

Abstract—The dusky rockfish (*Sebastes variabilis*) has recently been resurrected as a distinct species in the genus *Sebastes*. Reproductive biology and growth were examined for this redescribed species in the central Gulf of Alaska. Age and length at 50% maturity were 9.2 years and 365 mm fork length, respectively, which are lower than previously reported. Fertilized ova and eyed embryos were observed in April and evidence of postparturition was not observed until May. The gonadosomatic index decreased with the onset of postparturition in May. Von Bertalanffy growth parameters for female dusky rockfish, estimated from the maturity samples, were significantly different from growth parameters derived from Gulf of Alaska fishery-independent survey data.

Maturity and growth of female dusky rockfish (*Sebastes variabilis*) in the central Gulf of Alaska

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One quarter of the 65 rockfish species distributed throughout the Northeast Pacific reside in the Gulf of Alaska (Love et al., 2002). Life history information is limited for these temperate rockfish species, such as the reproductive biology and growth rates of the female dusky rockfish (*Sebastes variabilis*) (Pallas, 1814), which is the predominant pelagic rockfish species on the central Gulf of Alaska shelf. Reproduction in rockfish species is viviparous; fertilization of oocytes is internal and adult females provide some nutritional support for the developing larvae until parturition (Boehlert and Yoklavich, 1984). Length at 50% maturity in female rockfish is variable, occurring at a larger size in more northerly species. Rockfish species in the Gulf of Alaska also have wide ranging growth rates, with pelagic shelf rockfish growing faster than their demersal shelf congeners (Haldorson and Love, 1991; Munk, 2001).

Dusky rockfish have recently been redescribed as a separate species (Orr and Blackburn, 2004). The light and dark color variations previously described for *S. ciliatus* (Tilesius, 1813) have been defined as two distinct species: *S. ciliatus* and *S. variabilis*. *Sebastes ciliatus* is the shallow water, dark variant that is now commonly called “dark rockfish,” and *S. variabilis* is the deepwater, light variant which is now called “dusky rockfish.” Dark rockfish are caught on shallow, nearshore rocky reefs and dusky rockfish are found less frequently in nearshore habitats and are often captured in large aggregations over the outer

continental shelf (Orr and Blackburn, 2004). Dusky rockfish are patchily distributed; concentrated groups are found near the mouths of submarine gullies or canyons and along submerged banks (Reuter, 1999).

Before this study, estimates of dusky rockfish maturity for the Gulf of Alaska were based on visual observations of gonad maturity from a limited sample of this species in the Kodiak Island area. Previous work revealed the potential for incorrect identification of oocyte developmental stages with the macroscopic method in comparison to studies where the histological evaluation method has been used (McDermott, 1994; Zimmerman, 1997). Dusky rockfish growth parameters were derived from data sets collected before the redescription of dark and dusky rockfish.

The objective of this study was to provide improved life history data for the newly described dusky rockfish by 1) producing histologically derived estimates of the age and length at 50% maturity ($A_{0.5}$ and $L_{0.5}$); 2) describing the seasonal timing of ovary development in female dusky rockfish; and 3) comparing growth rates and weight-length relationships derived from the maturity-estimate samples to a larger data set collected in the central Gulf of Alaska for both male and female dusky rockfish.

In the Gulf of Alaska, management of the dusky rockfish resource is aided by the annual pelagic shelf rockfish stock assessment and fisheries evaluation process, with the use of a fishery-independent age-based

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Table 1

Summary of seasonal data and collection method for central Gulf of Alaska female dusky rockfish (*Sebastes variabilis*) samples used to estimate reproductive maturity, gonadosomatic index, and growth parameters. Sample collections: trawl = bottom trawl; hook-and-line.

Port sample collections	Chartered vessel collections	Trawl survey collections
February 2000 <i>n</i> =4	March 2000 <i>n</i> =9 (trawl) <i>n</i> =8 (hook-and-line)	July 2000 <i>n</i> =1
January 2001 <i>n</i> =15	April 2000 <i>n</i> =3 (hook-and-line)	January 2001 <i>n</i> =27
February 2001 <i>n</i> =3	November 2000 <i>n</i> =36 (trawl)	May 2001 <i>n</i> =18
March 2001 <i>n</i> =20	April 2001 <i>n</i> =14 (trawl) <i>n</i> =30 (hook-and-line)	June 2001 <i>n</i> =5

assessment model to determine the fishing quota for this rockfish species. Maturity estimates and growth parameters derived from this study could improve the estimation of spawning stock biomass and the stock recruitment relationship of future dusky rockfish stock assessments.

Materials and methods

Samples for the maturity estimates were randomly collected from three sources: 1) port sampling of commercial jig and trawl fisheries around Kodiak Island, Alaska; 2) hook-and-line and bottom trawl samples from chartered vessels around Kodiak Island; and 3) bottom trawl sampling during the Gulf of Alaska groundfish trawl survey conducted by the National Marine Fisheries Service (NMFS) in 2001. Samples were collected from February through April, June, and November of 2000, and from January through June of 2001 (Table 1). The majority of the samples were collected locally from nearshore waters on the southeast side of Kodiak Island. Specific catch locations were not available for many of the samples because of the confidential nature of the catch reporting system; however, Alaska Department of Fish and Game statistical areas were reported with each collection and are used here to show generalized collection locations (Fig. 1).

Sagittal otoliths and ovaries were collected from each individual female rockfish, as well as fork length (FL) to the nearest mm, total body weight (W) to the nearest gram, and individual ovary weight to the nearest gram. Otoliths were aged according to standard break and burn procedures (Chilton and Beamish, 1982). Tissue samples used for histological maturity examination were taken from the middle of the right ovary and fixed in a 10% neutral buffered formalin solution. Tissue was taken from the left ovary if the right ovary was torn because it has been determined in previous histological studies of rockfish maturity that there is

no difference in oocyte development between the left and right ovary (Shaw, 1999). These tissue samples taken at all macroscopic stages, except stage 5 (eyed larvae), were embedded in paraffin, thin sectioned to 7 μm with a rotary microtome, mounted on slides, and stained with standard hematoxylin and eosin (Sheehan and Hrapchak, 1980). Ovary samples with eyed larvae were fragile and not amenable to the paraffin and sectioning process.

A compound microscope and ocular micrometer were used to measure the diameter of the oocytes. The diameter of the fifth largest oocyte on a randomly selected transect along the histological cross section of the gonad was used as the decisive factor for evaluating the most advanced nonatretic oocyte and to determine the developmental stage of the ovary (West, 1990). This method eliminated the possibility of a single and largest oocyte misrepresenting the development stage of the ovary. These ovary stages were evaluated on the basis of seven maturity stages and corresponding oocyte development previously described for northern rockfish (*S. polypsinis*) (Chilton, 2006) (Table 2). Ovaries with vitellogenic oocytes developed to the migratory nucleus stage or the presence of postovulatory follicles were used as evidence of a mature ovary sample. Nichol and Pikitch (1994) found darkblotched rockfish (*S. crameri*) oocytes in the early vitellogenic stage (described as secondary yolk formation) with high levels of atresia (resorption of the unfertilized oocyte) and classified females with ovaries developed to this stage as functionally immature.

Age and length at 50% maturity ($A_{0.5}$ and $L_{0.5}$) were determined by fitting a logistic function to the maturity data as a function of age or length with generalized linear modeling generated by S-plus statistical software, and then evaluating the fitted model at a maturity proportion of 0.50 (S-plus, vers. 6.2; Insightful Corp., Seattle, WA). The variance of $A_{0.5}$ and $L_{0.5}$, as well as 95% confidence intervals (CI), were estimated by bootstrapping methods (Efron and Tibshirani, 1993).

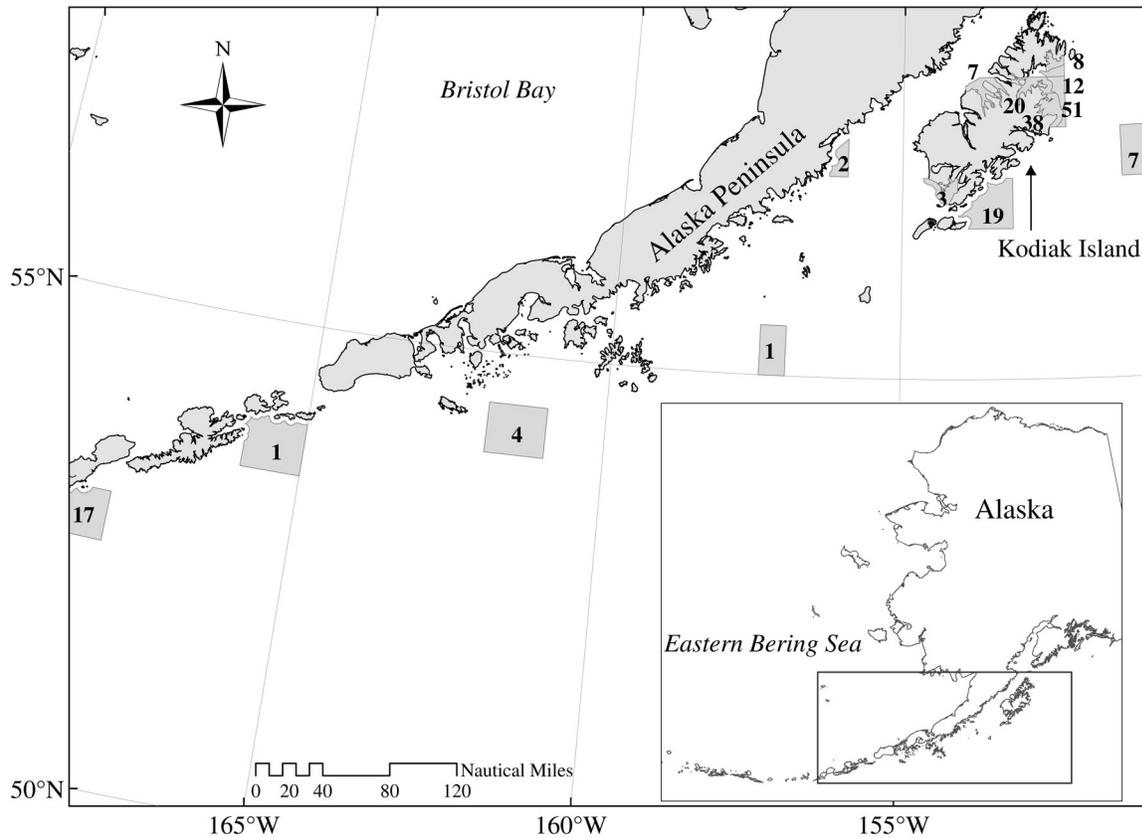


Figure 1

Locations in the central Gulf of Alaska where female dusky rockfish (*Sebastes variabilis*) samples were collected in 2000 and 2001 for the growth and maturity study. Number of samples collected within each Alaska Department of Fish and Game statistical area, delineated by shaded blocks, are reported in each block.

A gonadosomatic index (I_G) was calculated with the formula

$$[IG = 100(\text{gonad weight (g)} / \text{total body weight (g)})], \quad (1)$$

to show seasonal changes in development of the ovary with respect to the total body weight. Gonad weights were not collected in May of 2001.

Growth parameters for the female dusky rockfish collected in the Gulf of Alaska for the maturity estimates were calculated by using nonlinear least squares to fit the von Bertalanffy growth equation to age-length data. The von Bertalanffy equation can be expressed as

$$L_t = L_\infty(1 - e^{(-k*(t-t_0))}), \quad (2)$$

where L_t = the predicted length (mm FL) at age t (years);

L_∞ = the mean asymptotic length (mm) at maximum age;

k = the growth constant (per year); and

t_0 = the age (years) at which the fish would have been zero length.

Von Bertalanffy growth parameters for dusky rockfish in the central Gulf of Alaska were compared to the growth parameters derived from data collected for the maturity study (above). A larger set of age-length data, randomly collected from the 1996 to 2003 NMFS Gulf of Alaska groundfish surveys (GOAS), was used for male and female dusky rockfish separately and for combined sexes if no difference was found. A growth function was fitted to the data to test for significant differences in growth rate between the males and females and the combined-sex age-length data. Differences between sexes in the von Bertalanffy growth parameters were tested with a likelihood ratio test (Kimura, 1980; Haddon, 2001). This test was also used to determine whether growth parameters of female dusky rockfish caught in the NMFS GOAS were different from those values calculated from the maturity study collection.

An allometric weight-length function expressed as $W = aL^b$, where W is weight in grams, and L is length in millimeters, was fitted to the weight and length data from the maturity samples collected in 2000–01, and the NMFS GOAS data from 1996 to 2003. Values for constants a and b were estimated by linear regression of logarithmically transformed weight-length data

Table 2

Maturity criteria for staging gonads of female dusky rockfish (*Sebastes variabilis*) based on macroscopic and microscopic observations. Adapted from Chilton (2006).

Maturity stage	Macroscopic description	Histological description	Oocyte stages
1 Immature	Thin and thready ovaries, pink or light red in color; oocytes are not visible	Oogonial nests and unyolked oocytes, oocyte diameter is between 80 and 150 μm	Oogonia organized into nests (ON) with some oocytes at early perinucleus (EP) and late perinucleus (LP) development
2 Maturing or intermediate	Ovaries cream to light yellow in color with thin ovarian wall; oocytes visible	Initial yolk accumulation in oocytes with yolk globules very small, oocyte diameter 160 to 320 μm	LP and stage-1 through stage-2 yolk accumulation in oocytes, ON and EP stage oocytes are also present
3 Vitellogenesis	Individual eggs are visible, bright yellow in color; ovarian wall thickening and darkly pigmented	Yolk globules and oil vesicles present, oocyte diameter 400 to 600 μm	Tertiary yolk stage and initial oil vacuoles coalescing in oocytes
4 Fertilized	Large translucent eggs with pink to yellow tint, ovaries enlarged to accommodate large hydrated eggs	Embryo diameter is 600 to as large as 950 μm	Stage-8 migratory nucleus through early embryonic development
5 Eyed larvae	Ovary enlarged with eyed larvae, ovarian wall thin and transparent, easily torn or broken open	Embryos with dark pigmented eyes	Eyed larvae
6 Postparturition	Ovary flaccid and dark red in color, some eyed larvae are visible	Postovulatory follicles (POF) and atretic oocytes, residual larvae are present	Evidence of parturition based on POF, atretic oocytes and residual embryos
7 Resting	Ovary pink to reddish grey in color, eggs are small and opaque	Oogonial nests and resorption of POF as well as atretic oocytes	ON through EP stage oocytes, POF and atretic oocytes present

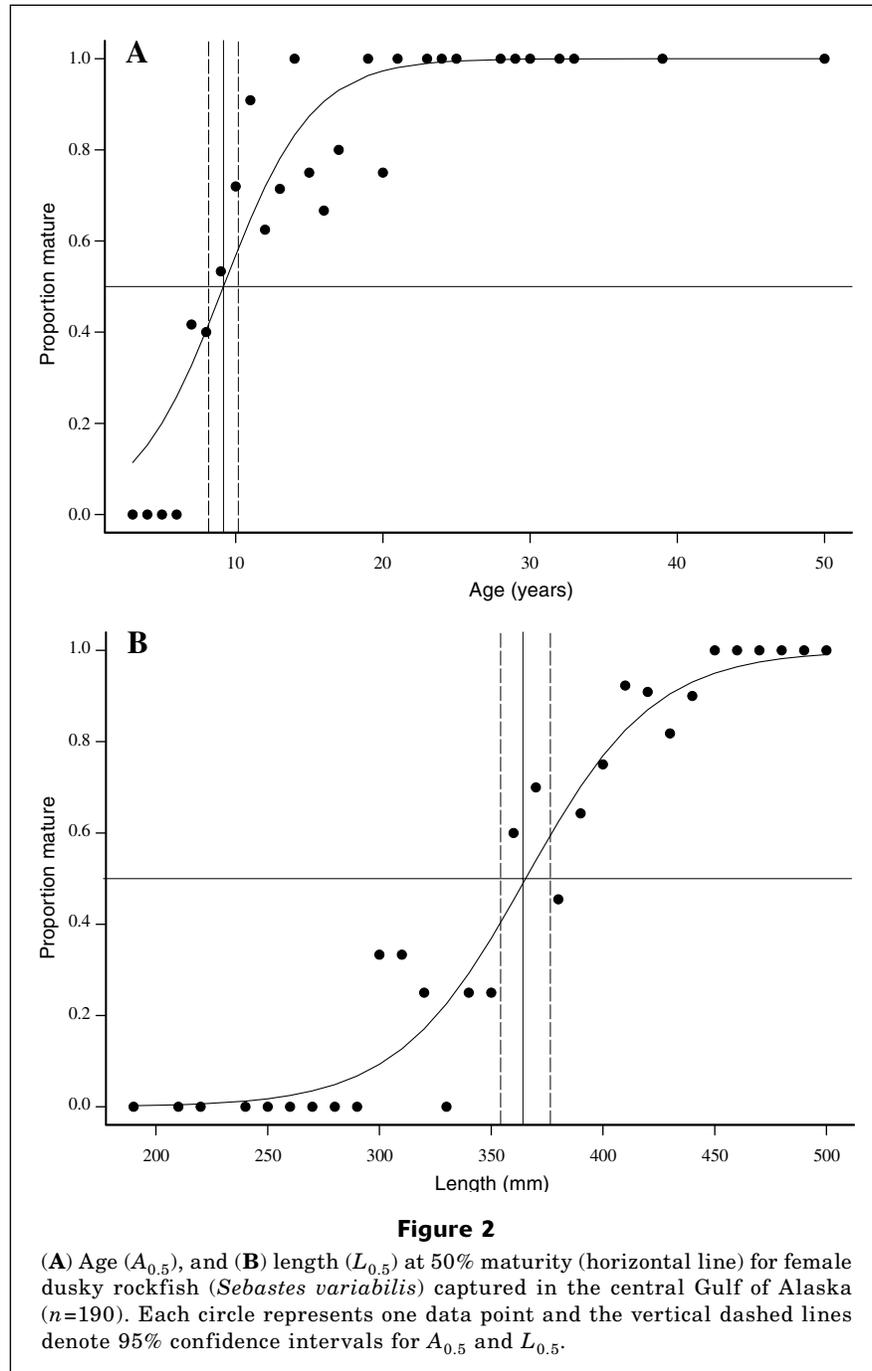
in the weight-length relationship. The residuals of the log-transformed weight-length data were approximately normally distributed and no transformations were made (Gerritsen and McGrath, 2007). Student's *t*-test was used to test for a significant difference in the weight-length relationship from the maturity-estimate samples compared to female dusky rockfish from the NMFS GOAS samples (Snedecor and Cochran, 1989).

Results

A total of 193 ovaries with corresponding otoliths and fish lengths were collected to estimate $A_{0.5}$ and $L_{0.5}$ of female dusky rockfish. Three otoliths were unreadable, resulting in 190 samples used for the age at 50% maturity estimate analysis of which 166 samples were collected along the east and south side of Kodiak Island and 24 were collected during May and June 2001 from the NMFS GOAS along the Alaska Peninsula. The ages of female dusky rockfish ranged from 3 to 50 years

and lengths ranged from 190 mm to 500 mm FL. The age at 50% maturity was estimated at 9.2 years (95% CI=8.2–10.2; Fig. 2A) and the length at 50% maturity was estimated at 365 mm FL (95% CI=354–378; Fig. 2B and Table 3).

Histological methods used to evaluate ovary development in this study resulted in observations of vitellogenic oocytes present in all seven months sampled; January through June, and November. Stage-4 fertilized ova, and stage-5 eyed embryos were observed only in April, and stage-6 postparturition was not observed until May, although a small number of ovaries were at stage 7 in April (Fig. 3). These results indicate that the peak of dusky rockfish fertilization in the central GOA occurred in April followed by parturition in May when postovulatory follicles (POFs) were present. The ovaries exhibiting POFs and extrusion of larvae, stage 7, in April were from females ranging in size from 300 to 360 mm (7 to 9 years of age) and could be an example of delayed oocyte development due to their smaller size.



The gonadosomatic index (I_G) began increasing in November and January, reaching a maximum in March, followed by a decrease in April. The lowest value observed was from one sample collected in June and qualitatively appeared to follow the decreasing trend (Fig. 4). This increase in I_G from late winter to spring shows an increase in the ratio of ovary weight to total body weight with the development of fertilized ova in April. The lowest I_G value in June corresponded with low ovary weight due to postparturition. The seasonal trend of decreasing I_G , coupled with the monthly ovary

development results of this study, indicates May as the peak month of parturition for dusky rockfish in the central Gulf of Alaska.

Von Bertalanffy growth parameters for female dusky rockfish from the maturity estimate sample were $L_\infty=449$ mm, $k=0.219$, and $t_0=0.855$ in contrast to values of $L_\infty=480$ mm, $k=0.211$, and $t_0=1.106$ for females from the NMFS GOAS. The female dusky rockfish from the NMFS GOAS were slower growing than females collected for the maturity estimate as reflected by the different mean asymptotic length and growth coefficients

(Fig. 5A). The likelihood ratio test showed a significant difference in growth parameters between the female dusky rockfish caught in the maturity study and females from the NMFS GOAS ($\chi^2=158.8$, $df=3$, $P<0.001$) (Table 4).

Von Bertalanffy growth parameters for male dusky rockfish from the NMFS GOAS were $L_\infty=461$ mm, $k=0.243$, and $t_0=1.232$ compared to values of $L_\infty=480$ mm, $k=0.211$, and $t_0=1.106$ for females; these results indicate that female dusky rockfish have a slower growth rate but a larger mean asymptotic length than males (Fig. 5B). The likelihood ratio test showed a significant difference between male and female dusky rockfish ($\chi^2=61.5$, $df=3$, $P<0.001$) from the NMFS GOAS (Table 4).

There was a significant difference detected in the slopes of the log-transformed weight-length data derived from the female dusky rockfish maturity sample when compared to female dusky rockfish caught in the NMFS GOAS according to the Student's t -test ($t=4.94$, $P<0.005$) (Table 5). Although the slope of the weight-length data from the maturity study was significantly different from the NMFS GOAS, both data sets had comparable length ranges with 190 to 500 mm FL for the maturity study and 170 to 530 mm FL for the NMFS GOAS. Consequently, this difference is not likely due to trawl gear selectivity in the NMFS GOAS.

Discussion

The maturity parameters presented in this study are not consistent with previously reported estimates of size and age at 50% maturity for female dusky rockfish of 11.3 years and 428 mm (Love et al., 2001), which are higher and larger than the results from the present study. The differences could be due to the timing, sample size, and method of determining the previous maturity estimates, where ovary development was evaluated at a macroscopic level from a small number of samples. The results of this study are based on a larger sample, collected over multiple months during a two-year period, and on an improved method to evaluate ovary development and may therefore represent a better estimate of maturity.

The seasonal timing of parturition in dusky rockfish is comparable to that of other Gulf of Alaska rockfish species, in April and May (Love et al., 2001; Chilton, 2006). Parturition begins to occur in female northern rockfish from the central Gulf of Alaska in April and higher numbers of POFs are found in May and June

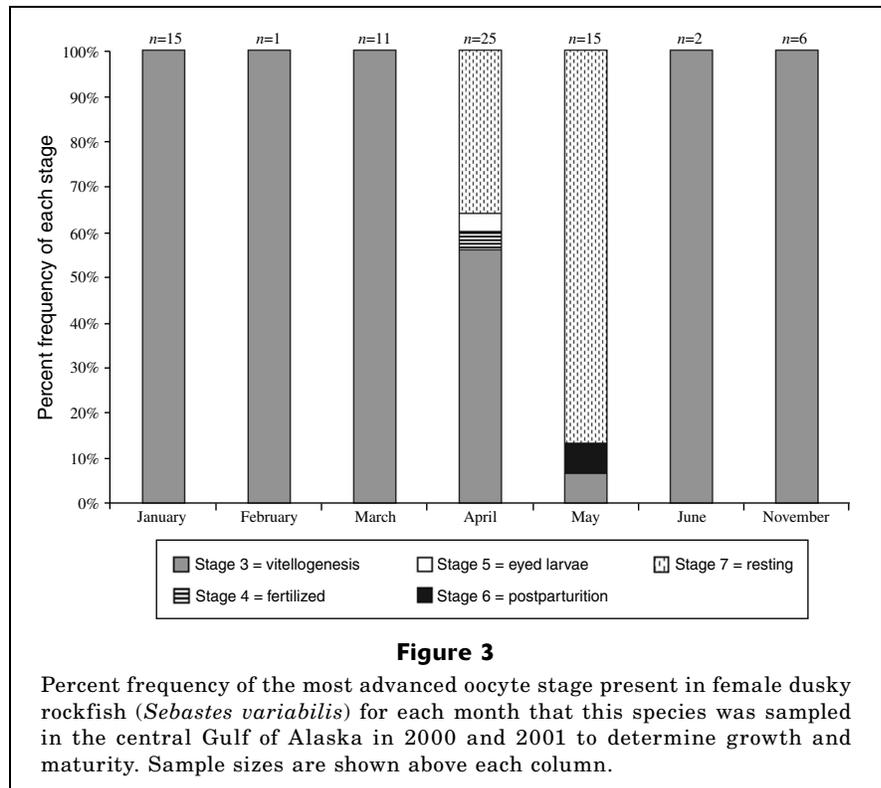


Figure 3

Percent frequency of the most advanced oocyte stage present in female dusky rockfish (*Sebastes variabilis*) for each month that this species was sampled in the central Gulf of Alaska in 2000 and 2001 to determine growth and maturity. Sample sizes are shown above each column.

Table 3

Maturity parameters and variances for female dusky rockfish (*Sebastes variabilis*) in the central Gulf of Alaska estimated by fitting a logistic function to the maturity data as a function of age or length with generalized linear modeling. a=scaling constant; b=allometric growth parameter.

	Value	Variance
$L_{0.5}$	365 mm	38.055
a	-12.728	3.581
b	0.035	2.408
$A_{0.5}$	9.2 years	0.254
a	-3.047	0.528
b	0.332	0.007

(Chilton, 2006). The small number of samples collected for this study in June prevented an estimation of the extent of parturition in dusky rockfish beyond the month of May. The smaller mature dusky rockfish exhibiting stage-7 ovaries in April were most likely fertilized in the previous reproductive season which could have occurred as late as July in the previous year. Nichol and Pikitch (1994) found that oocytes of smaller mature female darkblotched rockfish developed later in the season than oocytes from larger mature females.

The corresponding increase in female dusky rockfish ovary weight compared to total body weight, or gonadosomatic index (I_G), is a result of the advancement of

Table 4

Von Bertalanffy growth parameters for dusky rockfish (*Sebastes variabilis*) calculated from National Marine Fisheries Service, Gulf of Alaska groundfish survey data and the central Gulf of Alaska maturity study data. L_{∞} =mean asymptotic length at maximum age; k =growth constant; t_0 =age of fish at zero length; n =number of samples.

	L_{∞} (mm)	k	t_0	n
Gulf of Alaska groundfish survey (1996–2003)				
Females	480	0.211	1.106	752
Males	461	0.243	1.232	698
Sexes combined	472	0.223	1.117	1450
Gulf of Alaska maturity study (2000–01)				
Females	449	0.219	0.855	190

Table 5

Estimated weight-length parameters for dusky rockfish (*Sebastes variabilis*) captured in the National Marine Fisheries Service, Gulf of Alaska groundfish surveys and the central Gulf of Alaska maturity study. a =scaling constant; b =allometric growth parameter; n =number of samples.

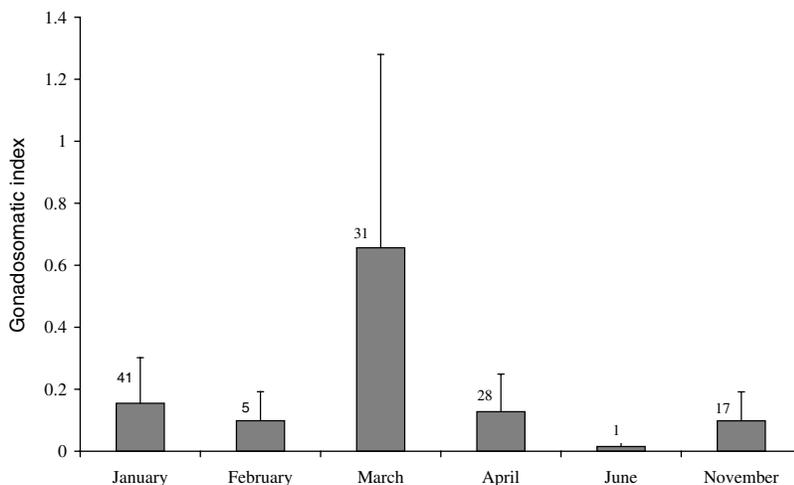
Weight-length constants	a	b	n
Gulf of Alaska combined sex from NMFS groundfish surveys (1996–2003)	0.0088	3.11	1581
Gulf of Alaska females (1996–2003)	0.0100	3.09	817
Maturity study females (2000–01)	0.0131	3.04	176

oocyte development in March, followed by a decrease in the I_G with the onset of parturition occurring from April through June. This pattern of increasing I_G until release of the developed larvae at parturition occurs in other rockfish species. The highest I_G values for *S. thompsoni* were recorded in March and a corresponding increase in the frequency of gestation (fertilized ova). Subsequently lower I_G values occurred in April and May because of an increased frequency of parturition during those months (Lee et al., 1998).

Previous research on dusky rockfish growth in the Gulf of Alaska (GOA) has revealed no differences between sexes or management regions. Reuter (1999) es-

timated growth parameters of dusky rockfish from the combined 1990–96 NMFS GOAS and commercial fisheries data and found no differences in growth between the three management regions, eastern GOA, central GOS, and western GOA, and no difference in growth between sexes with values of L_{∞} =457 mm, k =0.22, t_0 =0.74 for males, and females of L_{∞} =461 mm, k =0.25, t_0 =1.24. However, the results of the present study indicate significant differences between male and female growth parameters estimated from the fishery-independent data collected on the NMFS GOAS.

It is not unusual for female rockfish to grow larger than males but at a slower rate, because of the trade-off between somatic growth and growth for reproduction (Helser et al., 2007). The differences in growth parameters between previous research and this study could be due to the combination of dark and dusky rockfish species in the commercial fishing data or due to the NMFS GOAS data, which were collected before 1996. Before 1996, the light and dark color variant of dusky rockfish caught on the NMFS GOAS were combined into a single species group as dusky rockfish and this treatment prevents comparison of dusky rockfish growth parameters before 1996. Differences in von Bertalanffy growth parameters and the weight-length relationship between the NMFS GOAS and the maturity-estimate collection in this study could be due to the timing of the sample collection. The NMFS GOAS occurs in the months of June and July whereas samples

**Figure 4**

Mean monthly gonadosomatic indices for female dusky rockfish (*Sebastes variabilis*) captured in the central Gulf of Alaska ($n=124$). Sample sizes are shown above each column; bars indicate 5% confidence intervals.

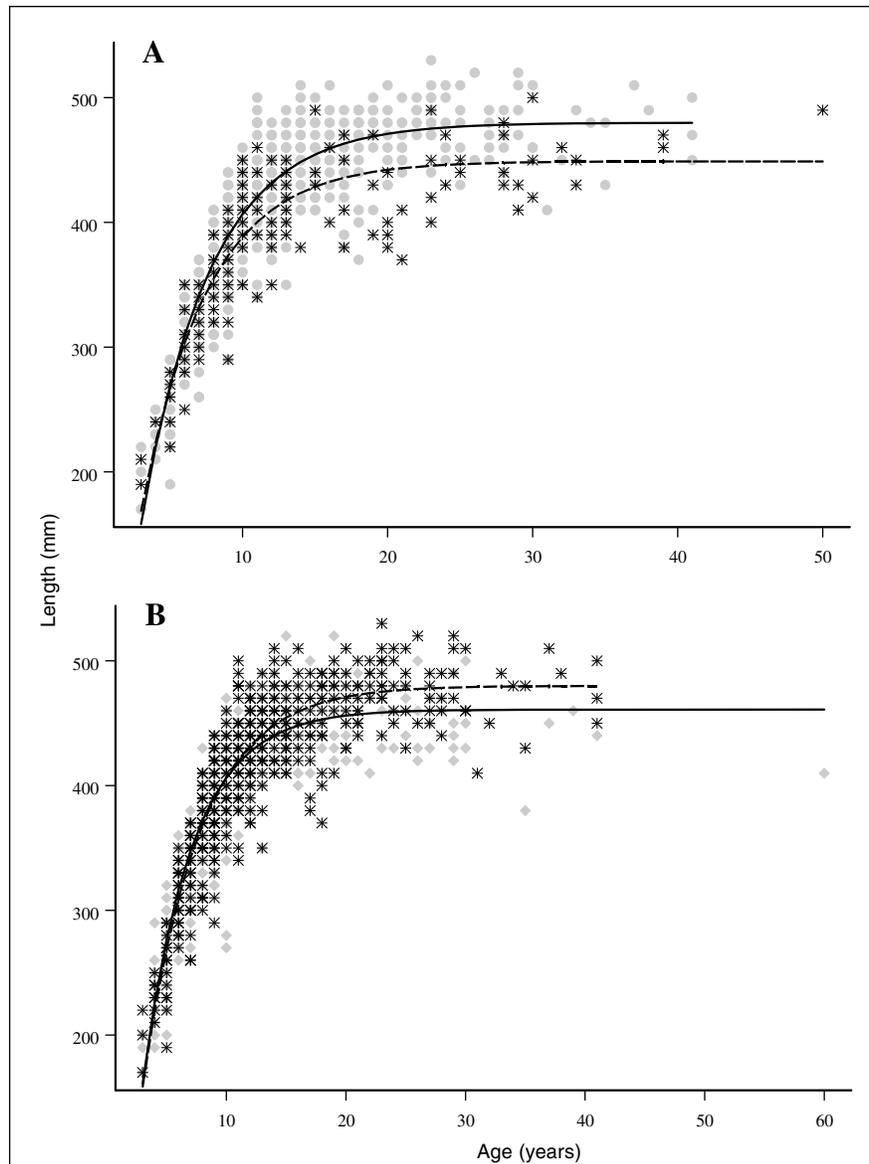


Figure 5

Growth curves for (A) female dusky rockfish (*Sebastes variabilis*) determined from 1996–2003 National Marine Fisheries Service (NMFS) Gulf of Alaska groundfish survey (GOAS) samples (gray circles) and the 2000–2001 central Gulf of Alaska maturity samples (asterisks) ($n=940$); and (B) NMFS GOAS male (gray diamonds) and female (asterisks) dusky rockfish ($n=1450$). Solid line (NMFS GOAS females) and dashed line (maturity sample females) in (A) illustrate the predicted relationship as do the solid (males) and dashed (females) lines in (B). Overlapping symbols in (A) and (B) represent two data points with the same value.

for the maturity estimate were collected throughout the year.

Future studies focusing on the reproductive maturity of rockfish would benefit from the collection of samples throughout the year. In this study, the seasonal timing of ovary collections for the maturity estimate was crucial for the histological evaluation of the most ad-

vanced oocytes within developing ovaries, as well as for highlighting the possibility of delayed development of small mature females within a year. In previous studies, where a histological method has been used to evaluate rockfish reproduction, the need for seasonal sampling has been emphasized (Nichol and Pikitch, 1994; Shaw, 1999; Chilton, 2006). The differences in growth

parameters and weight-length relationships between the maturity-estimate collection and the NMFS GOAS are an indication that sampling throughout the year, in months additional to those of the summer survey, could improve those estimates and could prove beneficial to the assessment of dusky rockfish and management of the pelagic shelf rockfish fisheries.

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