September 2004].

[4] DiCosimo, J., and N. Kimball. 2001. Groundfish of the Gulf of Alaska: A species profile. North Pacific Fisheries Management Council Report. Website: http://www.fakr.noaa.gov/npfmc/reports/goaspecies2001.pdf [accessed on 3 March 2003].

[5] Turnock, B. J., T. K. Wilderbuer, and E. S. Brown. 2003. Stock assessment and fishery evaluation: Gulf of Alaska flatfish. Website: http://www.afsc.noaa.gov/refm/docs/2003/GOAflats.pdf [accessed on 10 September 2004].

the trawl flatfish fishery once the allowed limit of Pacific halibut bycatch is captured (DiCosimo and Kimball[4]).

The life history, reproductive biology, and growth of rex sole were investigated off the Oregon coast from 1969 to 1973 (Hosie and Horton, 1977). Despite the wide geographic range of rex sole, no investigations have occurred elsewhere. Although rex sole in the GOA are managed as a single species unit with species-specific assessments of biomass and ABC estimates, there is no information on length or age at maturity to incorporate into analytical stock assessments. Thus, there is a substantial need for obtaining information on the reproductive biology of rex sole in the GOA for the purpose of stock-specific assessment and management.

To clarify the seasonal maturation dynamics and reproductive biology of female rex sole in the GOA, fish were collected year-round and their ovaries were analyzed by using standard histological techniques. To date, there have been no histological investigations on rex sole maturity (Castillo, 1995). Specific goals of this investigation were to determine the spawning season, length at first maturity, length at 50% maturity (ML_{50}), age at first maturity, and age at 50% maturity (MA_{50}). Additionally, inasmuch as possible, reproductive parameters and growth were compared between female rex sole in the GOA with those off the Oregon coast (data from Hosie and Horton, 1977). Reproductive parameters determined in this study will aid the development of a species-specific assessment of target fishing mortality rates and mature female biomass, yielding a more accurate management model for the GOA stock of rex sole.

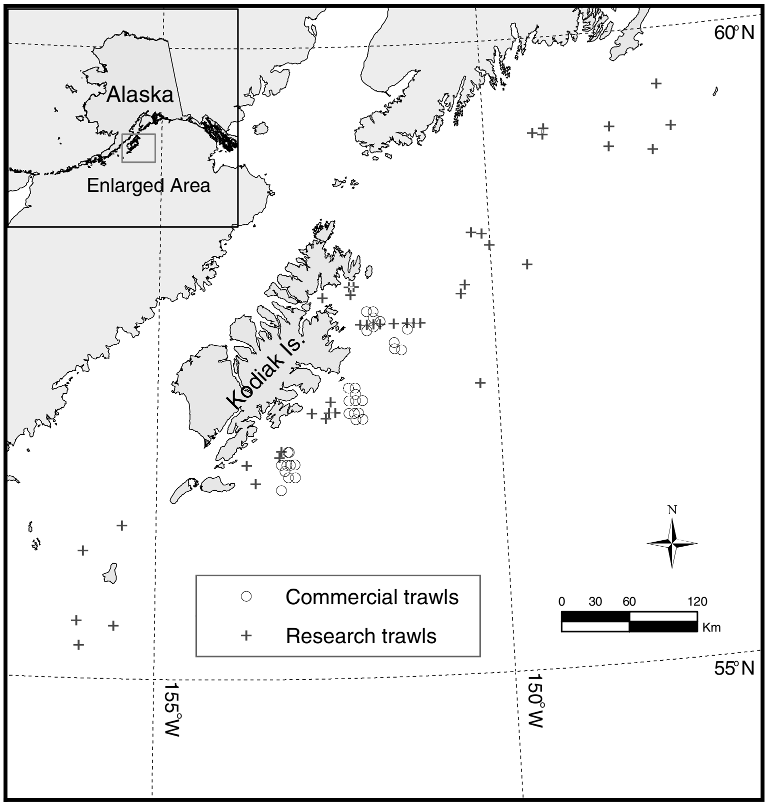

Figure 1

Collections of female rex sole (*Glyptocephalus zachirus*) in the Gulf of Alaska were concentrated around Kodiak Island, Alaska. Samples were obtained from the commercial trawl fishery (denoted by open circles) and from research survey trawls (denoted by crosses).

Materials and methods

Collections

Rex sole were collected from 14 February 2000 to 21 October 2001 in the central GOA (from 55°30′N, 156°00′W to 59°50′N, 147°15′W; Fig. 1). Approximately half (52%) of the samples were collected at fish processing plants in Kodiak, Alaska. The shore-side sampling data were dependent on the timing of the fishery, but allowed for the annual cycle of sexual maturation to be monitored. Shore-side sampling occurred in January, February, April, May, October, November, and December, and samples were obtained from boats that captured rex sole as bycatch while fishing for other species. Although there is no inherent biological difference in rex sole collected by commercial or research trawl, typically samples from the commercial fishery exclude young fish that are below the minimum landing size or escape through the meshes. However, because of the close proximity of the fishing grounds to the town of Kodiak, catches were not sorted at sea and very small rex sole (minimum total length [TL]=172 mm) were brought back to the processing plants where they were obtained for this study. The remaining 48% of samples were collected during research surveys in February, March, June, and July by the National Marine Fisheries Service (NMFS) and the University of Alaska Fairbanks with smaller-meshed trawls in the same waters fished by the commercial fishery.

Samples were stratified by length, so that up to five females per 1-cm length group were obtained each month. For each female, total length (to the nearest mm) and weight (to the nearest 0.1 gram) were measured, both sagittal otoliths were removed, and ovarian maturity was macroscopically staged. Each ovary was removed and weighed separately (to the nearest 0.1 gram). Ovaries were preserved in 10% buffered formalin for 2 months and then transferred to 70% ethanol. All ovaries collected at sea were weighed only after preservation; ovaries collected at processing plants were weighed both when fresh and after preservation.

Sagittal otoliths were removed from each fish, stored in a glycerol and thymol solution, and most (n=557)

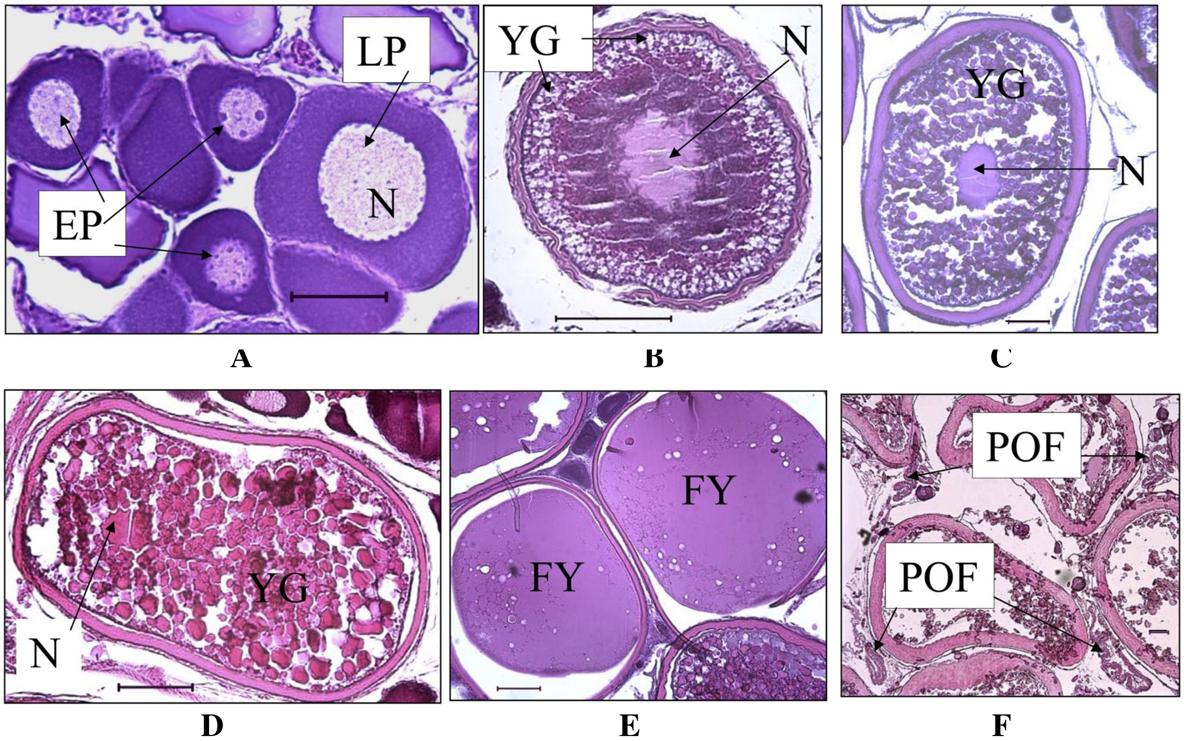

Figure 2

Photomicrographs of histological cross-sections of rex sole (*Glyptocephalus zachirus*) ovaries: (**A**) early perinuclear (EP) oocytes and late perinuclear [EP] oocytes, with a large central nucleus (N), that have not begun vitellogenesis; (**B**) early yolked oocyte beginning vitellogenesis with yolk globules (YG) at periphery of oocyte; (**C**) advanced yolked oocyte; (**D**) migratory-nucleus oocyte; (**E**) hydrated oocytes with fused yolk (FY); (**F**) postovulatory follicles (POFs). Each photomicrograph has a scale bar equal to 0.1 mm.

were analyzed for age determination. The left otolith, or blind-side otolith, was read because it is thicker along the proximal-distal axis, thereby allowing the annuli to be less compressed and easier to differentiate when counted from the core to the otolith edge along the sulcus (Anderl[6]). Otoliths were processed with standard break-and-burn techniques (Beamish and Chilton, 1982). Two experienced readers each read 117 otoliths and had initial agreement of 67%. The magnitude of the initial discrepancies within an age-group ranged from −2 to +3 years for females from age 2 to 18 years. All discrepancies of age estimates were resolved between readers through combined analysis. Once all discrepancies were resolved, the remaining otoliths were analyzed.

Histological analysis

Tissue from the middle portion of the right (ocular-side) ovary was embedded in paraffin Paraplast (McCormick Scientific, St. Louis, Missouri). Serial sections (5–8 microns thick) were prepared and stained with Harris hematoxylin (Sigma Aldrich, St. Louis, MO) followed by eosin counterstain (Sigma Aldrich, St. Louis, MO) (H&E). Each ovary section was examined for the presence or absence of the following oocyte stages (see Fig. 2): oocytes that had not begun vitellogenesis (early perinuclear [EP] and late perinuclear [LP]); oocytes in the first vitellogenic stages (early yolk [EY]); advanced yolked oocytes (AY); oocytes with a migratory-nucleus (MN); unovulated hydrated oocytes (HY); ovulated hydrated oocytes (ova); and postovulatory follicles (POF). During the initial stage of oocyte degeneration (known as alpha [α] atresia) the entire oocyte is resorbed by the hypertrophying granulosa cells of the follicle (Lasker, 1985). Presence of alpha atresia was noted for all histological stages of oocyte development, and the degree of alpha atresia in yolked oocytes was classified as either greater or less than 50% of all yolked oocytes in the ovary. The thickness of the ovarian wall was measured at five or more locations with an ocular micrometer.

Histological classification

Based on histological analysis, spawning categories were created for females (Table 1) according to the clas-

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[6] Anderl, D. 2003. Personal commun. Alaska Fisheries Science Center, National Marine Fisheries Service, 7600 Sand Point Way NE, Seattle, WA 98115.

Table 1

Histological criteria for female rex sole (*Glyptocephalus zachirus*) reproductive state and maturity. Active female ovaries contained a sufficient number of advanced yolked oocytes for one spawning. Abbreviations are as follows: migratory-nucleus oocytes (MN), hydrated oocytes (HY), postovulatory follicles (POFs), oocyte stage present (+); oocyte stage absent (○); oocyte stage not considered (–), and either one or both oocyte stages present (>). A postspawning fish has totally spent ovaries.

Ovary activity	Maturity stage	Spawning condition	Unyolked oocytes	Early yolked oocytes	Advanced yolked oocytes	MN or HY oocytes	POFs	>50% yolked atresia	Number of fish in stage
Inactive	Immature	Nonspawning	+	○	○	○	○	–	274
Inactive	Mature	Nonspawning	–	+	○	○	○	–	44
Inactive	Mature	Nonspawning	–	–	+	–	○	+	0
Inactive	Mature	Postspawning	–	–	+	–	+	+	96
Active	Mature	Nonspawning	–	–	+	○	○	○	26
Active	Mature	Spawning	–	–	–	+	○	○	27
Inactive	Mature	Postspawning	–	–	○	○	+	–	14
Active	Mature	Spawning	–	–	>	>	+	○	113
Total									594

sification from Hunter et al. (1992). Females were first classed as active or inactive by using the following criteria. Through histological analysis, ovaries that contained a sufficient number of AY/MN/HY oocytes for one spawning were classed as active. Active females were then classed as either spawning or nonspawning. Ovaries without AY oocytes or with major atresia of AY oocytes were classed as inactive. Inactive females were first classed as nonspawning or postspawning and then inactive nonspawning females were further classed as mature or immature (Table 1). Active spawning females showed evidence of past spawning (POF present) or imminent spawning (MN or HY present), whereas active nonspawning females had no evidence of recent or imminent spawning but were presumed capable of spawning in the near future. Females with ovaries containing oocytes in early stages of vitellogenesis (EY oocytes present) were considered mature but inactive. Immature females had ovaries without vitellogenic oocytes.

The fraction of active females and the fraction of postspawning females was calculated for each month. The start of the spawning season was defined by the first observance of a hydrated oocyte or a POF and the end of the spawning season was defined when the last female with hydrated oocytes was observed. A one-way ANOVA was used to test for differences in the ovary wall thickness of mature females among months. Assumptions of homogeneity of variances and normal distribution of observations were met for the ANOVAs. Bonferroni all-pairwise multiple comparison tests were used after the ANOVAs to test for differences among monthly mean values. Alpha was set at 0.05 for all tests of significance.

To estimate the length and age at which 50% of the female rex sole were mature ($ML_{50}$and MA_{50}), I used the logistic regression model:

$$Pmat = 1 / (1 + e^{a+bL}),$$

where $Pmat$ = the fraction of mature females per 15-mm length-class; and

L = total length in millimeters.

Similarly, for estimating MA_{50},age (in years) was substituted for length in the above equation. In each case, the equation was solved for $Pmat = 0.5$ to obtain the length and age at 50% maturity. The equation for the upper and lower 95% confidence limits around $Pmat$ when $Pmat = 0.5$ was solved to yield 95% confidence limits around $ML_{50}$and MA_{50}. Results were compared with existing length-at-maturity data for female rex sole off the Oregon coast by reconstructing a length-at-maturity logistic regression model from data presented by Hosie and Horton (1977), taking the log transformation of both the GOA and Oregon logistic regression curves to make them linear, and then comparing the slopes of the two lines according to Zar (1999). Direct statistical comparison with existing age-at-maturity data (e.g., the age at 50% maturity, and age at 100% maturity) for female rex sole off Oregon (Hosie and Horton, 1977) was not conducted because Hosie and Horton (1977) did not present standard error or logistic regression equations. Instead, the probability that a specific-size (or specific-age) female rex sole off the coast of Oregon would be considered mature in the GOA was calculated as the fraction of mature GOA females of the specified length divided by the GOA sample size of the specified length (Zar, 1999).

Size and growth

The relationship between weight and length for female rex sole in the GOA was estimated with the equation

$$W = aL^b,$$

where W = the total fish weight in grams; and
L = total length in cm.

This relationship was also determined for ovary-free weight. Because fresh ovarian weights were not measured for samples collected at sea, the fresh weight was estimated from a linear regression between fresh and preserved weights from the samples collected at processing plants. The linear regression $OW=1.127\,(OW_f)-0.024$ was used to convert formalin-preserved ovary weights, OW_f, to estimates of fresh ovary weights, OW ($n=446$, $r^2=0.997$, $P<0.0001$). When fresh and preserved ovary weights differed; fresh ovaries usually weighed more than ovaries preserved in formalin, and the maximum difference between fresh ovaries and formalin-preserved ovaries was 20%.

Parameters of the von Bertalanffy growth model (L_∞, k, and t_0) were estimated for female rex sole in the GOA by using nonlinear least squares regression with the equation

$$L_t = L_\infty\,(1 - e^{-k\,(t - t_0)}),$$

where L_t is length at age t.

All length and age data were used for the GOA growth model. Statistical comparison of growth rates for female rex sole in the GOA with those from the Oregon coast were less rigorous because Hosie and Horton (1977) used mean values of length at age to calculate the von Bertalanffy growth model, thereby decreasing the variability in length at age, which was not presented. Therefore, the parameters L_∞, k, and t_0 in the GOA growth model were each statistically compared with the parameters in the Oregon growth model for females age 1–15 years (data from Hosie and Horton, 1977) with three separate Z-tests (Zar, 1999). Alpha was set at 0.05 for all tests of significance.

Results

Maturity

Oocyte development and maturity stage were determined for 594 female rex sole. Histological examination revealed that 46% of the collected females were immature and 54% were mature. Both immature and mature females were collected in every month; however, no fish were sampled in August or September (Table 2). Year-round histological analysis of ovaries confirmed that rex sole are batch spawners, as seen in the presence of POFs, features associated with recent spawning, concurrent with advanced vitellogenic oocytes.

The spawning season of rex sole in the GOA was protracted; postovulatory follicles first appeared in October and hydrated oocytes occurred as late as May, indicating a spawning season that spans at least eight months. Active females were present from October through May and were absent in June and July (Table 2). Mature postspawning females with no healthy AY oocytes first appeared in April and increased in June and July; thus, the spawning season ended in April for some individuals, and by June all rex sole had completed spawning (Fig. 3). The high number of postspawning fish combined with the absence of spawning fish in June and July indicated that the duration of POFs in an ovary was several weeks. Active females had at least one of the following oocytes (AY, MN, or HY) and could have any combination of these advanced stage oocytes, or all three oocyte stages at once. These oocytes were large and stretched the ovary wall quite thin, whereas inactive postspawning females had shrunken ovaries and thicker ovary walls (Maddock and Burton, 1999). In May and July ovary walls in mature females were significantly thicker than in all other months sampled (ANOVA: $F_{9,274}=28.64$, $P<0.0001$; Fig. 4), corresponding to the high fraction of postspawning females present from May to July (Table 2, Fig. 3).

Female rex sole sampled for length and maturity ranged from 166 to 552 mm TL (Fig. 5). The smallest

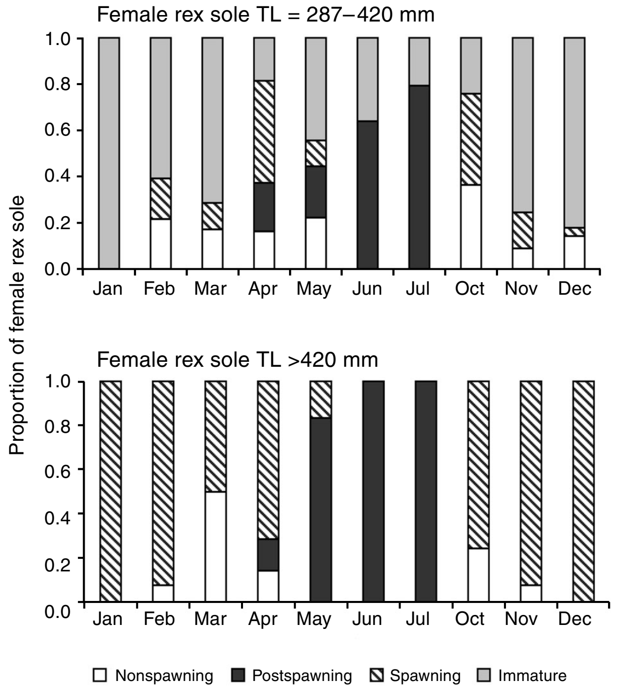

Figure 3

Monthly proportion of female rex sole (*Glyptocephalus zachirus*) maturity stages graphed separately for fish greater than size at first maturity (287–420 mm in upper graph) and fish greater than size at 100% maturity (>420 mm in lower graph). No data were collected in August or September. All mature rex sole were in the postspawning stage in June and July.

Table 2

Numbers of female rex sole (*Glyptocephalus zachirus*) in various histological subclasses, listed by month with years combined. Abbreviations are as follows: postspawning (PS), nonspawning (NS), spawning (S), early yolked oocytes (EY), advanced yolked oocytes (AY), migratory nucleus oocytes (MN), and hydrated oocytes (HY). Mature PS females had ovaries that contained postovulatory follicles (POF), and mature S females had ovaries that contained either MN or HY oocytes or AY oocytes combined with POF. The length distribution (minimum, maximum) and the total number of females sampled in each month are given. The percent active females in each month is given, and female rex sole were active from October through May. PS females were present from April to July. No collections were made in August or September.

Ovary activity	Maturity stage	Histological criteria	Jan	Feb	Mar	Apr	May	Jun	Jul	Oct	Nov	Dec	Total
Inactive	Immature	Unyolked oocytes	2	75	33	20	13	14	36	10	41	30	274
	Mature	EY; <50 % atresia	0	13	10	8	2	0	0	6	1	4	44
	Mature–PS	AY; >50 % atresia; POF	0	0	0	9	6	37	44	0	0	0	96
	Mature–PS	AY absent; POF	0	0	0	1	1	0	12	0	0	0	14
Active	Mature–NS	AY; POF absent	0	5	2	0	0	0	0	15	4	0	26
	Mature–S	MN or HY; POF absent	0	0	0	0	0	0	0	23	3	1	27
	Mature–S	AY, MN, or HY; POF present	5	37	10	24	2	0	0	18	16	1	113
Minimum length (mm)				353	166	250	214	215	257	176	267	172	220
Maximum length (mm)				513	529	552	547	460	503	450	476	460	452
Percent active females			71%	32%	22%	39%	8%	0	0	78%	35%	6%	
Percent postspawning females			0	0	0	16%	29%	73%	61%	0	0	0	
Total number sampled			7	130	55	62	24	51	92	72	65	36	594

mature female in the GOA was 287 mm TL. The nonlinear logistic regression model used to determine a length-at-maturity curve for females in the GOA had a very good fit (n=594, r^2=0.994; Fig. 6). The ML_{50} estimate for rex sole in the GOA was 352 mm (95% CI: 344–360 mm; Table 3), and length at 100% maturity was 420 mm (Fig. 5). Female rex sole in the GOA matured at a significantly larger size than off the Oregon coast (slope comparison: $t_{2,57}$=1356, P<0.0001; Fig. 6). Hosie and Horton (1977) estimated the ML_{50} as 24 cm off the Oregon coast, and at this length no GOA rex sole were mature. At the length that 100% of rex sole from Oregon waters were mature (30 cm; Hosie and Horton, 1977), only 15.8% (n=19) were mature in the GOA. The ML_{50} for female rex sole in the GOA was 46% greater than the ML_{50} for Oregon coast stock.

Female rex sole collected in this study ranged in age from 1 to 29 years. The estimated MA_{50} was 5.1 years (95% CI: 4.7–5.5 years) (n=557, r^2=0.988; Table 3, Fig. 7). Minimum age-at-maturity was 3 years, and all females had reached maturity by age 9, with the exception of two slow growing females who were still immature at ages 9 and 10 years (Fig. 5). These results are nearly identical to those obtained in Oregon (MA_{50}=5 yr, 100% mature at 9 years.; Hosie and Horton, 1977).

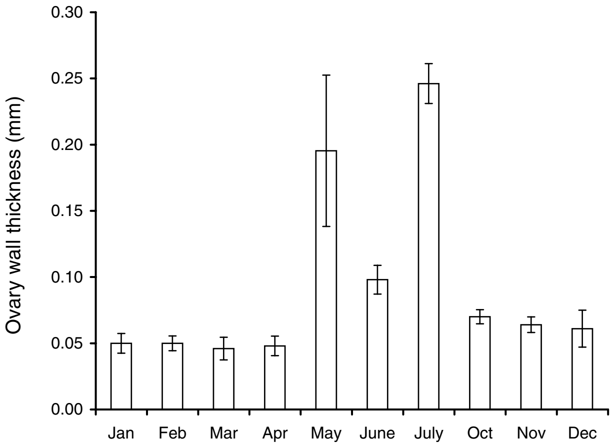

Figure 4

Monthly mean (±1 standard error) ovarian wall thickness (mm) for mature female rex sole (*Glyptocephalus zachirus*). No data were collected in August or September.

Size and growth

Parameters for the weight (g) to total length (cm) relationship for female rex sole in the GOA were

$W=0.000762L^{3.6127}$ ($n=573$, $r^2=0.963$, $P<0.0001$). Parameters for the ovary-free weight to total length (cm) relationship were $W=0.001277L^{3.4680}$ ($n=568$, $r^2=0.969$, $P<0.0001$). Parameters of the von Bertalanffy growth model for female rex sole in the GOA were $L_\infty=41.824$, $k=0.388$, and $t_0=-0.022$ ($n=556$, $r^2=0.480$, $P<0.0001$). All GOA parameters of the von Bertalanffy growth model differed from those off the coast of Oregon: L_∞ ($Z=8.01$, $P<0.0001$), k ($Z=5.61$, $P<0.0001$), and t_0 ($Z=2.29$, $P=0.0110$). Female rex sole age 1–15 years grew much more quickly in the GOA than off the Oregon coast (Fig. 8).

Discussion

A representative sample of fish can be challenging to collect during the spawning season, because samples from spawning aggregations may produce disproportionately large numbers of mature fish whereas samples from elsewhere may yield unusually large numbers of immature fish (Sampson and Al-Jufaily, 1999). The combination of samples from commercial trawls and randomly chosen trawls taken on research surveys provide a reasonable representation of the GOA population and are suitable for estimating spawning season, length and age at maturity, and growth rate. Shore-side sampling of the commercial catch enabled the annual cycle of rex sole sexual maturation to be monitored, and although a common problem in obtaining samples from commercial fishing gear is that the size-selectivity of trawls may produce biased estimates of size frequency and size at age (Sampson and Al-Jufaily, 1999), this concern was alleviated because small rex sole (minimum length=172 mm) were collected from processing plants.

One limitation in the sampling effort was that samples could not be obtained in August and September. This raises two concerns. First, the onset of the GOA spawning season was estimated to be October by the presence of POFs in mature ovaries; but, in all probability, it may begin earlier. Second, Hunter et al. (1992) argue that length and age at maturity are best estimated from fish collected prior to the spawning season, because during the spawning season the ovaries of some postspawning females are reabsorbed to the extent that they are indistinguishable from those of immature females. Their estimates of Dover sole (*Microstomus pacificus*) length at maturity from samples taken during the spawning season were 1.6–5.7 cm higher than estimates from samples taken prior to the onset of spawning (Hunter et al., 1992). Given that GOA collections were unavailable prior to the spawning season, estimates of ML_{50} in the present study may have been biased high. However, because 1) all postspawning females had POFs present and 2) there were no females that had atretic yolked oocytes without POFs, it is unlikely that mature females were misclassified as immature in this study.

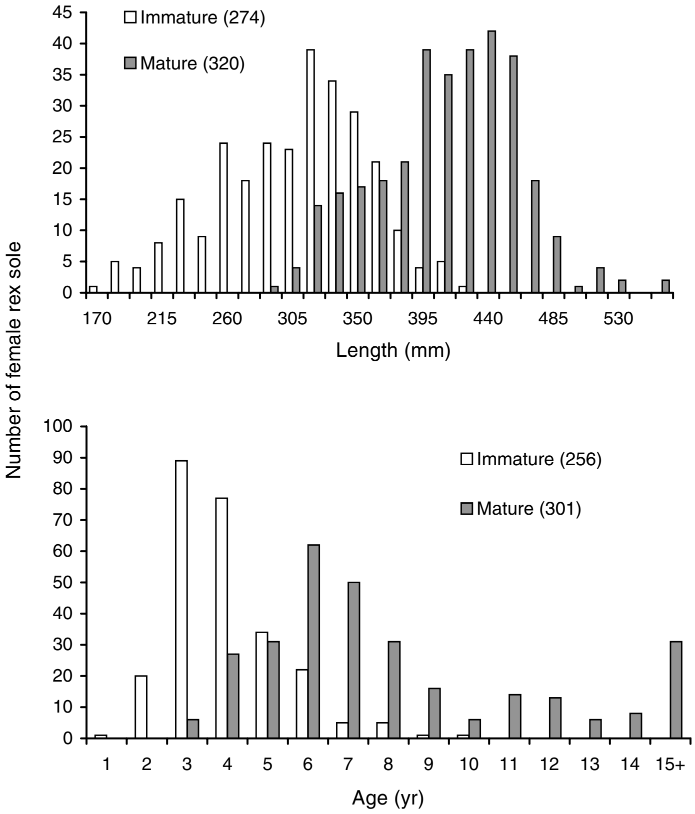

Figure 5

The number of immature and mature female rex sole (*Glyptocephalus zachirus*) by total length (upper graph) and age (lower graph). Sample size is given in parentheses. Lengths are binned at 15-mm increments and "age 15+" includes all females from 15 to 29 years old. Minimum size at maturity occurred in a fish with total length of 287 mm, and minimum age at maturity occurred at 3 years.

Spawning season

The spawning season for the population of female rex sole in the GOA ends in May and appears to commence in October, although it may begin earlier (see above). Castillo (1995) estimated the spawning season for rex sole in the GOA lasts from April through September, which differs markedly from results in the present study which are based on year-round histological examination of ovaries. Castillo (1995) based his estimation on the seasonal occurrence of rex sole larvae near Kodiak Island (Kendall and Dunn, 1985) rather than on collections of adult rex sole in spawning condition. Because rex sole larvae attain an exceptionally large size (up to 89 mm standard length) and have a prolonged pelagic life of

Table 3

Logistic regression model for female rex sole (*Glyptocephalus zachirus*) in the Gulf of Alaska: final maturity thresholds, length and age at 50% maturity (ML_{50} and MA_{50}), sample size (n), model parameter estimates, and the model r^2.

Variable	ML_{50}/MA_{50}	95% CI	n	a	SE	b	SE	Model r^2
Length (mm)	351.7	343.7–359.7	594	13.79	0.77	−0.0392	0.0022	0.994
Age (years)	5.1	4.7–5.5	557	5.29	0.45	−1.0375	0.0854	0.988

at least 12 months (Pearcy et al., 1977), the indeterminate pelagic larval phase may have confounded Castillo's (1995) estimates.

Fish may adjust their spawning season to synchronize larval hatching date with the season that is most favorable for larval feeding (Qasim, 1956). Because primary production at northern latitudes is restricted to a short, intense period during early summer, fishes at higher latitudes often delay and shorten their breeding season as an adaptation to synchronize the feeding of fish larvae with the zooplankton bloom (references in Qasim, 1956; Castillo, 1995). However, rex sole in the GOA spawn earlier in the year and for a longer duration than those off the Oregon coast, which spawn from January to June (Hosie and Horton, 1977). Hence, rex sole do not fit the typical pattern of geographic variation found in other pleuronectids, such as English sole (*Pleuronectes vetulus*; Kruse and Tyler, 1983; Sampson and Al-Jufaily, 1999), Dover sole (Abookire and Macewicz, 2003), and yellowtail flounder (*Limanda ferruginea*; Zamarro, 1991).

Maturity and growth

Size and age at sexual maturity are two important parameters of fish stock assessment models used to estimate spawning biomass and annual catch quotas, but these parameters may vary throughout the geographic distribution of a species (Roff, 1981; Nichol, 1997; Bromley, 2000) and can be influenced by food availability (Castillo, 1995; Sampson and Al-Jufaily, 1999), oceanographic conditions (Kruse and Tyler, 1983; Brodziak and Mikus, 2000), or population size (Morgan and Colbourne, 1999). Along the west coast of North America both English sole (Sampson and Al-Jufaily, 1999) and Dover sole (Brodziak and Mikus, 2000; Abookire and Macewicz, 2003) exhibit geographic variation in length at maturity and growth.

There is some indication that female rex sole mature at a smaller size in the southern portion of their range: off San Francisco, California, females were fully mature at 22.8 cm (in Hosie and Horton, 1977), and off the Oregon coast ML_{50} was 24 cm (Hosie and Horton,

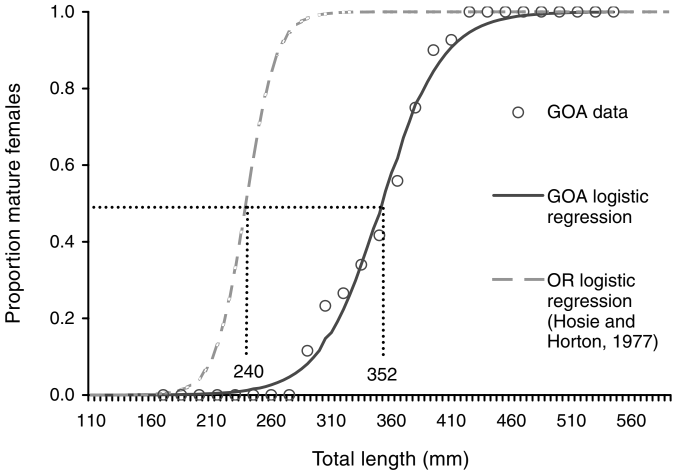

Figure 6

Proportion of female rex sole (*Glyptocephalus zachirus*) that were sexually mature in the Gulf of Alaska (GOA) as a function of total length (mm). Data points along the GOA curve represent the proportion of mature females in each 15-mm length-class interval. Logistic model parameter estimates are listed in Table 3. The dashed line denotes the length at which 50% of females are mature, and the actual size (mm) of ML_{50} is given. A maturity curve for female rex sole off the Oregon (OR) coast (from Hosie and Horton, 1977) is graphed for comparison. Female rex sole in the GOA mature at a significantly larger size than off the Oregon coast (P<0.0001).

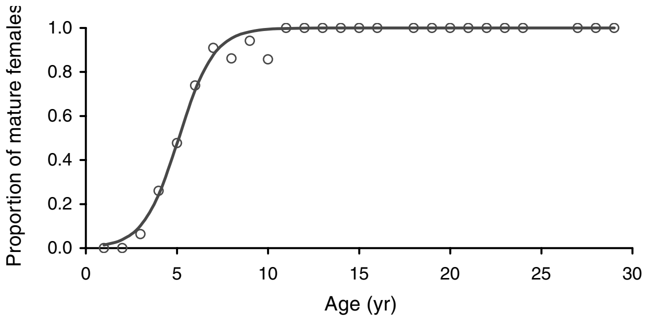

Figure 7

Proportion of female rex sole (*Glyptocephalus zachirus*) in the Gulf of Alaska that were sexually mature as a function of age (years). Datapoints along the curve represent females grouped in intervals of one year. Logistic model parameter estimates are listed in Table 3.

1977). Correspondingly, I found the ML_{50} in the GOA (35 cm) was 46% greater than that off the Oregon coast. Although there is a possibility that rex sole ML_{50} in the GOA was overestimated because sampling did not occur prior to the onset of spawning, the bias cited by Hunter et al. (1992) was relatively small and can not fully account for the 11 cm difference in ML_{50} between the GOA and Oregon. However, some caution must be exercised when maturity is compared between the GOA and Oregon (Hosie and Horton, 1977) because about 25 years elapsed between studies and different criteria were used to classify fish as mature.

Differences in the histological criteria used to define mature individuals and reliance solely on gross anatomical methods can lead to a misclassification of maturity and produce differences in estimates of ML_{50} (Hunter et al., 1992; Zimmermann, 1997). In a comparison of histological and gross anatomical methods, Hunter et al. (1992) found 1% of active female Dover sole were misclassified as inactive and 12% were visually classified as having advanced yolked oocytes and believed capable of spawning, whereas histological analysis indicated that they were inactive and future spawning was unlikely. Likewise, macroscopic examination of arrowtooth flounder misclassified 18.4% of maturing or spent females as immature and 4.4% of immature females as spent (Zimmermann, 1997). Unfortunately, in the only previous investigation on rex sole maturity, Hosie and Horton (1977) limited their analysis of ovaries to macroscopic staging. However, the enormous differences in ML_{50} between the GOA stock and the West Coast stock off Oregon likely stem from biological differences between stocks rather than from inconsistent methods used in the two studies. This interpretation is consistent with the dramatic difference in length at age between the two areas (Fig. 8) that was demonstrated in this study.

Given that Hosie and Horton (1977) used the otolith-surface aging technique to analyze rex sole otoliths, they may have underestimated ages and thereby biased their estimates of both age at maturity and growth rates. However, the tendency to underestimate age with the otolith-surface aging technique is greater for older fish where the outer edges of the otolith are worn (Anderl[7]). Surface analysis of several GOA rex sole otoliths revealed that, although break and burn is the preferred technique for aging rex sole otoliths, it is possible, depending on the clarity of the annular pattern, to age females less than 10 years old accurately by using otolith surfaces (Anderl[7]). Because the ages at 50% and 100% maturity off the Oregon coast were 5 and 9 years old, respectively (Hosie and Horton, 1977), there is a lower potential for bias caused by the surface aging technique because fish were <10 years old. Although these different aging methods may limit comparisons of age at maturity, the similarity in age at maturity between the GOA and Oregon is strongly indicated. Additionally, because the length-at-age data presented in growth curves from Oregon were only for rex sole <15 years old (Hosie and Horton, 1977), and a difference in growth is evident at young ages (Fig. 8), it seems unlikely that potential bias from otolith-surface aging methods—rather than from biological differences between stocks—could account for the markedly lower growth rate of Oregon rex sole. To be sure, it would be useful for future research to compare the reproductive biology and growth data of female rex sole in the GOA with a current study off the Oregon coast that employed similar aging techniques and histological criteria for maturity to determine if the distinct differences found in the GOA stock (i.e., larger size at maturity, similar age at maturity, faster growth rate) persist.

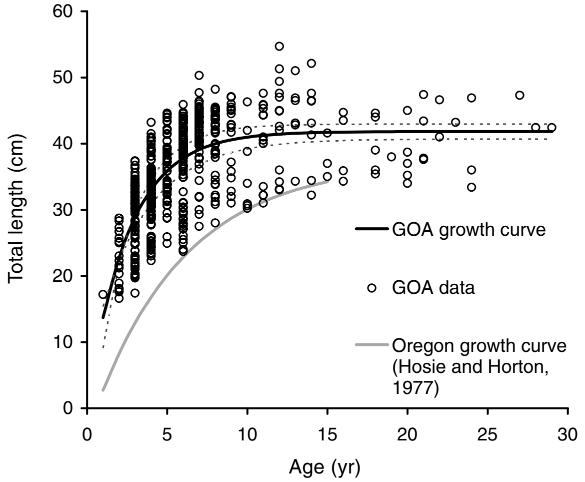

Figure 8

The von Bertalanffy growth curve with 95% confidence limits for female rex sole (*Glyptocephalus zachirus*) in the Gulf of Alaska. Parameters of the Gulf of Alaska growth model were $L_\infty = 41.82$, $k = 0.388$, and $t_0 = -0.022$. For comparison, the growth curve for age 1–15 female rex sole off the Oregon coast is graphed with data from Hosie and Horton (1977).

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