Natural mortality rate, annual fecundity, and maturity at length for Greenland halibut (*Reinhardtius hippoglossoides*) from the northeastern Pacific Ocean

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Mortality, fecundity, and size at maturity are important life history traits, and their interactions determine the evolution of life history strategies (Roff, 1992; Stearns, 1992; Charnov, 2002). These same traits are also important for population dynamics models (Hunter et al., 1992; Clark, 1999). It is increasingly important to accurately determine Greenland halibut (*Reinhardtius hippoglossoides*) life history traits and to correctly assess the status of its stocks because low recruitment or low biomass estimates have led to catch restrictions in the Bering Sea and Aleutian Islands (Ianelli et al.[1]), the Northeastern Arctic (Ådlandsvik et al., 2004), and the Northwest Atlantic (Bowering and Nedreaas, 2000).

Mortality has been estimated for stocks of Greenland halibut from the Northwest Atlantic (Bowering, 1983) and from the Bering Sea (Ianelli et al.[1]) from population age structures where a maximum age near 20 years has been assumed. However, recent age validation (Treble et. al[2]) and a new aging technique (Gregg et al., 2006) indicate that Greenland halibut may have a lower mortality rate and live longer. Fecundity estimates (Gundersen et al., 2000) and length at maturity estimates (Morgan et al., 2003) vary by geographic area and year for Greenland halibut in the Atlantic. Fecundity of Greenland halibut from the Bering Sea has been estimated once (D'yakov, 1982), and no estimates for Greenland halibut maturity at length have been reported from Alaskan waters.

A significant and positive relationship between natural mortality rate (M) and annual reproductive effort, as measured by gonadosomatic index (GSI=*ovary weight*/*somatic body weight*), was found for 28 fish stocks of a variety of species (M=1.79×GSI, r^2=0.75) (Gunderson, 1997). This GSI-M relationship can provide an estimate of M independent of age data, and is desirable for Greenland halibut because age data are still controversial for this species. The objectives of this study are to estimate annual fecundity, length at 50% maturity, and the rate of instantaneous natural mortality (M) by using GSI for Greenland halibut from the Bering Sea and Aleutian Islands.

Materials and methods

Ovaries were collected by fishery observers and scientists from the National Marine Fisheries Service (NMFS) in the Bering Sea and Aleutian Islands (Table 1, Fig. 1). Fork length (cm) and somatic weight (kg) (ovaries and stomach contents removed) were recorded at sea. Total weight was approximated by adding somatic weight and the estimated fresh ovary weight.

Ovaries were removed and placed in a 10% formalin solution buffered with sodium bicarbonate. Twenty-eight ovaries were weighed (±2 g) before being placed in formalin. The fresh weight was later compared to formalin weight to determine a conversion factor when fresh weight was not available. Ovaries were removed from the 10% buffered formalin, blotted dry, and weighed (±0.001 g). When possible, a whole cross section was removed from one lobe of an ovary for histological analysis. If the ovary cross section was too large to fit on a slide, a wedge-shaped sample was removed which included tissue from the center of the ovary to the ovarian wall. Ovary tissue samples were embedded in paraffin, sectioned at 4 μm, and stained with hematoxylin and eosin. All 56 specimens smaller than 40 cm were obviously immature because of their very small ovaries; therefore histological examination was completed on only six of these specimens to verify that they were immature.

[1] Ianelli, J. N., T. K. Wilderbuer, and D. Nichol. 2005. Stock assessment and fishery evaluation: Bering Sea and Aleutian Islands Greenland turbot. Website: http:www.afsc.noaa.gov/refm/docs/2005/BSAIGturbot.pdf (accessed on 28 June 2006).

[2] Treble, M. A., S. E. Campana, R. J. Wastle, C. M. Jones, and J. Boje. 2005. An assessment of age determination methods, with age validation of Greenland halibut from the Northwest Atlantic. NAFO SCR Doc. 05/43, 22 p. Northwest Atlantic Fisheries Organization, P.O Box 638, Dartmouth, Nova Scotia, Canada B2Y 3Y9.

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Each slide was analyzed for the oocyte stages present and for postovulatory follicles (POFs) according to the descriptions and images from Gundersen (2003) (Fig. 2). Maturity stages were assigned according to Gundersen et al. (2003).

Length-GSI relationship and instantaneous rate of natural mortality

For the GSI-M relationship, Gunderson (1997) defined GSI as the point in ovarian development when the ovaries had attained maximum weight due to vitellogenesis, but had not gained nonenergetic weight (due to hydration). For this study, fish with ovaries in maturity stage vitellogenesis 4 (Fig. 2) were used in the GSI-M estimate. Fish with ovaries containing hydrated oocytes or POFs were excluded. Fedorov (1968) found that dry weights of oocytes corresponding to the vitellogenesis-4 stage (yolk-filled oocyte in the trophoplasmic growth stage) were equal to dry weights of hydrated ova; this result indicates that yolk deposition is completed at the vitellogenesis-4 stage.

The length of the average mature female in an unexploited population is required for Gunderson's (1997) GSI-M relationship. The foreign trawl fishery prior to 1988 showed the best selectivity for fish in the widest size range (Ianelli and Wilderbuer[3]). Foreign trawl fishery data from the NMFS Observer program (Berger[4]) were analyzed, and the oldest complete data set (1977–87) was chosen to best approximate the true nature of the Greenland halibut population in the absence of fishing pressure. The mean length of mature females was determined from the weighted length by using data on the abundance at each length as weights.

Potential annual fecundity

To test for homogeneity of vitellogenic oocyte density throughout the ovaries, subsamples were selected from nine fish at three locations (anterior, middle, and posterior) on each ovary lobe (eyed side and blind side) for a total of six subsamples per fish. Cross sections were taken through the ovary and included the ovarian wall. For the anterior and middle sections, one half of the cross section was used as the subsample. The posterior cross sections of the ovary were much smaller and therefore the entire cross section was used. The subsamples had a mean weight of 2.07 grams (standard error [SE]=0.14) and a mean number of 553 vitellogenic oocytes (SE=43.11). Oocyte density (number of oocytes/gram of ovarian tissue) and diameters of 50 of the most advanced oocytes per fish were recorded.

Two-way ANOVAs were used to test for differences in oocyte density and diameter between ovarian lobes and among ovarian locations. Paired *t*-tests were used to identify differences among ovarian locations when the ANOVA detected significant differences.

Greenland halibut are reported to have determinate fecundity (Gundersen et al., 2001; Junquera et al.,

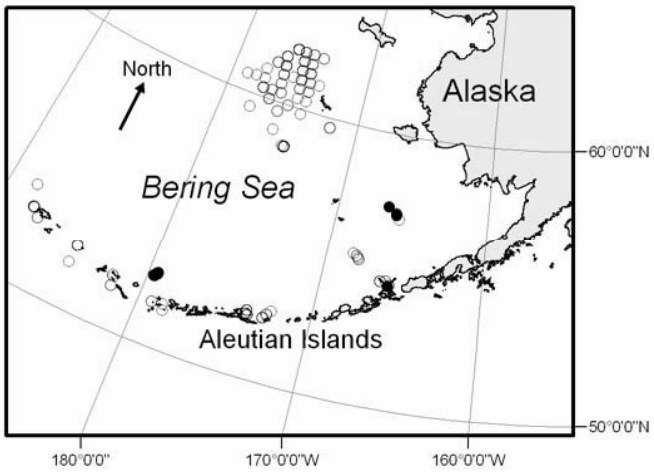

Figure 1

Map of locations where Greenland halibut (*Reinhardtius hippoglossoides*) were collected for ovary samples. Open circles mark locations where fish were collected for the ovary samples. Filled circles mark locations where fish were collected for the natural mortality (*M*) estimate.

Table 1

Number of Greenland halibut (*Reinhardtius hippoglossoides*) females collected by month and year.

	Year					
Month	1999	2000	2002	2003	2004	Total
January						
February						
March					19	19
April						
May						
June		13	3	1		17
July		44	8	101		153
August						
September	78	42				120
October		2				2
November						
December						
Total	78	101	11	102	19	311

[3] Ianelli, J. N., and K. T. Wilderbuer. 1995. Greenland turbot (*Reinhardtius hippoglossoides*) stock assessment and management in the Eastern Bering Sea. *In* Proceedings of the International Symposium on North Pacific flatfish, p. 407–441. Alaska Sea Grant report 95-04. Univ. Alaska Sea Grant College Program, P. O. Box 755040, Fairbanks, AK 99775.

[4] Berger, J. 2002. Personal commun. Alaska Fisheries Science Center, National Marine Fisheries Service, 7600 Sand Point Way NE, Seattle, WA 98115.

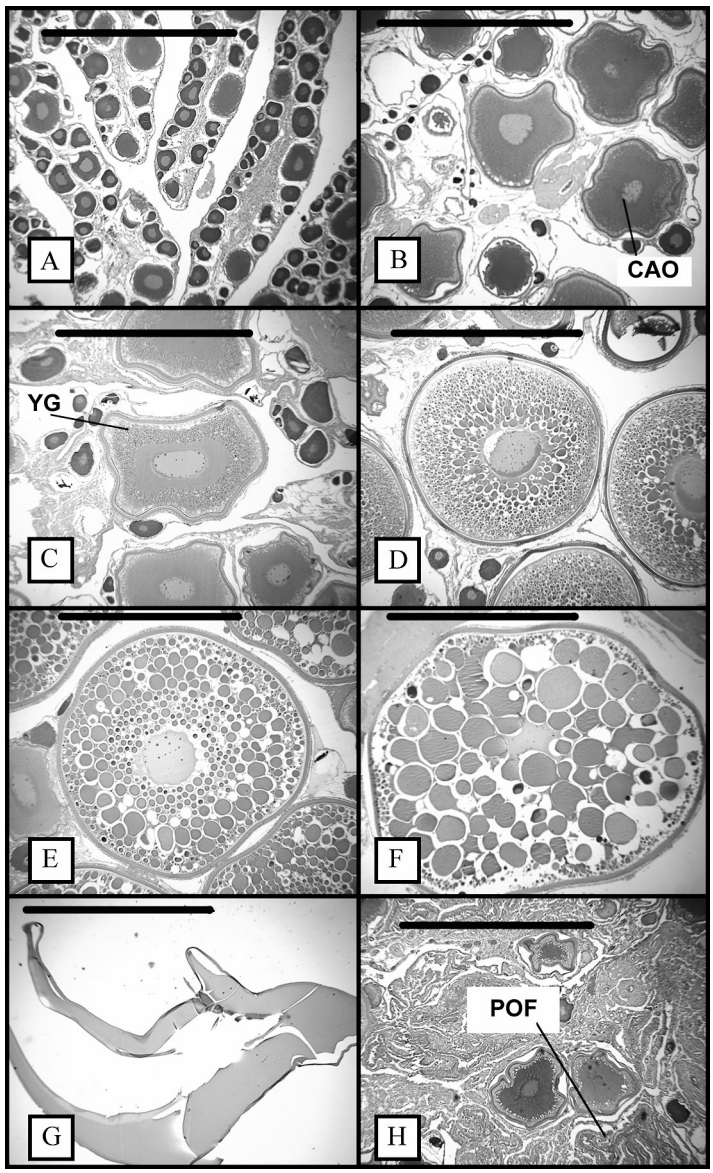

Figure 2

Ovary stages of Greenland halibut (*Reinhardtius hippoglossoides*) from histology. Ovary staging follows the methods of Gundersen (2003). All scale bars = 1.0 mm. (**A**) Immature. (**B**) Cortical alveoli. CAO = cortical alveolar oocyte. (**C**) Vitellogenesis 1. YG = yolk globules. (**D**) Vitellogenesis 2. Note the largest yolk globules are located near the nucleus. (**E**) Vitellogenesis 3. Note the yolk size gradient has been reversed and the largest yolk globules are near the periphery of the oocyte. (**F**) Vitellogenesis 4. The yolk globules are all large and have begun to fuse. (**G**) Spawning. (**H**) Spent. POF = postovulatory follicle.

2003). To confirm this for Greenland halibut in the Bering Sea, oocyte diameters were measured to determine if there is a hiatus in size between developing and reserve oocytes. Mean diameters of nonvitellogenic and vitellogenic oocytes were measured from whole oocyte tissue samples. All vitellogenic oocytes in a tissue sample of known weight were counted. The oocytes were placed in a dish on top of a sampling grid. All

oocytes touching the lines of the sampling grid were measured until 50 nonvitellogenic and 50 vitellogenic oocytes had been measured. Nonvitellogenic oocytes were reported as percent frequency, whereas vitellogenic oocytes were reported as number of vitellogenic oocytes per gram of ovary tissue. Because oocyte diameter may vary by ovary location (see "Results" section), all oocyte measurements were taken from the middle location of the ovaries.

To select ovaries suitable for fecundity estimates, the diameters of six vitellogenic oocytes sectioned through the nucleus were measured from the histological sections by using a microscopic image analysis system. Because oocytes were not perfectly round, oocyte diameter was calculated from oocyte area with the following equation:

$$Diameter = 2\sqrt{\frac{Oocyte\ Area}{\pi}}.$$

Females with the mean diameter of vitellogenic oocytes smaller than 1000 µm were excluded from the fecundity estimate because not all oocytes to be spawned in the current year could be identified (see "Results" section). To exclude fish that had already begun spawning, samples containing POFs or ova were excluded.

Fecundity was estimated gravimetrically by counting vitellogenic oocytes from weighed subsamples of ovarian tissue. The weight of the thick ovarian wall could not be discounted; therefore subsamples were cut with a proportionately weighted piece of ovarian wall attached. This procedure was accomplished by using either an entire cross section of the ovary, or a wedge-shaped sample cut from an entire cross section. Because small oocyte density differences were found between the posterior location and the anterior+middle locations, and between the eyed and blind lobes (see "Results" section), four subsamples were taken for each fish. The posterior region of each lobe and the area between the middle and anterior locations of each lobe were sampled. Weighting factors for the posterior and for the middle and anterior locations of the ovary were determined by calculating the proportional mass of these locations of the ovaries for 26 fish. The average proportional mass for the posterior and for the middle and anterior locations was 0.11 and 0.89 (SE: 0.0048), respectively. When divided by two (to account for the two ovary lobes), the average weighting factors for the posterior blind and eyed lobes = 0.06, and the average weighting factor of the anterior and middle locations for the blind and eyed lobes = 0.44. Fecundity of each female was estimated from the four subsamples by using the fecundity equation with weighting factors from Nichol and Acuna (2001) to account for the smaller proportional mass of the posterior sections.

The fraction of vitellogenic oocytes undergoing atresia was estimated for 174 fish from histological cross sections. The total number of vitellogenic oocytes and the number of atretic vitellogenic oocytes (Hunter and Macewicz, 1985) for each histological section were counted. The fraction of vitellogenic oocytes undergoing atresia was estimated as the number of atretic vitellogenic oocytes divided by the total number of vitellogenic oocytes.

Length at maturity

Maturity was determined histologically, by using all fish 40 cm and larger, and a subsample (n=6) of females less than 40 cm. Maturity stages were determined according to the method of Gundersen (2003).

Results

Length-GSI relationship and instantaneous rate of natural mortality

The conversion factor between ovary fresh weight and weight after fixation and storage in formalin was:

$$Fresh = (1.437 \times Formalin) + 6.8276, \quad (n=28,\ r^2=0.9903),$$

where $Fresh$ = fresh ovary weight (g); and
$Formalin$ = ovary weight after storage in formalin (g).

Maturity stages increased from spring (March) to summer (June and July) and again to autumn (September and October) (Fig. 3). In March, mature females were spawning, spent, or beginning vitellogenesis for the next spawning season. Most fish were in the vitellogenesis-1 stage. By June–July, the ovaries had advanced until most were in the vitellogenesis-2 stage, although some were also in stages vitellogenesis 1 and 3. By September–October, the majority of mature ovaries were in vitellogenesis-3 stage, although some had progressed to vitellogenesis 4 and a small percentage (4%) of the mature females collected in September were ready to spawn (presence of hydrated oocytes) or showed signs of recent spawning (presence of ova or POFs). The largest mean oocyte diameter (n=6 for histological examination) for any female with oocytes before hydration was 1720 μm.

The mean length of mature females was 79.2 cm during 1977–87, and the GSI data were derived from females smaller and greater than 79.2 cm. The GSI was very poorly correlated with length (r^2=0.04), and we used the mean GSI (0.063, σ^2=0.000018) in our sample to obtain a natural mortality estimate of M = 0.112. The variance of M ($Var\,\hat{M}$, 0.0002) was estimated according to the method of Gunderson et al. (2003) with the following equation:

$$Var\hat{M} = (\overline{GSI})^2 Var(\hat{k}) + \hat{k}^2 Var(\overline{GSI}),$$

where $Var\,\hat{M}$ = the variance of mortality;
$\overline{GSI}$ = mean value of GSI; and
$\hat{k}$ = constant from the GSI-M regression (Gunderson, 1997).

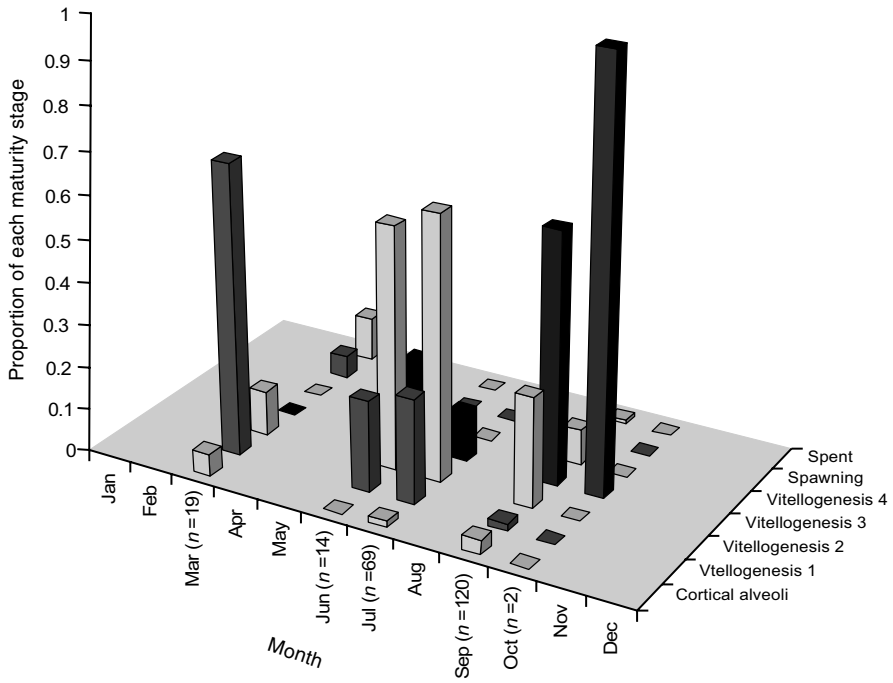

Figure 3

Proportion of Greenland halibut (*Reinhardtius hippoglossoides*) females in each histological maturity stage by month. The number of females (n) is noted for each month along the x-axis. Ovaries were collected in March 2004; June 2000, 2002, 2003; July 2000, 2002, 2003; September 1999, 2000; and October 2000.

The final estimate of instantaneous natural mortality (M) in our study had a standard error of 0.0138, yielding a 95% confidence interval of 0.08–0.14).

Potential annual fecundity

When nine females were tested for the difference in mean oocyte density by ovary location, the difference was significant (two-way ANOVA, $P<0.01$, df=2 , $F=19.7$). Mean oocyte densities were 280, 276, and 240 in the anterior, middle, and posterior locations in ovaries, respectively. Paired t-tests indicated that the posterior location had a significantly lower oocyte density than middle ($P<0.001$) or anterior locations ($P<0.001$), whereas the middle and anterior locations were not significantly different from each other ($P=0.19$). Oocyte density was also slightly lower in the eyed (259 eggs/gram) than in the blind lobe (272 eggs/gram; two-way ANOVA, $P=0.034$, df=1, $F=4.8$).

Mean oocyte diameters also varied significantly by ovary location (two-way ANOVA, $P=0.047$, df=2, $F=3.4$). Mean oocyte diameters for the anterior, middle, and posterior locations were 1611, 1627, and 1609 μm, respectively. We observed two distinct and separate oocyte size-frequency modes corresponding to nonvitellogenic and vitellogenic oocytes when the average vitellogenic oocyte diameter exceeded 1000 μm (Fig.4). On the basis of these results, we decided to include only those samples where the mean vitellogenic oocyte diameter was greater than 1000 μm ($n=6$ oocytes per specimen for histological examination).

Potential annual fecundity data conformed more closely to a linear regression on total weight:

$$Fec = 13.438\ (Wt_{total}(g)) - 436.4438 \quad r^2=0.6206,\ n=47$$

where Fec = fecundity; and
Wt_{total} = total weight,

than to a nonlinear regression on length (Fig. 5):

$$Fec = 0.0266\ (ForkLength(\text{cm}))^{3.3654}, \quad r^2=0.4969,\ n=47$$

where Fec = fecundity; and
$ForkLength$ = fork length.

The highest fractions of atretic vitellogenic oocytes occurred in females with oocytes in early stages of vitellogenesis. Once the largest cohort of vitellogenic oocytes reached a diameter of 750 μm, the fraction of atresia was greater than 0.20 for only one of 153 specimens. Over 77% of females with developing oocytes had fractions of atresia of 0.05 or less, and over 90% of females had fractions of atresia of 0.10 or less. For fish that met oocyte diameter criteria for fecundity estimates

Table 2

Greenland halibut (*Reinhardtius hippoglossoides*) female length (cm) at 50% maturity determined in the present study and in other studies. Examination method column indicates whether visual macroscopic gonad inspection or histological examination was used to assign maturity stages.

Study	Examination method	Area	Length
This study	Histological	Bering Sea, Aleutian Islands	65–70
Walsh and Bowering (1981)	Histological and visual	Northern Labrador	75–80
Nielsen and Boje[1]	Histological	West Greenland Fjords	65
Junquera et al. (1999)	Visual, checked with histological	Flemish Cap (N. Atlantic)	64.5–69.5
Gundersen (2003)	Visual, checked with histological	Barents Sea	57.8
Morgan et al. (2003)	Visual	Gulf of St. Lawrence 1978–1981	58.2
Morgan et al. (2003)	Visual	Gulf of St Lawrence 1996–2000	48.2
Morgan et al. (2003)	Visual	Labrador-eastern Newfoundland	78.5
Morgan et al. (2003)	Visual	Eastern Greenland	62.7
Morgan et al. (2003)	Visual	Iceland	64
Morgan et al. (2003)	Visual	Barents Sea (Norwegian data)	57.3
Morgan et al. (2003)	Visual	Barents Sea (Russian data)	60.6

[1] Nielsen, J. G., and J. Boje. 1995. Sexual maturity of Greenland halibut at West Greenland based on visual and histological observations. NAFO SCR Doc. 95/18, 7 p. Northwest Atlantic Fisheries Organization, P.O Box 638, Dartmouth, Nova Scotia, Canada B2Y 3Y9.

(mean diameter of vitellogenic oocytes >1000 μm), the mean fraction of atretic vitellogenic oocytes was 0.04 (standard deviation [SD]=0.05, n=108).

Length at maturity

All females smaller than 65 cm were categorized as immature, although few females were collected between 51 and 60 cm (2 females between 61 and 65 cm, and 4 females between 56 and 60 cm). All females larger than 70 cm were categorized as mature.

Discussion

Maturity at length

No precise estimate of female length at 50% maturity was possible because of a scarcity of collected samples near the presumed length at 50% maturity. The data indicate length at 50% maturity is somewhere between 65 and 70 cm and is higher than the 60 cm value currently used in stock assessment (Ianelli et al.[1]). Estimates for female length at 50% maturity for this species in other geographic regions range from 48–80 cm (Table 2).

Fecundity

Atresia followed the same general pattern as reported by Gundersen (2003) and did not have a large effect on annual fecundity. Fecundity at length from our study was somewhat higher than that reported by D'yakov (1982) from samples collected in 1978 in the Bering Sea. The results from both our study and D'yakov's study (1982) fall within reported ranges of fecundity from other regions; however there is strong variation between the regions in fecundity at length (Fig. 5). Gundersen (2003) hypothesized a geographic variation in fecundity for Greenland halibut. This variation may be caused by a trade-off between egg size and fecundity (Roff, 1992). The largest vitellogenic oocytes before hydration in our study were about 1700 μm, compared to 2800 μm reported by Gundersen (2003) for samples collected in the Barents Sea. Fecundity estimates by Gundersen (2000) from samples collected in the Barents Sea in 1996, 1997, and 1998 were all lower than the fecundity estimates from our study (Fig. 5).

Length-GSI relationship and instantaneous rate of natural mortality

The estimated rate of instantaneous natural mortality of 0.112 from our study is lower than the value of M currently used in the Bering Sea and Aleutian Islands stock assessment. The stock assessment uses a maximum age of 21 to estimate M to be 0.18 (Ianelli et al.[1]).

Our estimate for M corresponds more closely with results from Gregg et al. (2006) who aged Greenland halibut from the Bering Sea up to 36 years, corresponding to an M of 0.115. A recent age validation study has revealed that Greenland halibut in the Atlantic live up to 33 years, which is also older than previous estimates (Treble et al.[2]). Overestimating M may result in unsustainably high target harvest rates (Clark, 1999).

This study provides a length range for estimated length at 50% maturity, annual fecundity, and an

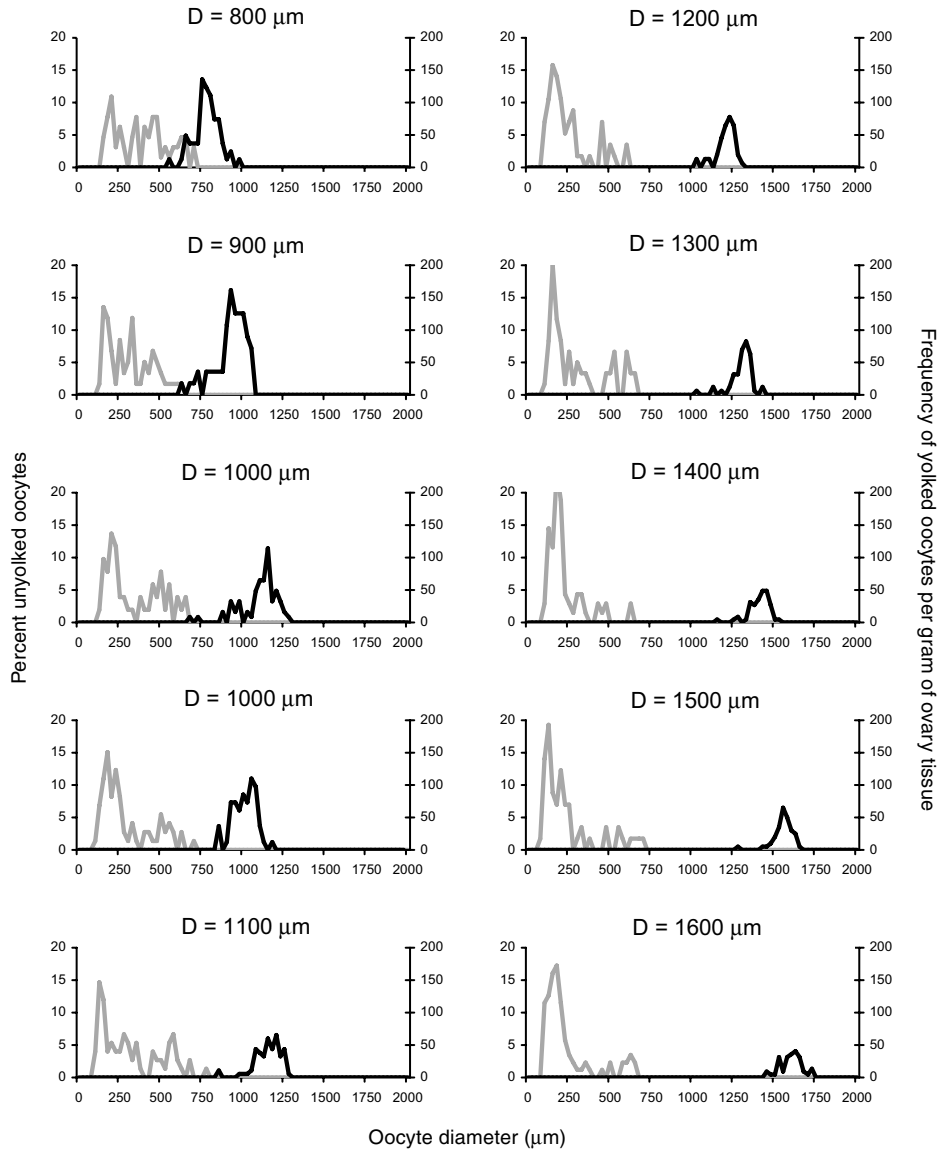

Figure 4

Frequency of oocyte diameter for 10 female Greenland halibut (*Reinhardtius hippoglossoides*) arranged in progression of vitellogenic oocyte mean diameter (D). Data for non-vitellogenic oocytes (in gray) are plotted in terms of percent frequency, and vitellogenic oocytes (in black) in terms of number of oocytes per gram of ovary tissue.

estimate of instantaneous natural mortality independent of age data for a species with an uncertain age structure. Fecundity was higher and eggs were smaller in Greenland halibut from Alaskan waters than the reported values for the Barents Sea. This may be due to a trade-off between number of eggs and egg size (Roff, 1992). Based on the energy invested in annual reproduction (GSI), Greenland halibut mortality (M) appears lower than the values used currently in population models.

Acknowledgments

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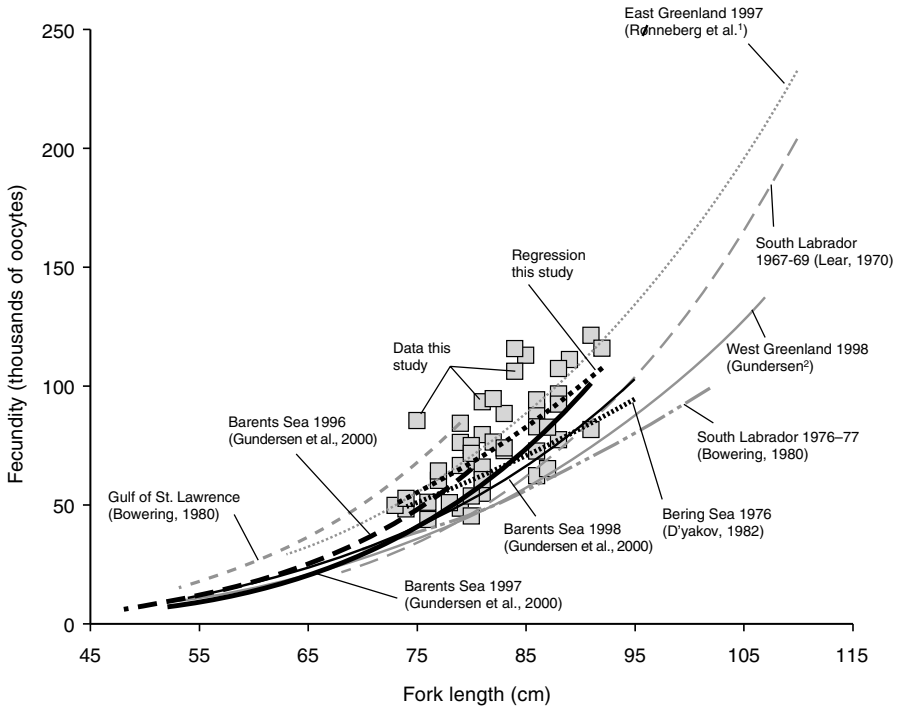

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Figure 5

Greenland halibut (*Reinhardtius hippoglossoides*) fecundity-at-length data and fitted regression lines for this (n=47, r^2=0.50) and other studies.

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