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[Article]

Reproductive Characteristics and Mortality of Female Giant Grenadiers in the Northern Pacific Ocean

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Abstract.—Giant grenadiers *Albatrossia pectoralis* are caught as bycatch in deep-sea commercial fisheries in relatively large numbers. The population appears to be stable, although there is no directed fishery, catch limits, or reporting requirements. The purpose of our study was to describe and quantify the reproductive life history characteristics and natural mortality of female giant grenadiers. During the summers of 2004 and 2006, a total of 338 specimens were collected from the Gulf of Alaska. Every phase of reproductive development was found, suggesting a protracted annual spawning season. An ovarian wall thickness technique was used to successfully place 31% ($n = 24$) of the fish with an unknown maturity status into a known category. Female age at 50% maturity was 22.9 years, and preanal fin length at 50% maturity was 26 cm. Total fecundity ranged from 35,000 to 231,000 oocytes (mean = 106,761), with a mean mature oocyte diameter of 1.26 mm. We developed a new technique for preparing otoliths for age determination by grinding off the distal surface to elucidate the growth zones; age ranged from 14 to 58 years. Estimates of natural female mortality ranged from 0.052 to 0.079 and estimates of total female mortality from 0.061 to 0.149. This life history information will be essential for future management of giant grenadier populations in the North Pacific Ocean.

Giant grenadiers *Albatrossia pectoralis* inhabit the continental slope to depths in excess of 2,000 m from Baja California, Mexico, around the arc of the North Pacific Ocean to Japan, including the Bering Sea and the Sea of Okhotsk (Mecklenburg et al. 2002). The giant grenadier is by far the most abundant fish species in terms of biomass at depths of 200–1,000 m on the continental slope of Alaska (Clausen 2008). There has never been a directed fishery for giant grenadiers in the Gulf of Alaska (GOA), but they are frequently taken as bycatch in the sablefish *Anoplopoma fimbria* longline fishery. Currently, there are no catch limits or reporting requirements for giant grenadiers. Because they are relatively large (>14 kg), numerous, and widespread, they have economic potential, like other grenadiers that have been commercially exploited, such as roughhead grenadier *Macrourus berglax* (Fossen et al. 2003), roundnose *Coryphaenoides rupestris* (Atkinson 1995), and Pacific *Coryphaenoides acrolepis* (Clausen 2008).

Because of their abundance, giant grenadiers are likely to be an important component of the continental slope ecosystem in the North Pacific Ocean. The general characteristics of grenadier species (late maturity, slow growth, and high mortality after being discarded by a fishery) make giant grenadiers susceptible to overexploitation, although their biomass is currently stable (Clausen 2008). Many deep-sea fishes that share these life history traits have been declared endangered according to World Conservation Union criteria, and eight other deep-sea fishes have exhibited significant population declines (Devine et al. 2006; Baker et al. 2009). Of the eight that are endangered, two are grenadier species (roundnose and roughhead).

A study of giant grenadier age and growth off the U.S. West Coast, GOA, and Aleutian Islands found that age ranged from 13 to 56 years based on radiometric aging and otolith readings (Burton 1999). However, there was not good agreement between the results of the radiometric and otolith aging methods. More recently, giant grenadier catch and distribution have been described off Alaska (Clausen 2008), Kamchatka, and the northern Kuril Islands (Orlov and Tokranov 2008). Tuponogov et al. (2008) described the distribution of giant grenadiers from the

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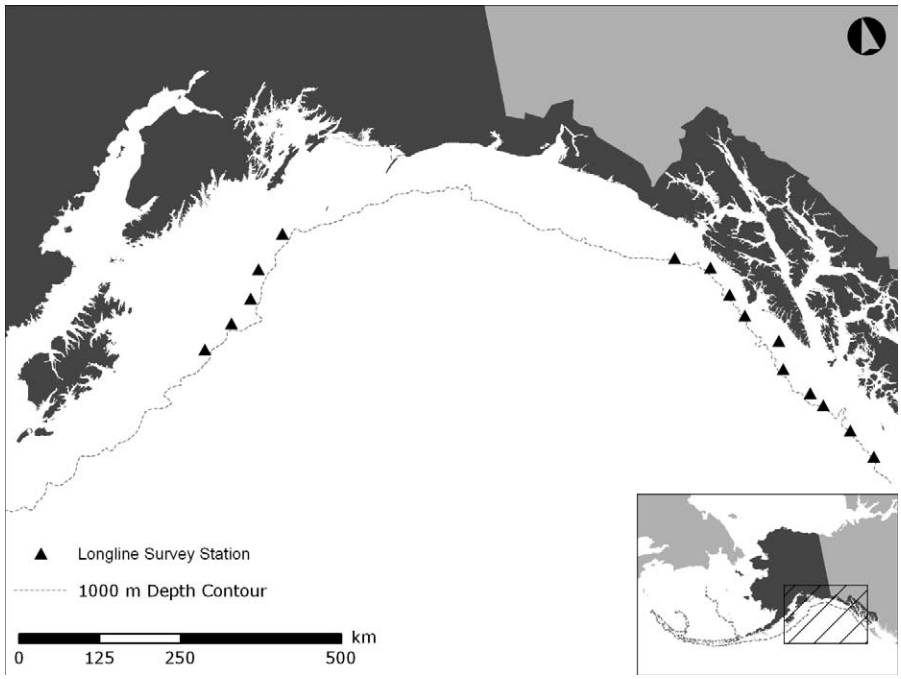


FIGURE 1.—Map showing the locations of the National Marine Fisheries Service longline survey stations at which female giant grenadiers were sampled in 2004 (central Gulf of Alaska) and 2006 (eastern Gulf of Alaska).

Sea of Okhotsk, western Bering Sea, and Kuril Islands and presented fecundity and age-at-maturity data from macroscopic evaluations of ovaries; however, their analysis was based on scales.

Because of the paucity of information on the basic reproductive and mortality life history characteristics of female giant grenadiers, we conducted a study of their ovarian development, fecundity, age, length and age at maturity, and natural mortality. This information will be necessary for future management of the giant grenadier in the North Pacific Ocean.

Methods

Sampling.—Ovaries were obtained from 157 giant grenadiers from the central GOA during August 10–16, 2004, and from 181 individuals from the eastern GOA during July 10–19, 2006. All samples were collected as part of the annual National Marine Fisheries Service (NMFS) Alaska longline survey (Figure 1). The survey sets longline gear at fixed stations on-bottom from 200 to 1,000 m to assess groundfish abundance. Giant grenadiers were caught at depths exceeding 400 m on the continental slope. Different stations were chosen in 2006 because very few immature fish were found in 2004 and smaller fish were known to occur in the eastern GOA from previous NMFS longline surveys. Preanal fin lengths (PAFLs; i.e., from the tip of the snout to the start of the anal fin) were measured to the nearest centimeter. This length measurement is typically used for grenadiers because their long, fragile tail is often damaged during capture (e.g., Kelley et al. 1997). Fish mass was measured to the nearest 10 g with an electronic, motion-compensating scale. Otoliths were removed and preserved in 50% solutions of ethanol.

Reproductive maturity assessment.—Ovaries were assigned an initial sexual maturity classification based on macroscopic assessment at the time of collection (Table 1), then preserved in 10% solutions of neutral buffered formalin for later analysis of fecundity and histological slide preparation. Samples were taken from the middle of the right ovary and included a piece of the ovarian wall so that its thickness could be measured.

Samples were embedded in paraffin, sectioned at 5–6 μm, stained with hematoxylin, and counterstained with eosin; the oocyte stages present were identified. Some tissue sections were stained with a carbohydrate stain (periodic acid–Schiff [PAS]) to identify prominent transparent, intracytoplasmic organelles found in the oocytes.

Macroscopic sexual maturity (Table 1) and histological oocyte staging information (Table 2) were used to define the phases of ovarian development. The

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TABLE 1.—Phases of ovarian development for female giant grenadiers from the Gulf of Alaska using ovarian macroscopic observations and histological criteria.

Phase	Condition	Macroscopic description	Histological staging
1	Immature	Oocytes not visible; tissue white to light pink with compact structure compared with later phases; ovarian wall thin and translucent.	Early-developing oocytes in the perinucleolar stage and often also in the early vacuole stage; oocytes typically tightly packed together; ovarian wall thin.
2	Immature	Very small white oocytes visible.[a]	Stage defined by the presence of late-vacuole-stage oocytes; perinucleolar oocytes are also always present and sometimes early-vacuole-stage oocytes.
3	Mature, early vitellogenic	Ovaries full of well-defined cream-colored oocytes.	Stage defined by the presence of early vitellogenic oocytes. Ovaries in this stage also contain perinucleolar oocytes and sometimes have early vacuole oocytes present.
4	Mature, advanced vitellogenic	Ovary full of large oocytes that are often orange but sometimes cream colored; ovarian tissue not noticeable because oocytes are so large.	Advanced vitellogenic oocytes present as well as perinucleolar. Early vacuole oocytes are also often present.
5[b]	Mature, spawning	Ovary large and full of semi-translucent cream-colored eggs that flow out when pressure is applied to the ovary.	Hydrated eggs present as well as perinucleolar and often early-vacuole-stage oocytes; new postovulatory follicles (POFs) are present.
6[c]	Mature, spent	Deteriorating eggs can appear as white or orange flecks macroscopically. The fresh ovarian tissue looks cloudy, owing to the POFs; ovary flaccid and ovarian wall thick.	POFs present indicating that spawning was relatively recent; various stages of atresia of large oocytes common; perinucleolar oocytes present as well as early vacuole or late vacuole oocytes.
7	Mature, between spawnings	Ovary flaccid with larger white or orange flecks inside but not cloudy.	Perinucleolar oocytes present as well as either early-vacuole- or late-vacuole-stage oocytes. Ovaries have an overall empty scattered appearance, thick ovarian tissue separating oocytes accompanied by atretic-yolked oocytes or eggs.

[a] Because the late-vacuole-stage oocytes are visible, they can be confused with atretic oocytes and be misclassified as stage 6 or 7.
[b] Only one fish was found in this condition, so the details are not well known.
[c] If atretic vitellogenic eggs are present, they appear as a few scattered orange or white larger dots or flecks. This indicates that the fish is in phase 6 or 7 rather than phase 2.

presence of vitellogenic yolk was taken to indicate mature ovaries. Ovaries that were large and flaccid and that contained few scattered, large, atretic, yolked oocytes or remnant ova were categorized as stage 7 (mature, between spawnings; Table 1). Immature fish were defined as those with only perinucleolar and vacuole stage oocytes and no evidence of past or immanent spawning (i.e., only early-stage oocytes).

The ovarian wall thickness was used to classify fish maturity when no postovulatory follicles or atretic, yolked oocytes or remnant ova were present to classify the ovary as postspawned. Two wall thickness measurements were taken from each sample (at the thickest and thinnest points), averaged, and then square root transformed to fit a normal distribution. The ovarian wall widths of fish of unknown maturity were compared with the distribution of wall widths of postspawned and immature fish. If the wall width was at least as thin as the smallest 97.5% of the distribution of postspawned wall widths (i.e., left of the 2.5% point

TABLE 2.—Stages of oocyte development for female giant grenadier from the Gulf of Alaska determined using histology.

Oocyte stage	Oocyte description
Perinucleolar	Multiple nucleoli visible inside the oocyte nucleus but no vacuoles (transparent, circular intracytoplasmic organelles) present in the cytoplasm.
Early vacuole	Small vacuoles present in the cytoplasm near the oocyte nucleus.
Late vacuole	Vacuoles larger and more numerous, but still near the oocyte nucleus; oocyte diameter greater, perivitelline envelope has thickened and appears as a defined edge around the oocyte.
Early vitellogenic	Vacuoles have moved toward the periphery of the cytoplasm; small yolk bodies (pink staining) begin to form near the cytoplasmic periphery of the oocytes in between the plasma membrane and vacuoles.
Advanced vitellogenic	Large vacuoles are interspersed with larger yolk bodies; oocyte nucleus still centrally located and nucleoli visible.
Hydrated	Yolk spheres become very large and coalesce into a solid mass; oocyte shape becomes irregular instead of circular.
Postovulatory	Ovarian follicle is irregularly shaped, hyperplastic, and ruptured, with the oocyte absent.

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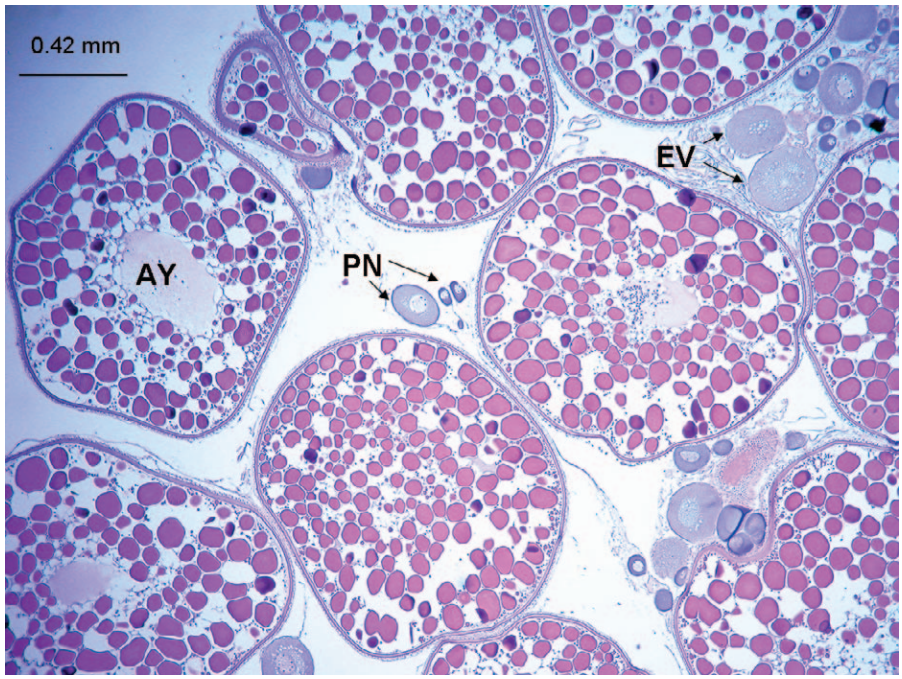


FIGURE 2.—Photograph of a histological section through the mid-portion of an ovary of a giant grenadier from the Gulf of Alaska stained with hematoxylin and counterstained with eosin at 4× magnification. Identified features include advanced vitellogenic oocytes (AY), perinucleolar oocytes (PN), and early-vacuole-stage oocytes (EV). Based on these features, this individual was classified stage 4 ("mature, advanced vitellogenic").

on the cumulative distribution function), the individual was declared immature. Conversely, if it was thicker than the largest 97.5% of immature ovarian walls, the individual was declared postspawned (or mature).

Fecundity.—Ovaries (from 2004 only) were chosen for fecundity estimation if they had advanced vitellogenic oocytes and no postovulatory follicles in histological cross sections (Murua 2003; Table 2). In these ovaries, the advanced (mature) cohort of oocytes was clearly separable from the early-developing (immature) cohort based on size and appearance (Figure 2).

Fecundity was measured using the gravimetric method (Murua et al. 2003). To test for vitellogenic oocyte density differences within each ovary, samples were taken from the anterior, mid, and posterior sections of the ovary. Ovarian wall mass was measured after first scraping away all the oocytes and internal ovarian tissue to determine whether fecundity estimates were affected by the proportion of mass from the ovarian wall. Diameters of whole, advanced yolked oocytes were measured from each of the 34 females sampled for fecundity ($n = 20$ oocytes per female).

Preanal fin length, ovary-free body mass, ovary mass, and age were regressed against fecundity to determine the strength and nature of the relationship. Correlations between fecundity and these variables as well as egg density were examined, along with those between the proportion of ovarian mass that could be attributed to the wall PAFL, and age, egg density, and ovary mass.

Age determination.—Otoliths were used to age the fish with either a transverse thin-section method (Smith et al. 1995) or a ground distal surface method developed during this study. The latter was the primary method used because the thin-section method left dark indiscernible areas near the core (Figure 3). For the ground distal surface method, the top surface layer was ground off using a Buehler Ecomet grinding wheel with 320-grit sandpaper to elucidate the growth zones. First, the posterior half of the distal surface was ground; then the otolith was rotated 180° and the anterior half was ground. When the otolith pattern was deemed readable, the otolith was aged by enumerating the growth zones on the ground distal surface. The otoliths were viewed in a water-filled petri dish with a black background using a dissecting microscope and reflected light under 8× magnification. A subset of the otoliths (66%) were read by two readers to guard

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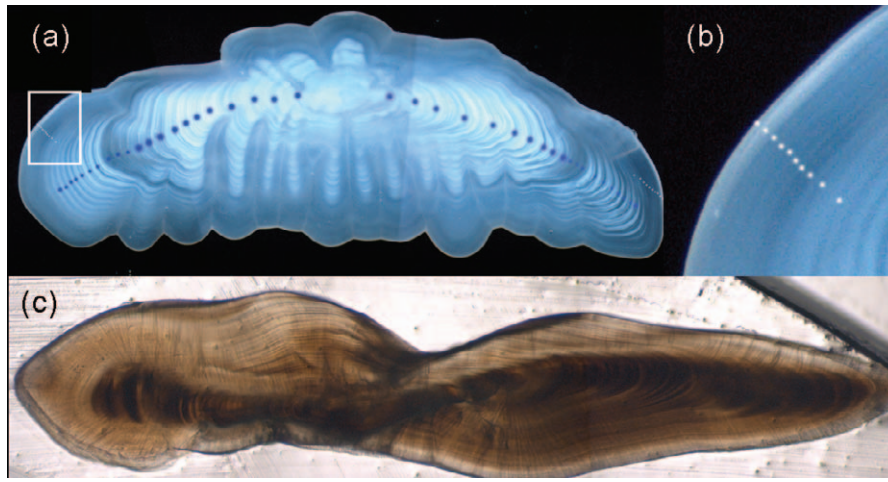


FIGURE 3.—Giant grenadier otoliths prepared with **(a)**–**(b)** the distal ground method and **(c)** the thin-section method. Panel (a) shows a photograph taken at 8× magnification using a dissecting microscope. Each dot represents a yearly annulus; the dots on the right and left sides are from the same annuli. Panel (b) shows a close-up of the boxed area in (a) in which the dots represent yearly annuli. Panel (c) shows a photograph taken at 40× magnification using a dissecting microscope. The thin-section method resulted in dark areas where the annuli were difficult to distinguish.

against reader bias. Age discrepancies were resolved by having both readers agree on a single age.

For older fish, the otolith edge contains narrowly spaced annuli that can be inadvertently ground off when the ground distal surface method is used. Thin sections were therefore made using the methods of Smith et al. (1995), with the following adjustments: the otoliths were embedded in Artificial Water resin, and transverse sections (approximately 0.50 mm thick) were made at intervals surrounding the core region using a Tyslide table saw; the sections were reduced to a thickness of approximately 0.30 mm using a Hillquist grinding wheel followed by an Ecomet grinding wheel with 600-grit sandpaper.

Age and length at maturity.—Logistic functions were fit to the proportion mature in each age and PAFL group to estimate the age and PAFL at 50% maturity for females (A_{50} and L_{50}, respectively). The proportions were grouped by 2-cm and 2-year increments, respectively, for PAFL and age. Logistic curves were fit to two data sets, one for which maturity was evaluated macroscopically and one for which histology was used to aid in the classification. The logistic curves for age were of the form (Seber and Wild 1989)

$$P_x(A) = 1/(1 + e^{-\kappa[A-\gamma]}), \qquad (1)$$

where $P_x(A)$ is the proportion mature at age A, and κ and γ are parameters in the model (κ affects the curvature, and γ is the age at which the inflection point occurs). Similar curves were derived for PAFL.

Mortality.—We used two methods each to describe natural mortality (M) and total mortality (Z). The longevity method and the simplified-maximum-age method (Hoenig 1983) were used to estimate M, and catch-curve analysis (Quinn and Deriso 1999) and the length frequency method (Beverton and Holt 1957) were used to estimate Z. We used PAFL data collected in the NMFS longline survey from the eastern GOA in 2006 for the catch-curve analysis and an age–length key to extrapolate ages from PAFLs. Raw frequency-at-age data were $\log_e$ transformed and a linear regression fit to the downslope of the curve. For the length frequency method, L_c was the minimum observed PAFL of the samples from this study. Because the samples were not randomly chosen, $\overline{L}$ was calculated as the average PAFL of giant grenadiers from the longline survey in the eastern GOA in 2006.

Results

Reproductive Maturity Assessment

Giant grenadier ovaries showed oocyte stages ranging from perinucleolar to hydrated, which is typical of other fishes and ovaries during the summer months (Figure 4). Early-stage oocytes lacked a Balbiani body and had large transparent cytoplasmic organelles (vacuoles appearing). These took up neither carbohydrate (PAS) nor hematoxylin and eosin stains, indicating that they were not cortical alveoli but may have been lipid inclusions (Figure 2). Oocytes with a migratory nucleus were only observed in one ovary (spawning [stage 5]; Table 1). Ovaries that contained

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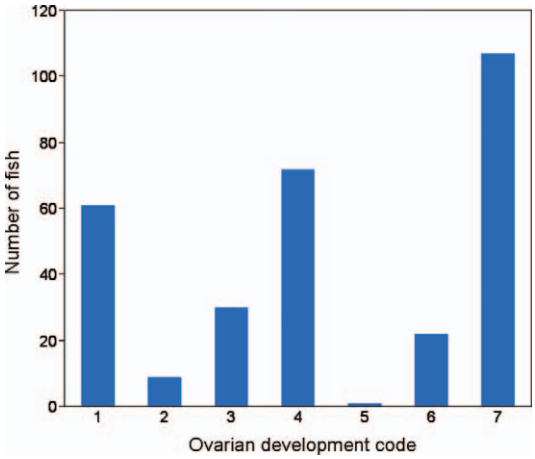


FIGURE 4.—Number of female giant grenadiers with ovaries in stages 1–7 of development. Development stages were assigned using histology (see text).

oocytes in the early vacuole stage or later also contained a cohort of smaller, early-stage oocytes. In ovaries that contained advanced vitellogenic oocytes, there was a distinct hiatus in size and developmental stage between a larger, maturing cohort and a smaller, immature cohort (Figure 2). For example, in an ovary that contained advanced vitellogenic oocytes the average diameter of the advanced vitellogenic oocytes was 0.97 mm (SE = 0.008, $n = 20$) and the diameter of the next most advanced oocytes (early vacuole) was 0.21 mm (SE = 0.010, $n = 20$). For this analysis, only oocytes that were cut through the center were measured. This particular ovary had very dense oocytes (advanced oocytes are smaller and possibly less developed than those in other ovaries used for fecundity estimates), and as such can be considered to provide conservative estimates of the size distribution gap.

Histological assessments of maturity often differed from the initial macroscopic assessment; 15% ($n = 10$) of the ovaries that were classified as immature using histology and 18% ($n = 42$) of those that were classified as mature according to histology were incorrectly classified using only macroscopic criteria.

Seventy-seven ovaries (23%) could not be categorized as postspawned or immature based solely on histology. In these instances, ovarian wall thickness was sometimes used to assign maturity. Ovarian wall thickness was determined for 222 fish that were positively identified as immature ($n = 60$), postspawned ($n = 85$), or of unknown maturity status ($n = 77$). The ovarian wall thickness of immature fish averaged 0.77 mm (SD = 0.25), whereas that of postspawned individuals averaged 1.11 mm (SD = 0.25). Four unknowns were assigned to the immature category based on their ovarian wall thickness (range = 0.20–0.44 mm), and 20 were assigned to the postspawned category (range = 1.40–2.89 mm). Fifty-three unknowns were not assigned a maturity because there was no evidence of mature oocytes or previous spawning and their ovarian walls were of intermediate thickness. These samples were not used for analysis of age or PAFL at maturity. The average age of the unknowns was less than that of the immature fish, so it is likely that many of these fish were immature. There were a total of 132 samples with known maturity from 2004 and 167 from 2006.

TABLE 3.—Pearson's correlation coefficients (r) between total fecundity or percent wall mass (the proportion of the ovary mass attributable to the ovarian wall) and other features of female giant grenadiers from the Gulf of Alaska. All data were $\log_e$ transformed except age. Significant correlations are denoted by asterisks.

Variable 1	Variable 2	r	P	N
Fecundity	Ovary mass	0.43	0.0116*	34
	Body mass	0.77	<0.0001*	34
	PAFL	0.71	<0.0001*	34
	Egg density	0.58	0.0003*	34
	Age	0.38	0.0343*	32
% Wall mass	Age	0.22	0.2576	28
	PAFL	0.40	0.0296*	30
	Ovary mass	0.04	0.8213	30
	Egg density	0.61	0.0004*	30

Fecundity

Potential fecundity ranged from 35,000 to 231,000 oocytes (mean = 106,761, SD = 58,687, $n = 34$). The average oocyte diameter (measured from whole advanced yolked oocytes) of the fish sampled for fecundity was 1.26 mm (SD among ovaries = 0.19, number of ovaries = 31). The density of vitellogenic oocytes did not differ among locations within the ovary (analysis of variance; P-values ranged from 0.2 to 0.6 for each fish), so fecundity was calculated from the average oocyte density. The fraction of the ovary mass that could be attributed to the ovarian wall varied greatly among fish (range = 6–20%, mean = 9.1%, SD = 3.5%, $n = 30$). Fecundity was related to the fish's ovary-free body mass, PAFL, and oocyte density more strongly than to the ovary mass and age (Table 3; Figure 5). The relationships between the natural logarithm of fecundity and PAFL, mass, and ovary mass were linear, whereas that between the natural logarithm of fecundity and age was curvilinear. The fraction of ovarian mass represented by the ovarian wall was correlated with PAFL and oocyte density, indicating that (1) larger fish had relatively thicker

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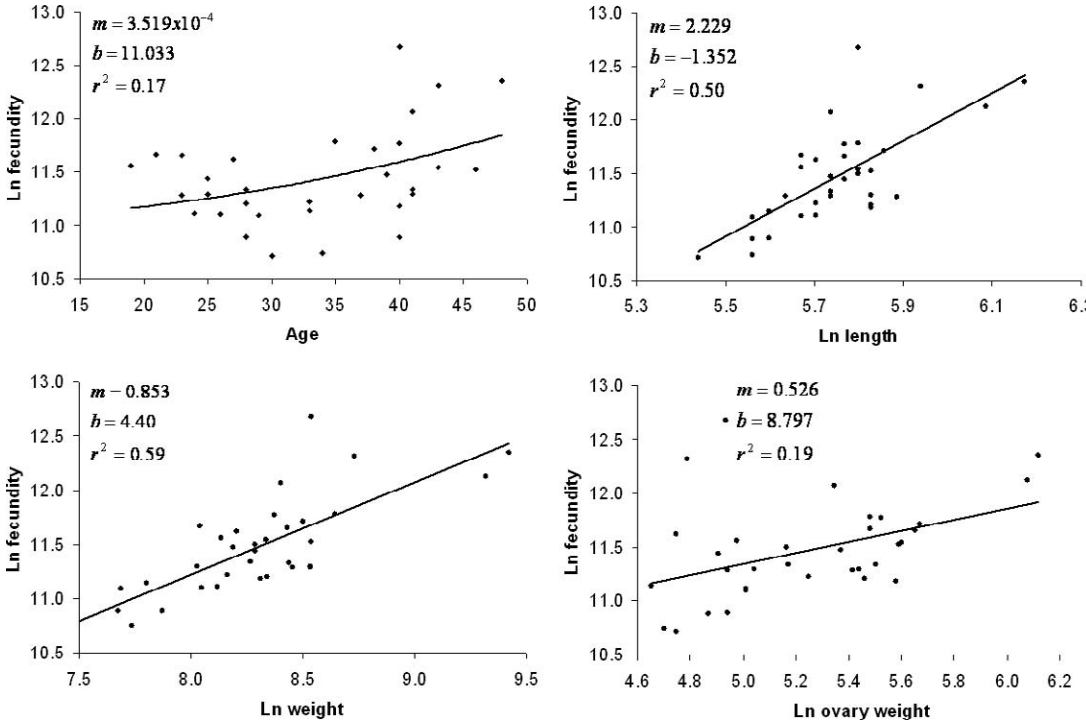


FIGURE 5.—Regressions of giant grenadier fecundity on age, preanal fin length, ovary-free body mass, and ovary mass. All variables except age were $\log_e$ transformed to meet the assumptions of normality. All of the fits are linear except that for age, which is quadratic.

ovarian walls and (2) smaller, more dense oocytes had less mass and therefore a greater fraction of the ovarian mass could be attributed to the ovarian wall (Table 3). The number of oocytes per gram of ovary-free fish mass was 24.5 (linear regression; $r^2 = 0.59$, $n = 34$), and the number of oocytes per centimeter of PAFL was 3,197 (linear regression; $r^2 = 0.50$, $n = 34$).

Age and Length at Maturity

The A_{50} from a logistic curve fit to the histologically classified maturity data was 22.9 years (95% confidence interval, 21.1–26.9). The PAFL at 50% maturity using histology was 26 cm for both the pooled data and the 2006 data. Only 127 and 165 samples from 2004 and 2006, respectively, could be used for age-at-maturity analysis.

Mortality

Estimates of M ranged from 0.052 to 0.079 and estimates of Z from 0.061 to 0.149. The highest estimates of M were from the Hoenig longevity (1983) method and the Hoenig simplified maximum age (1983) method ($P = 0.01$). The maximum age used in the Hoenig (1983) method was 58. The estimate of Z from the length frequency method was similar to estimates of M. The estimate of Z using catch-curve analysis was approximately twice all the other estimates of Z and M. The r^2 of the linear regression for the catch-curve analysis was 0.71 (Table 4).

Discussion

Similar to other grenadiers (Eliassen and Falk-Petersen 1985; Murua 2003), giant grenadiers have group-synchronous ovarian development and determinate fecundity. The presence of a hiatus in oocyte size between the vitellogenic and previtellogenic oocytes further supports this conclusion. When advanced vitellogenic oocytes were present, other oocytes were at least two stages of development behind (i.e., one of the vacuole stages versus the advanced vitellogenic stage) and were many times smaller in diameter (Figure 2). Monitoring the decline in vitellogenic oocytes during the spawning season would help determine whether oocytes are being recruited, but that is not feasible for giant grenadiers because the spawning season appears to be protracted.

Although we did not conduct seasonal sampling, our data suggest that the spawning season for giant

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TABLE 4.—Estimates of natural mortality (M) and total mortality (Z) for female giant grenadiers from the Gulf of Alaska and other grenadier species. Variable P is the proportion of fish surviving to the maximum age of 58. The calculation column specifies the values that were used to compute the estimates of M and Z.

Grenadier species	Method	Study	Calculation	M	Z
Giant	Simplified maximum age (Hoenig 1983)	Current	$\hat{M} = -\log_e(P) \times 58^{-1}$		
			$P = 0.01$	0.079	
			$P = 0.02$	0.067	
			$P = 0.03$	0.060	
			$P = 0.04$	0.055	
			$P = 0.05$	0.052	
	Longevity (Hoenig 1983)		$\log_e(\hat{M}) = 1.440 - 0.982 \times \log_e(58)$	0.078	
	Length frequency (Beverton and Holt 1957)		$\hat{Z} = 0.025 \times [(52 - 28.9) \times (28.9 - 19)^{-1}]$		0.061
	Catch curve (Quinn and Deriso 1999)		$\hat{Z} = -\text{slope} = 0.149$		0.149
			$\log_e(\text{frequency}) = -0.149 \times \text{age} + 8.91$		
Giant	Simplified maximum age	Burton (1999)		0.074	
Roughhead	Catch curve	Murua (2003)			0.236
Bigeye	Pauly (1980)	Morley et al. (2004)		0.090	
Roundnose	Length frequency	Lorance et al. (2001)		0.100[a]	

[a] Assumed to be equivalent to M because data are from surveys prior to exploitation.

grenadiers in the GOA is in fact protracted. Because ovaries in all stages of development were found in the summer, it is likely that some fish had spawned in the preceding months. Fish with early- and advanced-stage vitellogenic oocytes would probably spawn in the coming months. There is no information on the development time of giant grenadier oocytes or the degradation time of postovulatory follicles, so precise estimates of the spawning dates for individual fish are not possible. Additional collection during other times of the year may help characterize the spawning season for this species. Novikov (1970) also concluded that giant grenadiers had a protracted spawning season. Additionally, female grenadier species worldwide are found with ripe oocytes nearly year-round (Massuti et al. 1995; Coggan et al. 1999; D'Onghia et al. 1999; Allain 2001; Morley et al. 2004).

We found the width of the ovarian wall to be somewhat reliable for categorizing ovaries as immature or postspawned. Atlantic cod *Gadus morhua*, which are taxonomically related to grenadiers (both are in the order Gadiformes), also have thicker ovarian walls after spawning than do immature fish (Holdway and Beamish 1985; Burton et al. 1997). This measurement may be useful for classifying maturity in other species and taxa of fish.

Differences between macroscopic and histological classifications are not uncommon. For example, Vitale et al. (2006) found that macroscopic staging of Katteget Atlantic cod causes an overestimation of $A_{50.}$ Estimates of A_{50} and L_{50} for species that have a protracted spawning period can be difficult because there is no season when maturity status can be assigned with confidence to all individuals. Unknown giant grenadier ovaries may have been in a seasonal condition that was more difficult to classify. Also, many ovaries were classified differently when macroscopic criteria were used because evidence of spawning was sometimes only visible with histology. In some cases ovaries were classified as postspawned using macroscopy but as immature using histology (23% [16/70]) or as immature using macroscopy but as postspawned using histology (10% [13/129]). This discrepancy is likely because both of these classes may contain oocytes that are not vitellogenic but that are visible to the naked eye (Table 1).

Age estimation of giant grenadiers was successful in 157 samples in 2004 and 181 in 2006, largely with the ground distal surface method. The ages of individuals in 2004 ranged from 19 to 49 years, and the between-reader coefficient of variation (CV = 100 • SD/mean) was 10.57%. The ages of individuals in 2006 ranged from 14 to 58 years, and the CV improved to 7.63%. The distal ground surface method proved to be the best in terms of precision. When age was determined from the otoliths of 32 randomly sampled individuals in 2004 with both the distal ground surface and thin-section methods, the CV between readers was 9.03% for the former and 13.2% for the latter. Of the 338 otoliths used to determine ages, ages derived using the thin-section method were used in only 24 cases.

The potential fecundity of the giant grenadiers in this study was higher than that of most other grenadier species (up to 231,000 oocytes per female), which is not surprising given that giant grenadiers have the largest maximum body size and some of the smallest vitellogenic oocyte diameters. The significant, positive relationship between egg density and fecundity clearly

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implies that there are losses of advanced oocytes, possibly from atresia, during the advanced yolked phase of oocyte development. The fecundity estimates may therefore be biased upward. The estimates would have been even higher if the ovarian wall masses had been used in the extrapolations, as in other studies, which did not account for wall mass. Roughhead grenadiers had lower fecundities and their vitellogenic oocytes (1.2–4.3 mm) were larger than those of the giant grenadiers (1.26 mm) (Eliassen and Falk-Petersen 1985). Bigeye grenadiers had fecundities similar to those of the giant grenadiers (22,000–260,000), even though their PAFL is smaller (21 cm), because they have smaller oocytes (~1 mm in diameter; Morley et al. 2004).

Compared with the grenadiers in other studies, the giant grenadiers in the GOA are longer-lived (maximum age = 58) and later to mature (A_{50} = 22.9). Tuponogov et al. (2008) found that the A_{50} of giant grenadiers in the northwest Pacific Ocean was 8–9 years, but they determined fish ages using scales. In their study, the age at first maturity for females was 6–15 years and the PAFL 18–34 cm. In our study, fish of this size were 15–36 years old. Other grenadiers mature sooner and have lower maximum ages. For example, bigeye grenadiers (A_{50} = 9, maximum age = 25; Morley et al. 2004), roughhead grenadiers (A_{50} = 15–16, maximum age = 18; Murua 2003), and roundnose grenadiers (A_{50} = 9–11, maximum age = 60–72; Bergstad 1990; Kelley et al. 1997) all had younger ages at 50% maturity.

Each estimate of M is based on particular assumptions and has its limitations. For the giant grenadier stock assessment (Clausen and Rodgveller 2008), the Hoenig (1983) longevity estimate of M was chosen. When choosing between the two Hoenig methods, Hewitt and Hoenig (2005) suggest using the longevity regression equation instead of the simplified-maximum-age approach because the regression is fit to extensive data sets. The length frequency estimate of Z (total mortality) was sensitive to small changes in average PAFL. For example, when the average PAFL was increased by 2.7 cm (the difference between eastern Bering Sea and eastern GOA fish), mortality dropped by 26%. The estimate of Z from catch-curve analysis was 0.149. Clausen (2008) estimated that the percentage of the giant grenadier biomass caught annually in the GOA was 2.2%. Subtracting 0.022 from 0.149 gives an estimate of M of 0.127, which is still much higher than all other estimates and would be more reliable if a cohort were tracked through time.

There are few published values of M or Z for grenadiers. Burton (1999) reported an estimate of M for giant grenadiers that was similar to the values we calculated (Table 4). The estimates for bigeye (Morley et al. 2004) and roundnose grenadiers (Lorance et al. 2001) are slightly higher. The value of Z is higher for roughhead grenadiers than for other grenadiers (Murua 2003), probably because they mature relatively early (at a smaller size) and are commercially harvested. Other grenadiers probably have larger M values than giant grenadiers because their maximum ages are far lower than 58 years (reviewed in Swan and Gordon 2001).

Our study on the reproductive life history characteristics of female giant grenadiers in the GOA shows that sexual maturity is reached late in life and natural mortality is low. Based on these features (which are similar in some respects to those of other exploited grenadier species; Atkinson 1995), giant grenadier populations may be susceptible to rapid decline if they are overfished. A unique aspect of their reproductive biology that could partially offset fishery exploitation is their high fecundity compared with that of other grenadiers. Because of their potential sensitivity to overfishing, this species will need to be managed with caution to prevent overharvest.

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