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Source: Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science, 5(5) : 21-27

Published By: American Fisheries Society

URL: <https://doi.org/10.1080/19425120.2012.751941>

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ARTICLE

## Reproductive Biology of Pacific Ocean Perch in the Gulf of Alaska

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### Abstract

Despite the ecological and economic importance of rockfish fisheries in Alaska waters, little information is available concerning the reproductive biology of the majority of federally managed rockfish species in the Gulf of Alaska. Pacific Ocean Perch *Sebastes alutus* are the most abundant and commercially important rockfish in this region. This study examines the reproductive biology of Pacific Ocean Perch within the Gulf of Alaska, utilizing histological techniques to microscopically examine ovarian tissue. Pacific Ocean Perch samples were obtained throughout the year during National Marine Fisheries Service and Alaska Department of Fish and Game scientific surveys, as well as scientific charters. Ovaries of Pacific Ocean Perch began to ripen during the month of August with yolk increasing until February. Embryos appeared within the ovaries during February and continued to grow and develop until parturition in May. Results from this study indicate the fork length at 50% maturity is 33.4 cm and the age at 50% maturity is 8.4 years. Both of these values are smaller than those currently utilized in the stock assessment of Gulf of Alaska Pacific Ocean Perch. Results from this study will improve the stock assessment of this species by providing more accurate estimates of reproductive parameters and reducing the uncertainty in estimates of length and age at maturity.

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Pacific Ocean Perch *Sebastes alutus* occur from Japan to Cape Navarin in the Bering Sea, along the Aleutian Islands, throughout the Gulf of Alaska, and along the North American West Coast as far south as southern California (Allen and Smith 1988). Adult Pacific Ocean Perch are found predominantly off-shore on the outer continental shelf and on the upper continental slope in depths of 200–300 m (Chikuni 1975) but appear to occupy deeper depths during the winter months (Westrheim 1970). All members of the genus *Sebastes* are live-bearers: they employ internal fertilization and give birth to a large number of planktonic larvae (Kendall and Lenarz 1987). Fecundity of Pacific Ocean Perch, which ranges from 10,000 to 300,000 larvae per female, is probably related to body size of the female (Leaman 1991). Evidence suggests that the reproductive mode of these species is true viviparity; that is, the embryos receive some

additional maternal nutrition beyond what is provided from the yolk during gestation (Boehlert et al. 1987).

Pacific Ocean Perch are the most abundant rockfish in the Gulf of Alaska and are the most commercially important rockfish in this region. Landings of Pacific Ocean Perch increased dramatically during the 1960s due to development of foreign fisheries in the Gulf of Alaska. Catches peaked in 1965 at around 350,000 t and then declined through the 1970s. In 1976, the U.S. Government passed the Magnuson–Stevens Fishery Conservation and Management Act, which led to the phasing out of foreign fishing in the Exclusive Economic Zone; in 1985, trawling by foreign fishers in the Gulf of Alaska was prohibited. A domestic fishery developed in 1985 and expanded until 1991, when stricter management measures were enacted (Hanselman et al. 2010). This fishery has predominately been a bottom trawl

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Received July 30, 2012; accepted November 16, 2012

fishery but recently a significant portion of the catch has been captured using pelagic trawls. Increasing quotas have led to increased catches in recent years; the recent catch rates are more likely a reflection of management quotas than fishery-driven trends in abundance (Hanselman et al. 2010).

The stock assessment for Pacific Ocean Perch in the Gulf of Alaska utilizes a separable age-structured model as the primary assessment tool. This model incorporates maturity estimates that directly influence the estimation of stock biomass, and a very small change in this parameter can have a significant impact on the determination of total allowable catch calculated as a percentage of the stock biomass (Hanselman et al. 2009). Therefore, it is critical to have accurate data on the reproductive parameters of this rockfish species. The values for age and length at maturity of this species currently utilized in the stock assessment model are derived from a non-peer-reviewed study in which visual techniques were used to assess maturity status and oocyte development (Hanselman et al. 2009). Previous studies have revealed a greater potential for incorrect identification of maturity stages during macroscopic staging than during histological evaluations, which may bias maturity estimates (Hunter et al. 1992; Zimmermann 1997). The objective of this study is to examine the seasonality of the reproductive cycle and update the estimates of age and length at maturity for Pacific Ocean Perch in the Gulf of Alaska by utilizing more accurate histological techniques.

## METHODS

Pacific Ocean Perch samples were collected opportunistically throughout the year during National Marine Fisheries Service and Alaska Department of Fish and Game scientific surveys, from the Alaska Fisheries Science Center's Fisheries Monitoring and Analysis Division, and from dedicated charters. Samples were collected predominately from the central Gulf of Alaska, but some samples were taken from both the eastern and western Gulf, particularly in the late summer months (Table 1; Figure 1). Each fish was measured for fork length (FL), and the ovary was removed and preserved in 10% neutral buffered formalin. Total weight was measured before ovary collection and a fresh ovary weight was measured for samples obtained fresh from observers. In the laboratory, a formalin-fixed ovary weight was measured. The otoliths were removed and preserved in 70% ethanol until later transfer to a glycerol-thymol solution. Otolith samples were analyzed by the Alaska Fisheries Science Center's Age and Growth Program, utilizing standard break and burn procedures (Chilton and Beamish 1982). A subsample of 20% of otoliths was analyzed by a second reader and the percent agreement between readers and the coefficient of variation were calculated.

A cross-section taken from the middle of one ovary from each sample was embedded in paraffin and cut into 6- $\mu$ m-thick sections. These sections were stained with hematoxylin and eosin using standard histological techniques. Maturity stages were defined utilizing the terminology of Bowers (1992) but were modified specifically for this species in this region (Table 2).

TABLE 1. The number of Pacific Ocean Perch samples collected by month within the western Gulf of Alaska (federal statistical region 610), the central Gulf of Alaska (regions 620 and 630), and the eastern Gulf of Alaska (regions 640 and 650).

Month	No. of Pacific Ocean Perch samples collected			Total
	Western Gulf of Alaska	Central Gulf of Alaska	Eastern Gulf of Alaska	
January		88		88
February	14	1		15
March		86		86
April		7		7
May	4	38		42
June	17	48		65
July		15	14	29
August		6	49	55
September		18		18
October		16	4	20
November		99		99
December		90		90

One histological section for each ovary was chosen and scanned with a compound microscope to determine the most advanced oocyte stage present in that ovary. The most advanced oocyte stage identified at least five times within the section was used to classify the maturity stage of that fish. Maximum oocyte diameter (MOD) was measured with an ocular micrometer. The histological section was scanned, and five of the largest non-atretic oocytes in the most advanced stage were measured. The largest of these was determined to be the MOD. The monthly mean MOD from mature fish was plotted to determine whether there were seasonal trends in this parameter. MOD values were calculated only for fish that had developing oocytes because degenerative oocytes were difficult to measure. Sections were examined for atresia, that is, the degeneration and resorption of oocytes. Sections that had atretic oocytes were classified as low intensity (<5%) or high intensity (>25%) following McDermott (1994).

Pacific Ocean Perch were determined to be mature if their oocytes had evidence of development that would lead to the completion of spawning within the upcoming reproductive season. Samples classified as maturity stage 3 (advanced yolk) or higher were considered to be mature. Samples classified as stage 2 (maturing) were not considered to be mature; studies have shown rockfish within this stage may be functionally immature and therefore may not spawn within the year (Nichol and Pikitch 1994). Seasonality of the reproductive cycle was examined by plotting the frequency of samples in each maturity stage collected during each month of the year, using only mature (stage 3 and higher) fish. In addition, a gonadosomatic index (GSI) was calculated for all mature fish as the gonad weight divided by the total body weight.

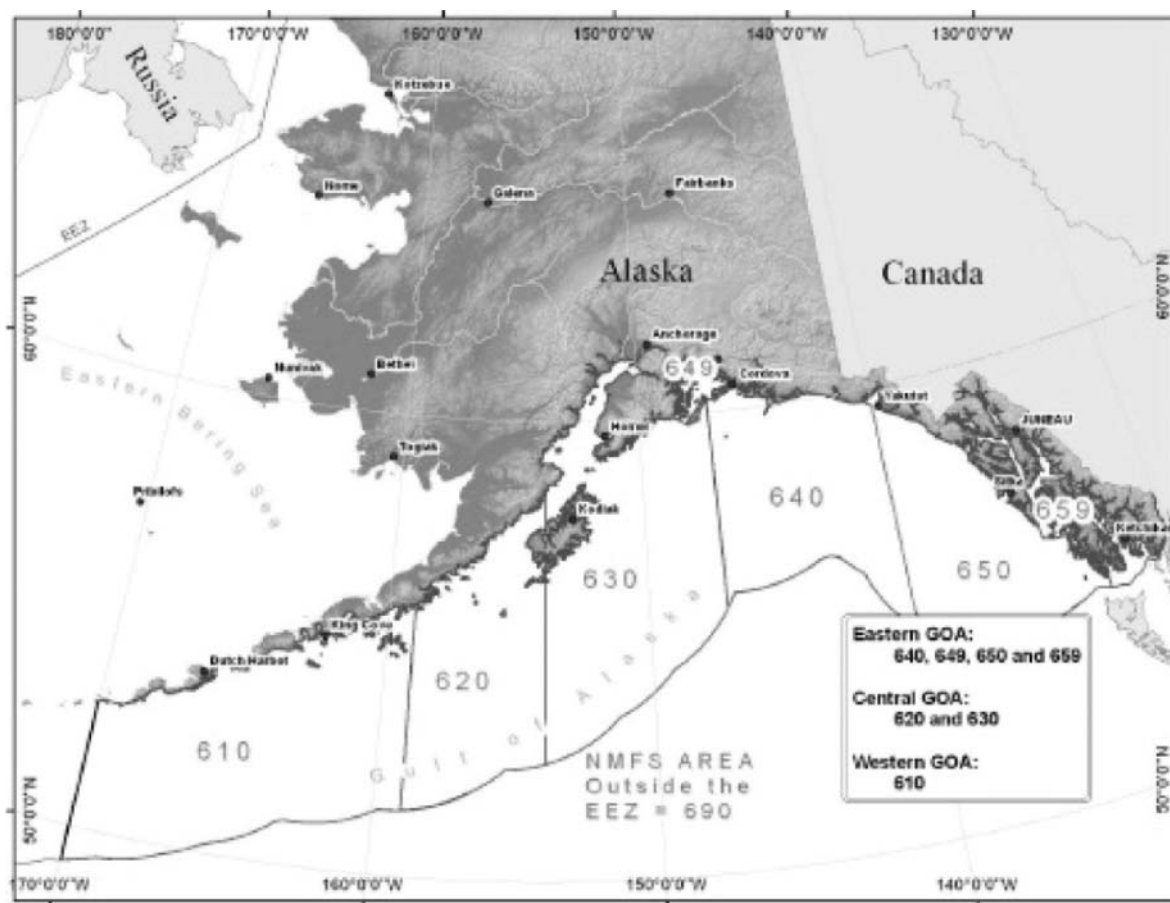


FIGURE 1. Map of Alaska federal management regions showing the western Gulf of Alaska (federal statistical region 610), the central Gulf of Alaska (regions 620 and 630), and the eastern Gulf of Alaska (regions 640 and 650). Source: NMFS, 2011.

The mean and standard error of these values for each month were determined. A correction factor was developed for ovary weights from samples that had been preserved in formalin by using weights from fresh and formalin-preserved samples where

both weights were available. Ovary and total weights were unavailable for some fish; collection of the complete ovary from those fish was not possible due to the difficulty of maintaining the structure of ovaries that were in a late stage of development.

TABLE 2. Histological maturity stages of Pacific Ocean Perch.

Stage	Physical description
1. Immature	Oogonia, early perinucleus, and late perinucleus stages are present; mean MOD = 269 $\mu$ m
2. Maturing	Earliest signs of yolk accumulation, small spherical globules of yolk in the periphery of the oocyte; mean MOD = 355 $\mu$ m
3. Advanced yolk	Oocyte content is at least 50% yolk droplets, nucleus still well defined; mean MOD = 566 $\mu$ m
4. Migratory nucleus	Nucleus migrates to the periphery of the oocyte, nuclear membrane becomes irregular, nucleoli disappear; mean MOD = 748 $\mu$ m
5. Ovulation/fertilization	Yolk material begins to merge and form a single united mass; mean MOD = 827 $\mu$ m
6. Early embryo	Blastoderm cap present with a large yolk mass; mean MOD = 997 $\mu$ m
7. Embryo body	Embryo body appears, blastoderm cap of cells develops into recognizable tissue; mean MOD = 1,170 $\mu$ m
8. Eyed embryo	Retinal pigmentation becomes apparent; mean MOD = 1,551 $\mu$ m
9. Embryo reduced yolk	Yolk attached to the embryo is reduced in size and may be present only as droplets; mean MOD = 1,973 $\mu$ m
10. Post-ovulatory/resting	Presence of postovulatory follicles and cell degeneration

Length and age at 50% ( $L_{50}$  and  $A_{50}$ ) maturity were estimated by fitting the data to the logistic equation

$$P = 1/(1 + (X/X_{50})^b),$$

where  $P$  is the proportion of mature fish,  $b$  is a parameter of the model,  $X_{50}$  is the length or age at 50% maturity, and  $X$  is the length or age of the fish. Parameters were fitted to the logistic equation by using maximum likelihood estimation. All statistical tests were completed in the computer program R, version 2.15.1 (The R Foundation for Statistical Computing, Vienna).

## RESULTS

### Seasonality

A total of 614 samples were collected, representing all months, although only 7 samples were collected during April (Table 1). Pacific Ocean Perch oocytes began to develop during the months of July through September. Advanced vitellogenesis occurred primarily between October and January. Yolk increased in the oocytes until February. Embryos appeared within the ovaries during February and March, and embryogenesis continued to April or May, when parturition occurred. Parturition began in April but occurred primarily during May (Figure 2).

The results from the GSI also show an increase in the size of ovary through March, a decrease in May as parturition occurs, and a sharp drop off in June after parturition (Figure 3). The mid-value and high variability of the GSI for May reflect that fish examined were captured both before and after parturition. The mean MOD also follows the same trend but, since it includes only oocytes that are developing the value for MOD, peaks in May. Values for MOD in June and July, the resting stage period of Pacific Ocean Perch oocytes, were absent (Figure 3). The reproduction of this species was highly synchronous with a prolonged period of development from the onset of vitellogenesis in July and August to parturition in May. Vitellogenesis occurred during a 5- to 6-month period from July/August through December/January; this was followed by embryogenesis, which occurred during a 4- to 5-month period from December/January through May. The spent/resting period of Pacific Ocean Perch was very short, only about 2 months from the end of May through July, before vitellogenesis began again.

### Atresia and Abortive Maturation

Low-intensity alpha (early stage) atresia was widespread and documented in 95 samples ranging in size from 25 to 48 cm (FL) and in age from 7 to 58 years. This phenomenon was documented in fish in a variety of ages, lengths, and reproductive stages and occurred throughout the year. High-intensity alpha atresia or abortive maturation was observed in 24 samples

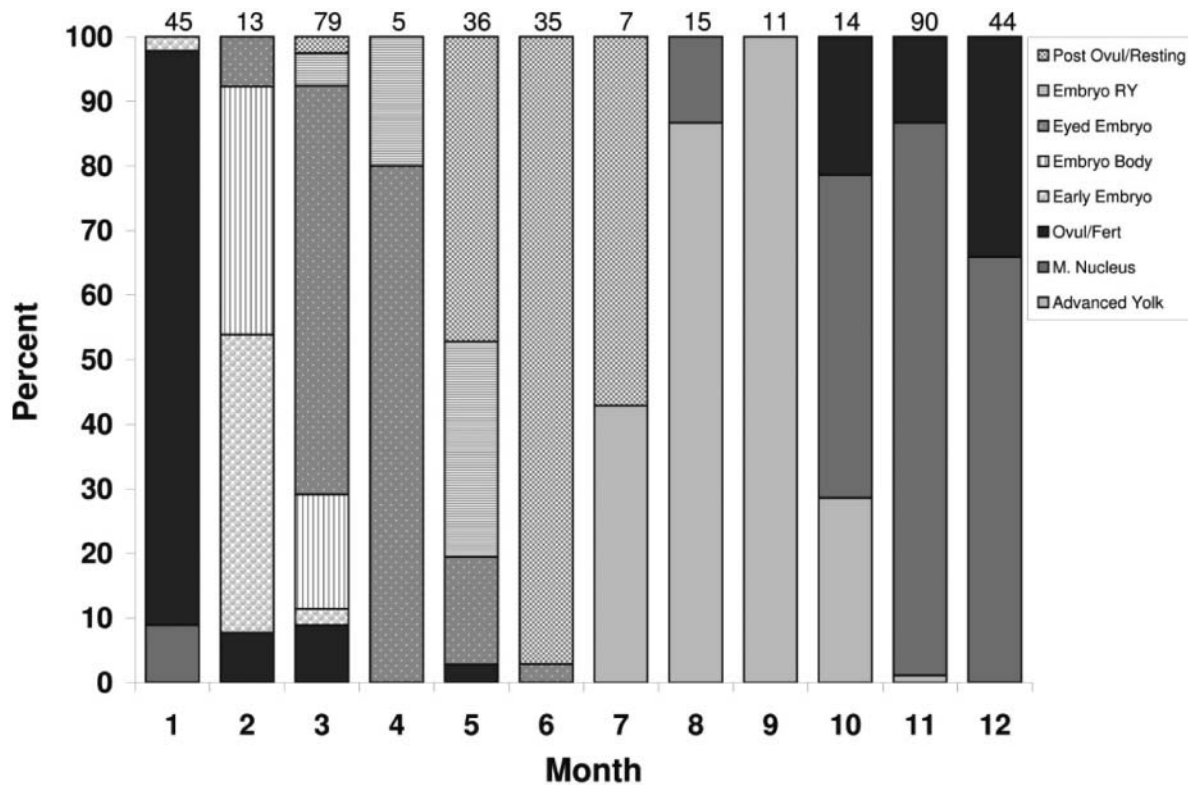


FIGURE 2. Seasonal changes in the maturity stage of female Pacific Ocean Perch. The proportion of fish in each stage during each month is presented. Numbers above each bar indicate sample size.

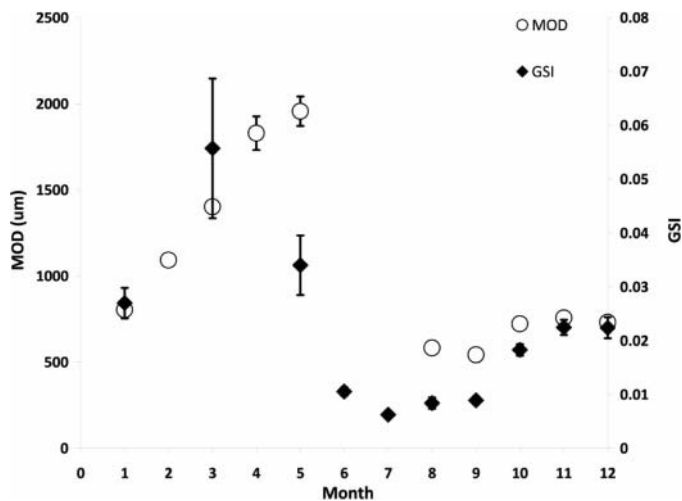


FIGURE 3. Mean monthly gonadosomatic index (GSI) and maximum ova diameter (MOD) values for Pacific Ocean Perch. Error bars are standard error of the mean.

ranging in size from 31 to 36 cm and at ages 7–13 years; the age of the majority of fish ranged between 7 and 10 years old. High-intensity atresia was documented in several months but was most frequently noted in December and January, although this may be a reflection of the high-intensity sampling during those months. High-intensity atresia was most commonly associated with oocytes that were in stage 2 or early vitellogenesis.

### Age Analysis

A total of 595 Pacific Ocean Perch samples were successfully aged. Ages ranged from 2 to 65 years with an average age of 13.8 years. Perfect agreement of all tested specimens was over half (50.8%) and agreement within 2 years was 98.0%. The coefficient of variation was 81.9%.

### Maturity

Due to the difficulty of distinguishing maturing and resting stage fish during the late summer months, fish collected during July and August were not included in the length at maturity calculation. This exclusion also ensured that fish that might be classified incorrectly as immature during the earliest stages of development (stage 2, which is prevalent in August) would not be included in the analysis. The smallest mature fish was 30.8 cm FL and the largest immature fish was 40.0 cm FL (Figure 4A). Length at 50% maturity was calculated to be 33.4 cm FL (SE = 0.301, 95% confidence interval [CI] = 32.8–34.0 cm). The youngest mature fish was age 7 and the oldest immature fish was age 23. A 58-year-old fish was not developmentally mature but was considered to be mature because the ovary contained high proportions of delta (late-stage) atresia, indicating it had previously spawned. This was the only fish sampled that appeared to be skipping spawning in the upcoming year. Age at 50% maturity was calculated to be 8.4 years (SE = 0.206, CI = 8.0–8.8 years, Figure 4B).

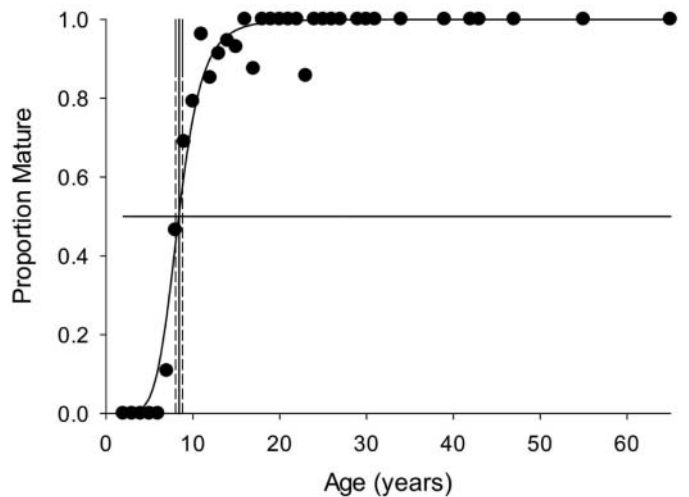
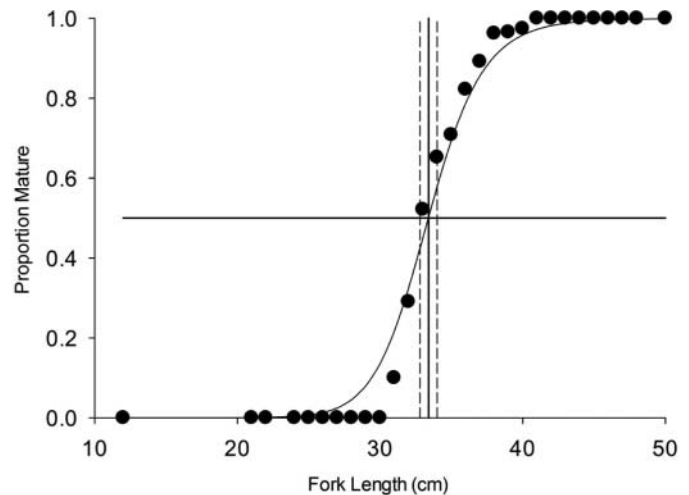


FIGURE 4. Logistic maturity curve for (top) fork length of Pacific Ocean Perch; and (bottom) for age of Pacific Ocean Perch. The dotted lines represent the 95% confidence values for  $A_{50}$  and  $L_{50}$ .

### DISCUSSION

Seasonality of the reproductive biology of Pacific Ocean Perch was similar to that reported for this species in the Gulf of Alaska by Lunsford (1999). Parturition appeared to occur predominately within the month of May. Pacific Ocean Perch appear to spawn later in higher latitudes. Parturition occurred in March off British Columbia and in April in the southeastern Gulf of Alaska (Westrheim 1975). This study found the period between fertilization and parturition to be 3 to 4 months, with embryonic development occurring between February and May. This is longer than previously reported for this species (Westrheim 1975; Gunderson 1977) in other regions and may relate to the later time of parturition in the Gulf of Alaska.

The management of Pacific Ocean Perch in the Gulf of Alaska is dependent upon accurate estimates of life history parameters, including length and age at 50% maturity. This study estimated an  $L_{50}$  of 33.4 cm FL, which is smaller than the 35.7 cm FL

currently utilized in stock assessment models (Lunsford 1999; Hanselman et al. 2009). Both of these estimates are significantly larger than the previously reported value of 28.5 cm (Chikuni 1975) for Pacific Ocean Perch in this region. Our estimate of  $L_{50}$  is also similar to values reported for Pacific Ocean Perch off the coasts of Washington state, Oregon state, and British Columbia, which ranged from 31.1 to 36.3 cm FL (Gunderson 1977, 1997; Hannah and Parker 2007). This study also estimated the  $A_{50}$  value to be 8.4 years, younger than the age (10.5 years) currently used in stock assessment models (Lunsford 1999; Hanselman et al. 2009). Previously reported  $A_{50}$  maturity values for Pacific Ocean Perch within the Gulf of Alaska range from 7 years (Chikuni 1975) to 10–12 years (Westrheim 1975), though Chikuni's estimates were based on aging from scales, which may be biased. In lower latitudes these values range from 5.2 years off the coast of Oregon (Hannah and Parker 2007) to 9.3–11.4 years (Gunderson 1977) in Canadian waters, and 8.1–10.1 years off the coast of Washington (Gunderson 1977, 1997). However, some of these ages were not directly measured but were derived from applying length at maturity data to growth curves.

The discrepancy between the current study and Lunsford's (1999) results may be attributable to either differences in technique, differences in the primary area of sampling, or a temporal change in parameters. Histological evaluations of maturity stage allow for a more precise and detailed examination of ovarian state than does visual staging and therefore the probability of misidentifying maturity stages is decreased. The current study obtained samples collected primarily from the central Gulf of Alaska, whereas Lunsford's (1999) age at maturity value was derived from samples obtained from the eastern Gulf of Alaska. It is possible that the age at maturity may differ between the two regions. Lunsford (1999) found that lengths at maturity between Gulf of Alaska regions were similar to one another but increased from the western Gulf of Alaska to the eastern Gulf of Alaska.

While Pacific Ocean Perch are distributed throughout the Northeast Pacific, the Gulf of Alaska has been and continues to be the dominant region in terms of Pacific Ocean Perch abundance (Ito, 1987). The biomass of Pacific Ocean Perch in the Gulf of Alaska is highest in the central Gulf of Alaska, and 60% of the apportionment of the total allowable catch is for statistical regions 620 and 630 (Figure 1; Hanselman et al. 2010). It is therefore most appropriate for age and length at maturity values to be derived predominately from central Gulf of Alaska specimens if one value is going to be applied for the entire region. Pacific Ocean Perch have been shown to have significant geographically related genetic and demographic structure in several localities within their range. Adult members of this species in Alaska waters belong to neighborhoods at geographic scales less than 400 km (Palof et al. 2011). Also two populations of Pacific Ocean Perch inhabit the eastern and western portions of Queen Charlotte Sound in British Columbia (Withler et al. 2001). It has been suggested that the metapopulation structure of some rockfish in the North Pacific is the result

of mesoscale oceanographic barriers to dispersal, the dispersal being limited between oceanographic domains (Gunderson and Vetter 2006). It is therefore likely that Pacific Ocean Perch captured in different areas of the Gulf of Alaska have differences in life history parameters and utilizing one value for this region may not be appropriate. While ultimately it will be worthwhile to examine differences in life history parameters in different localities, utilizing samples from the central Gulf of Alaska is most appropriate for the current management scenario.

An on-going challenge with rockfish reproductive research in the Northeast Pacific Ocean is the occurrence of abortive reproductive efforts of young rockfish reaching maturity. This phenomenon has been noted by a variety of authors and has been called a variety of terms, including a "maturity cycle" (Nichol and Pikitch 1994) and "abortive maturity" (Hannah and Parker 2007). The mechanism, duration, and frequency of this phenomenon are unclear as are how it may relate to environmental factors encountered by the individual or to the energetic condition of the fish. It has been suggested that these fish have a maturing period that lasts at least 1 year (Westrheim 1975; Lunsford 1999). Some authors have suggested that the frequency of fish in this state may vary with environmental factors (Hannah and Parker 2007). It may also be possible that until the appropriate energy reserves have been established, fish may be mature but not reproducing every year. The current study found that abortive maturity predominately occurs in younger fish (age 7–13 years). Abortive maturity was also found to be more predominant in younger Pacific Ocean Perch (age 5–9) collected from waters off Oregon state (Hannah and Parker 2007). A few older fish also experienced abortive maturity and while it is possible these fish were not yet mature, it may be more likely that energetic demands keep them from reproducing in a given year. There is a need for additional research on the prevalence, mechanics, and variability of this phenomenon to define the maturity levels of rockfish species in the North Pacific Ocean.

## ACKNOWLEDGMENTS

The authors wish to acknowledge the many individuals and agencies that collected samples from this project including R. Swanson, D. Jones, C. Rooper, P. Spencer, M. Martin, M. Zimmermann, D. Hanselman, D. Urban, K. Spalinger, A. Ellsworth, the North Pacific Groundfish Observer Program, and the Alaska Department of Fish and Game. In addition, we thank C. Worton for assistance with histological techniques and B. Mjos for valuable assistance in processing samples for this project. We also thank the crew of the F/V *Gold Rush*, including B. Ashley, D. Ashley, and M. Smith, for assistance in collecting samples during charter operations.

## REFERENCES

- Allen, M. J., and G. B. Smith. 1988. Atlas and zoogeography of common fishes in the Bering Sea and northeastern Pacific. NOAA Technical Report NMFS 66.

- Boehlert, G. W., M. Kusakari, and J. Yamada. 1987. Reproductive mode and energy costs of reproduction in the genus *Sebastes*. Pages 143–152 in B. R. Melteff, editor. Proceedings of the international rockfish symposium. University of Alaska, Alaska Sea Grant Report 87-2, Anchorage.
- Bowers, M. J. 1992. Annual reproductive cycle of oocytes and embryos of Yellowtail Rockfish *Sebastes flavidus* (Family Scorpaenidae). U.S. National Marine Fisheries Service Fishery Bulletin 90:231–242.
- Chikuni, S. 1975. Biological study on the population of Pacific Ocean Perch in the North Pacific. Bulletin Far Seas Fisheries Research Laboratory 12:1–119.
- Chilton, D. E., and R. J. Beamish. 1982. Age determination methods for fishes studied by the groundfish program at the Pacific Biological Station. Canadian Special Publication of Fisheries and Aquatic Sciences 60.
- Gunderson, D. R. 1977. Population biology of Pacific Ocean Perch, *Sebastes alutus*, stocks in the Washington–Queen Charlotte Sound region, and their response to fishing. U.S. National Marine Fisheries Service Fishery Bulletin 75:369–403.
- Gunderson, D. R. 1997. Spatial patterns in the dynamics of slope rockfish stocks and their implications for management. U.S. National Marine Fisheries Service Fishery Bulletin 95:219–230.
- Gunderson, D. R., and R. D. Vetter. 2006. Temperate rocky reef fishes. Pages 69–117 in J. P. Kritzer and P. F. Sale, editors. Marine metapopulations. Elsevier, Burlington, Massachusetts.
- Hannah, R. W., and S. J. Parker. 2007. Age-modulated variation in reproductive development of female Pacific Ocean Perch (*Sebastes alutus*) in waters off Oregon. Pages 1–20 in J. Heifetz, J. DiCosimo, A. J. Gharrett, M. S. Love, V. M. O'Connell, and R. D. Stanley, editors. Biology, assessment, and management of North Pacific rockfishes. University of Fairbanks, Alaska Sea Grant Program, Report AK-SG-07-01, Fairbanks.
- Hanselman, D., S. K. Shotwell, J. Heifetz, J. T. Fujioka, and J. N. Ianelli. 2009. Assessment of Pacific Ocean Perch in the Gulf of Alaska. Pages 743–816 in Stock assessment and fishery evaluation report for the groundfish resources of the Gulf of Alaska. North Pacific Fishery Management Council, Anchorage, Alaska.
- Hanselman, D., S. K. Shotwell, J. Heifetz, and J. N. Ianelli. 2010. Assessment of Pacific Ocean Perch in the Gulf of Alaska. Pages 543–546 in Stock assessment and fishery evaluation report for the groundfish resources of the Gulf of Alaska. North Pacific Fishery Management Council, Anchorage, Alaska.
- 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. U.S. National Marine Fisheries Service Fishery Bulletin 91:101–128.
- Ito, D. H. 1987. Comparing abundance and productivity estimates of Pacific Ocean Perch in waters off the United States. Pages 287–298 in B. R. Melteff, editor. Proceedings of the international rockfish symposium. University of Alaska, Alaska Sea Grant Report 87-2, Anchorage.
- Kendall, A. W., Jr., and W. H. Lenarz. 1987. Status of early life history studies of northeast Pacific rockfishes. Pages 99–128 in B. R. Melteff, editor. Proceedings of the international rockfish symposium. University of Alaska, Alaska Sea Grant Report 87-2, Anchorage.
- Leaman, B. M. 1991. Reproductive styles and life history variables relative to exploitation and management of *Sebastes* stocks. Environmental Biology of Fishes 30:253–271.
- Lunsford, C. 1999. Distribution patterns and reproductive aspects of Pacific Ocean Perch (*Sebastes alutus*) in the Gulf of Alaska. Master's thesis. University of Alaska Fairbanks, Juneau.
- McDermott, S. F. 1994. Reproductive biology of Rougheye and Shortraker Rockfish, *Sebastes aleutianus* and *Sebastes borealis*. Master's thesis. University of Washington, Seattle.
- Nichol, D. G., and E. K. Pikitch. 1994. Reproduction of Darkblotched Rockfish off the Oregon coast. Transactions of the American Fisheries Society 123:469–481.
- NMFS (National Marine Fisheries Service). 2011. Gulf of Alaska reporting areas. NMFS, Alaska Regional Office, Juneau. Available: [www.fakr.noaa.gov/tr/figures/fig3.pdf](http://www.fakr.noaa.gov/tr/figures/fig3.pdf). (October 2011).
- Palof, K. J., J. Heifetz, and A. J. Gharrett. 2011. Geographic structure in Alaskan Pacific Ocean Perch (*Sebastes alutus*) indicates limited lifetime dispersal. Marine Biology 158:779–792.
- Westrheim, S. J. 1970. Survey of rockfishes, especially Pacific Ocean Perch, in the northeast Pacific Ocean, 1963–66. Journal of the Fisheries Research Board of Canada 27:1781–1809.
- Westrheim, S. J. 1975. Reproduction, maturation, and identification of larvae of some *Sebastes* (Scorpaenidae) species in the northeast Pacific Ocean. Journal of the Fisheries Research Board of Canada 32:2399–2411.
- Withler, R. E., T. D. Beacham, A. D. Schulze, L. J. Richards, and K. M. Miller. 2001. Co-existing populations of Pacific Ocean Perch, *Sebastes alutus*, in Queen Charlotte Sound, British Columbia. Marine Biology 139:1–12.
- Zimmermann, M. 1997. Maturity and fecundity of Arrowtooth Flounder, *Atheresthes stomias*, from the Gulf of Alaska. U.S. National Marine Fisheries Service Fishery Bulletin 95:598–611.