Oocyte maturation in Hecate Strait English sole (*Pleuronectes vetulus*)

Jeff Fargo
Department of Fisheries and Oceans, Pacific Biological Station
Biological Sciences Branch, Nanaimo, British Columbia V9R 5V6

Albert V. Tyler
School of Fisheries and Oceans
University of Alaska, Fairbanks, Alaska 99775

English sole, *Pleuronectes vetulus*, is an important component of the bottom trawl fishery in Hecate Strait, British Columbia, Canada. It is a small-mouthed flounder that feeds on sedentary invertebrates associated with sandy substrate and is most common at depths of 80–150 m (Hart, 1973). The species is characterized by moderate growth (k=0.22), mortality (M=0.20) and longevity (20 years) (Fargo, 1993). It recruits to the fishery at an age of four years, which is roughly equivalent to the age of sexual maturity (Ketchen, 1956; Tyler et al., 1987[1]). Most of the exploited population is under 12 years of age (30–45 cm in length) (Fargo, 1993). Results from tagging studies (Ketchen, 1956; Fargo et al., 1984) and analysis of landing statistics and age composition data (Fargo, 1993) indicate that a single stock exists in Hecate Strait.

Since 1955, abundance for this stock has fluctuated, primarily because of changes in recruitment (Fargo, 1993). Factors influencing recruitment for this stock are poorly understood. Ocean temperature and circulation have been found to influence spawning time and oocyte maturation for the stock off the Oregon coast (Kruse and Tyler, 1989). These authors postulated that 1) the rate of gonadal development for English sole was inversely related to summer bottom temperatures in the same manner as is somatic growth, and 2) spawning was delayed by rapid increases in bottom temperature caused by upwelling. In Hecate Strait, where Ekman transport is weak, these temperature changes may be brought about by the fall transition when strong winds from the south cause mixing of the warm surface waters to depths of 150 metres (Dodimead, 1980[2]). Relatively little information exists on spawning time and egg development for the Hecate Strait stock. We investigated oocyte growth and development to examine the length of the oocyte maturation period and the time and duration of spawning for the English sole stock in Hecate Strait.

Materials and methods

Samples of English sole ovaries were obtained from research cruises and at ports-of-landing from commercial vessels between November 1987 and November 1990. The fish were caught with bottom trawls at five locations throughout Hecate Strait (PMFC Areas 5C-D, Table 1, Fig. 1). Length-stratified samples were collected to ensure that ovaries were obtained throughout the size range of fish collected. For each collection we attempted to sample fifteen sexually mature fish from each 5-cm length interval over a range of 30–50 cm, though this was not always possible. The minimum size fish (30 cm) from which an ovary was dissected corresponds to the length at first maturity for this stock (Ketchen, 1956; Tyler et al., 1987[1]). Total length and the condition of maturity for each fish sampled was recorded. The right ovary was then removed and preserved in a buffered formalin-saline solution (Foucher et al., 1987[3]). Sampling methods have been described in previous reports (Foucher et al., 1987[3]; Tyler et al., 1987[1]). A list of ovary samples examined is given by sample type and month in Table 1.

Preserved ovaries were prepared for histological examination by soaking in Davidson's fixative for approximately 24 hours. Subsequently, tissue sections were dissected from the anterior portion of the ovary (which contained the greatest amount of eggs), embedded in paraffin wax, sectioned at 5 μ, stained with haematoxylin and counterstained with eosin (Yasutake and Wales, 1983).

Oocyte diameter was measured with a light microscope calibrated

[1] Tyler, A. V., J. Fargo, R. P. Foucher, and J. B. Lucas. 1987. Studies on the reproductive biology of Pacific cod and English sole in Hecate Strait from the cruise of the FR/V *W.E. Ricker*, November 25–29, 1986. Can MS. Rep. Fish. Aquat. Sci. 1937, 43 p.

[2] Dodimead, A. J. 1980. A general review of the oceanography of the Queen Charlotte Sound-Hecate Strait-Dixon Entrance region. Can. MS. Rep. Fish. Aquat. Sci. 1574, 248 p.

[3] Foucher, R. P., J. Fargo, and J.B. Lucas. 1987. Cruise of the FV *Nucleus*, January 5–17, 1987 to Hecate Strait to study reproductive biology of Pacific cod and English sole. Can. MS Rep. Fish. Aquat. Sci. 1941, 25 p.

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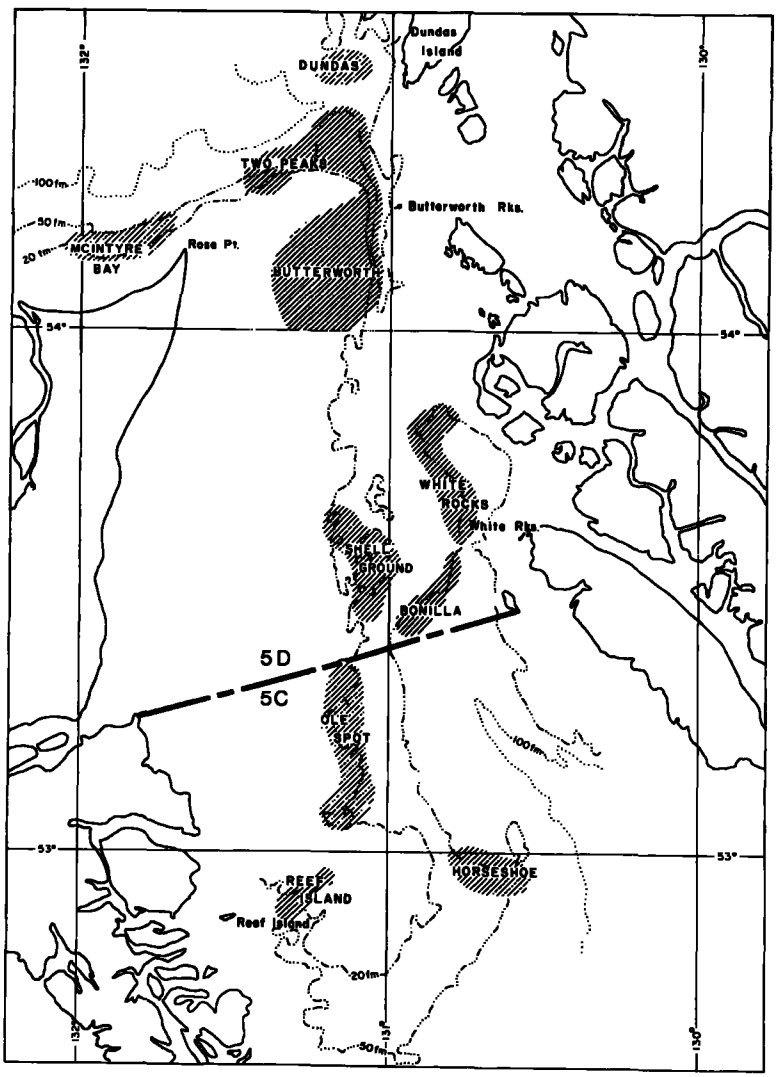

Figure 1

Location of trawling grounds in the study area, Hecate Strait, British Columbia, Canada.

to the nearest 5 μ, or with a projection microscope calibrated to the nearest 4 μ. Three hundred oocytes were measured from at least one fish for every cm length interval for each sample (Table 1). Measurement of 300 oocytes per fish was necessary to provide complete information on the size composition of developing oocytes. Only oocytes that had been sectioned through the nucleus, close to the center of the oocyte, were measured. Mean diameter was estimated as the mean of the minimum and maximum diameters for each oocyte (Foucher and Beamish, 1980). For smaller oocytes (10–20 μ), precision of the measurement was lower because of distortion of the oocyte by surrounding maturing oocytes (Dunn, 1970). A description of the histological stage of oocyte development (Fargo and Sexton, 1991[4]) was also recorded.

We were unable to obtain oocyte measurements from ovaries collected from ripe fish in October and November 1990. These samples were taken from commercial vessels at ports of landing. Ovaries from these samples had combinations of hydrated and non-hydrated oocytes with many burst cells. These fish had been held in chilled seawater for several days prior to sampling, probably exacerbating the state of hydrated oocytes and causing them to burst. Since oocyte diameter data for these samples would have been biased (because most measurable oocytes would not have reached the hydrated state) the slides from these samples were used only to assess the histological stage of the oocytes. This problem did not occur with the November 1987 sample collected at sea on a research vessel.

Prior to statistical testing of the data, we tested oocyte size distributions for normality using the Shapiro-Wilk test. We applied two sample *t*-tests to test for differences in the mean diameter of previtellogenic and vitellogenic oocytes between months within years and among years. We used linear regression to investigate the relation 1) between fish length and mean oocyte diameter within months and 2) between fish length and mean oocyte diameter at the time of spawning.

Results

Oocyte development

Ovaries were examined from 174 fish (Table 1) caught at five locations in Hecate Strait (Fig. 1). The sampling period encompassed seven different months over three years. Descriptions and micro-

[4] Fargo, J., and T. Sexton. 1991. A quide to the ovarian histology of English sole (*Parophrys vetulus*). Can. MS. Rep. Fish. Aquat. Sci. 2133, 19 p.

graphs of the stages of maturation for English sole oocytes have been summarized by Fargo and Sexton (1991).[4] Examples of oocyte size distributions for fish of different lengths sampled during the same period, August 1988, are presented in Figure 2. For all sizes of English sole collected, we observed the simultaneous presence of only two modes in the oocyte size distributions. The smaller mode (10–150 μ) consisted of previtellogenic oocytes and the larger mode (150–500 μ) of vitellogenic oocytes. No previtellogenic ooctyes >150 μ were observed. The size modes for previtellogenic oocytes were similar among fish ranging in size from 33 to 46 cm. The mode for vitellogenic oocytes shifted to the right (increased) with increasing fish length.

Vitellogenic oocytes increased in size from early summer until they became hydrated prior to spawning in the fall (Fig. 3). We observed no trend in the size composition of previtellogenic oocytes over the same period. As the month of spawning was approached a complete separation between the two modes became apparent. The irregular shape of the modal distribution for vitellogenic oocytes in Figure 3 is caused by combining data for fish of different lengths and developing at different rates. The more normal distribution for this mode during the month of spawning is due to two factors. First, the size range of fish for this sample was smaller than for other samples and, second, egg diameter at the time of spawning was similar for fish of different length. Fargo and Sexton (1991)[4] described the events of oocyte maturation for English sole in detail. Briefly,

Table 1

A summary of ovary samples examined in the study of oocyte maturation in Hecate Strait English sole (*Pleuronectes vetulus*).

Date	Sample type	Location	Length class (cm) (No. ovaries examined)
7–13 January 1987	Research cruise	Two Peaks	30–34 (2)
		White Rocks	35–39 (6)
			40–44 (5)
			45–49 (5)
			50–54 (4)
			55–59 (1)
		Total	(23)
19 January 1988	Port sample	White Rocks	30–34 (1)
			35–39 (1)
			40–44 (1)
		Total	(3)
17 March 1987	Research cruise	Horseshoe	30–34 (2)
			35–39 (2)
			40–44 (3)
			45–49 (2)
			50–54 (1)
		Total	(10)
16 March 1988	Port sample	Horseshoe	30–34 (1)
			35–39 (4)
			40–44 (2)
			45–49 (1)
		Total	(8)
May 5 1988	Port Sample	Horseshoe-White Rocks	30–34 (1)
			35–39 (1)
			40–44 (2)
			45–49 (6)
		Total	(10)
6 June 1987	Research cruise	Horseshoe-Bonilla	30–34 (1)
			35–39 (3)
			40–44 (3)
			45–49 (3)
			50–54 (3)
		Total	(12)
2 June 1988	Port sample	Horseshoe	30–34 (1)
			35–39 (3)
			40–44 (3)
			45–49 (3)
			50–54 (2)
		Total	(12)
27 August 1987	Research cruise	Horseshoe	30–34 (1)
			34–39 (7)
			40–44 (5)
			50–54 (1)
		Total	(14)

Table 1 (continued)

Date	Sample type	Location	Length class (cm) (No. ovaries examined)
22 August 1988	Port sample	Horseshoe	30-34 (2)
			34-39 (5)
			40-44 (8)
			45-49 (6)
			50-54 (1)
		Total	(22)
28 August 1990	Port sample	Two Peaks	35-39 (4)
			40-44 (4)
			45-49 (4)
			50-54 (1)
		Total	(13)
27 January 1988	Port sample	Two Peaks-Butterworth	30-34 (4)
			35-39 (2)
			40-44 (3)
			45-49 (1)
			50-54 (1)
		Total	(11)
19 January 1990	Port sample	Horseshoe	30-34 (1)
			35-39 (6)
			40-44 (8)
			45-49 (1)
		Total	(16)
5–6 November 1987	Research cruise	Horseshoe-Butterworth-White Rocks	30-34 (5)
			35-39 (7)
			40-44 (4)
			45-49 (2)
			50-54 (1)
3 November 1990	Port sample	Butterworth	30-34 (1)
			35-39 (1)
			40-44 (2)
			45-49 (1)
			50-54 (1)
		Total	(6)

vitellogenesis occurred when oocytes reached a diameter of about 150 μ. Vacuolization occurred in oocytes ranging from 180 μ to 250 μ Deposition of yolk in the outer cortex occurred in oocytes ranging in size from 200 μ to 430 μ, and hydrated oocytes ranged in size from 375 μ to 550 μ.

We began our investigation of the timing and duration of oocyte maturation by examining the size composition and histological stage of oocytes collected from fish sampled between January and November. Ovaries examined from 68 of 72 fish collected during winter and spring (January 1987–88 and March 1987–88) contained mainly previtellogenic oocytes. The fish examined from the January samples contained previtellogenic oocytes only. Four of 22 fish examined from samples collected during the month of March contained vitellogenic oocytes. Three of these (36–40 cm in length) contained vitellogenic oocytes that were hydrated and translucent (405–429 μ mean diameter). The fourth fish (46 cm in length) contained oocytes that had recently undergone vitellogenesis (mean diameter=230 μ).

Vitellogenesis for most fish occurred in the early summer. In May 1988, we observed vitellogenic oocytes in six of nine fish examined, ranging from 40 to 49 cm in length. All of these oocytes were in the early stages of development, prior to vacuolization, with mean diameters ranging from 174 to 263 μ. Smaller fish (length range 33–42 cm) contained previtellogenic oocytes only . In June (1987, 1988) vitellogenic oocytes, ranging in mean diameter from 178 μ to 269 μ, were present in 23 of 24 fish examined (length range 36–52 cm). Vitellogenic oocytes in one fish of 52 cm were at an advanced stage of development (mean diameter=252 μ), with yolk granules formed in the outer cortex. The relation between mean diameter of vitellogenic oocytes and fish length was not significant for the months of May (1988) and June (1987, 1988) (linear regression, $P>0.1$ for all three, $n=6, 11, 12$)

By August the oocytes in some of the larger fish (45–50 cm) were nearing hydration. Mean diameters for vitellogenic oocytes from fish sampled in August (1987, 1988, 1990) ranged from 226 μ to 429 μ. There were significant, positive linear relationships between fish length and mean oocyte diameter for all of these samples (Table 2, Fig. 4).

The size distributions for previtellogenic and vitellogenic oocytes did not differ significantly (Shapiro-Wilk test, $P<0.05$) from that of the normal distribution for any of the following cases. There was no significant difference in mean diameter of previtellogenic oocytes for the same months across

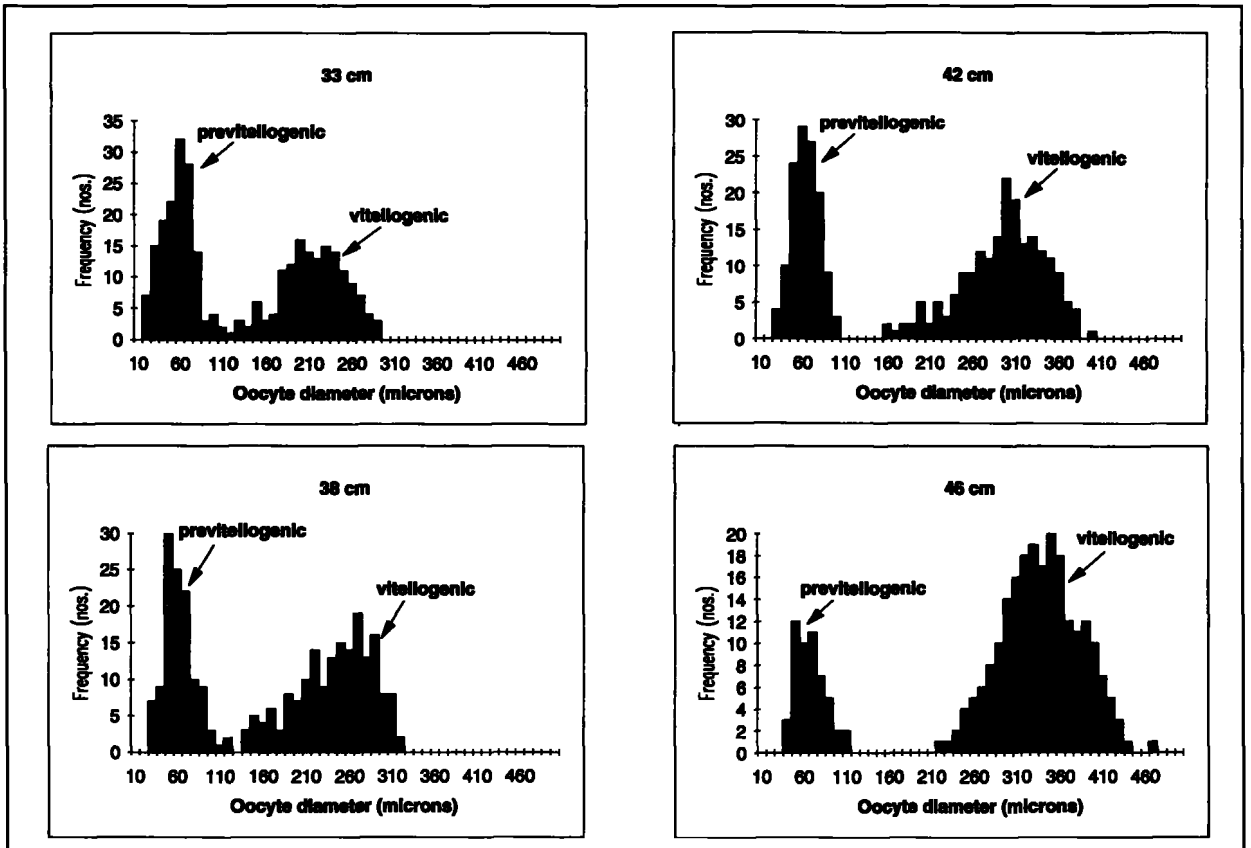

Figure 2

Oocyte size compositions determined from ovary samples collected from Hecate Strait English sole (*Pleuronectes vetulus*) in August 1988.

the two years (Table 3). However, there were significant differences in mean diameter for previtellogenic oocytes among months within both years (Table 4). No obvious trend in mean diameter over time was apparent for previtellogenic oocytes. There were significant differences in the rate of oocyte development between 1987 and 1988 (Table 3). The mean diameter of vitellogenic oocytes in June and August of 1987 was significantly larger than for the same months in 1988, suggesting that vitellogenesis occurred earlier in 1987 than in 1988. There were also significant differences in the mean diameter of vitellogenic oocytes among months within years (Table 5). The mean diameter of vitellogenic oocytes increased significantly, coinciding with advancing oocyte development, between June–November in 1987 and June–October in 1988.

Spawning

Ovaries obtained from spawning fish (October 1988, 1990 and November 1987, 1990) were examined to investigate 1) size-dependent spawning and 2) the relation between fish length and egg diameter at the time of spawning. For the October 1988 sample, we observed the presence of vitellogenic oocytes only in fish smaller than 40 cm. The mean diameter of vitellogenic oocytes in these fish ranged from 287 to 408 μ. Fish ranging in length from 43 to 52 cm contained spent ovaries with previtellogenic oocytes only. Thus, we concluded that the larger fish had spawned prior to the time of the sample collection. In the October 1990 sample, taken two weeks earlier than the 1988 sample, some of the fish larger than 40 cm contained hydrated oocytes while others had spent ovaries with resorbing oocytes, suggesting that they were spawning in early October. Oocytes examined from samples collected in November (1987, 1990) also indicated that larger fish had spawned previous to this time. Fish larger than 42 cm contained only pre-vitellogenic oocytes and there was no sign of resorbing oocytes. Most smaller fish were in spawning condition during this month. Vitellogenic oocytes were present in fish ranging from 30 to 42 cm. Mean diameter ranged from 373 to 483 μ and these oocytes were hydrated and trans-

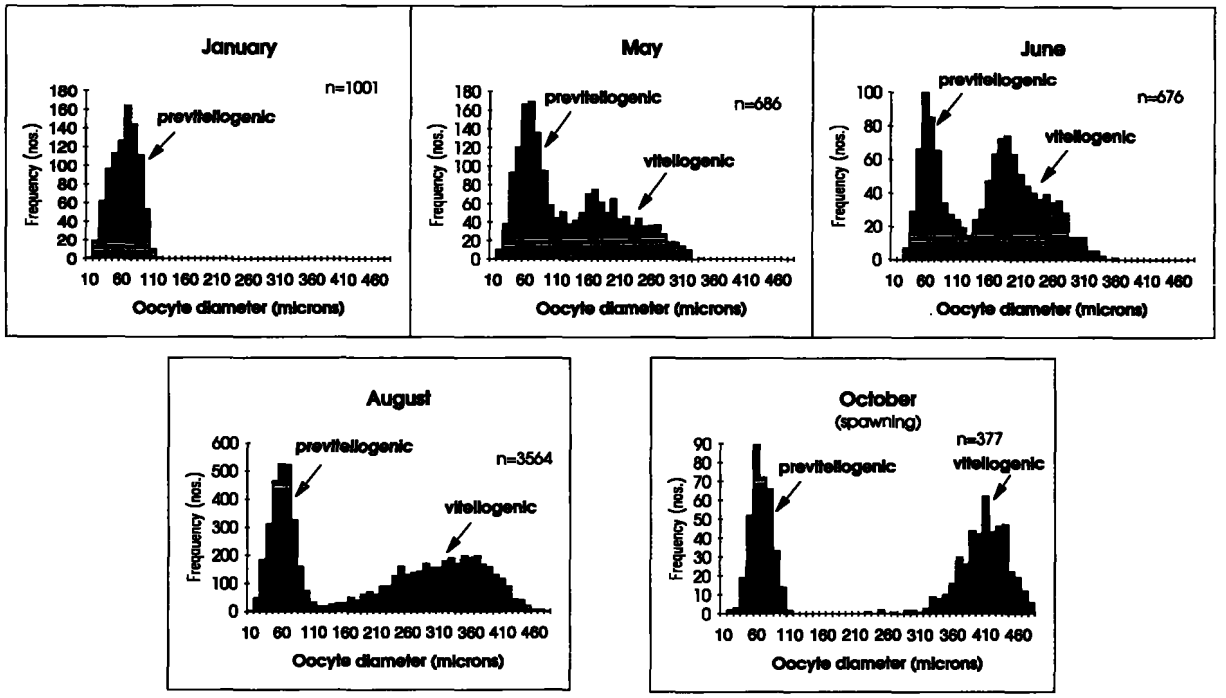

Figure 3

Oocyte size composition determined from ovary samples collected from Hecate Strait English sole (*Pleuronectes vetulus*) during January-October in 1988 (samples combined).

lucent. We then combined all the data on mean egg diameter for spawning fish and there was no relationship between mean egg diameter at the time of spawning (hydrated and translucent) and fish length (linear regression, $P>0.1$, $n=19$).

Table 2

Linear regression statistics for the relationship between vitellogenic oocyte mean diameter and fish length for English sole (*Pleuronectes vetulus*) for the month of August 1987, 1988, and 1990.

Year	Degrees of freedom	*F*-statistic	*P*	Regression equation[1]	*r*
1987	13	10.72	0.007	$Y = 122 + 5.93X$	0.687
1988	20	20.93	<0.0001	$Y = -93 + 9.44X$	0.910
1990	12	44.01	<0.0001	$Y = -237 + 12.6X$	0.724

[1] Y = oocyte mean diameter (μ).
X = total length of fish (cm).

Discussion

Oocyte development

Dunn and Tyler (1969) and Dunn (1970) determined the length of time required for oocyte maturation in winter flounder (*Pleuronectes americanus*). They observed two size modes of previtellogenic oocytes at any particular time. They documented the rate of increase in size for these modes for three consecutive years and concluded that the oocyte maturation period for this species was three years.

We observed only a single mode for both previtellogenic and vitellogenic oocytes in fish sampled during all the months examined in our study. Johnson et al. (1991) reported similar results in their study of Puget Sound English sole. If oocytes produced in year i were spawned in year $i+1$, we would expect to see two size classes of immature oocytes in year $i+1$, corresponding to those oocytes that were produced in year i (large immatures) to be spawned in year $i+1$ and those that were produced in year $i+1$ (small immatures) to be spawned in year $i+2$. The fact that there were no significant differences in the mean diameter of previtellogenic oocytes for the same months in consecutive years (1987–88) suggests that the oocyte maturation period for Hecate Strait English sole is probably one year.

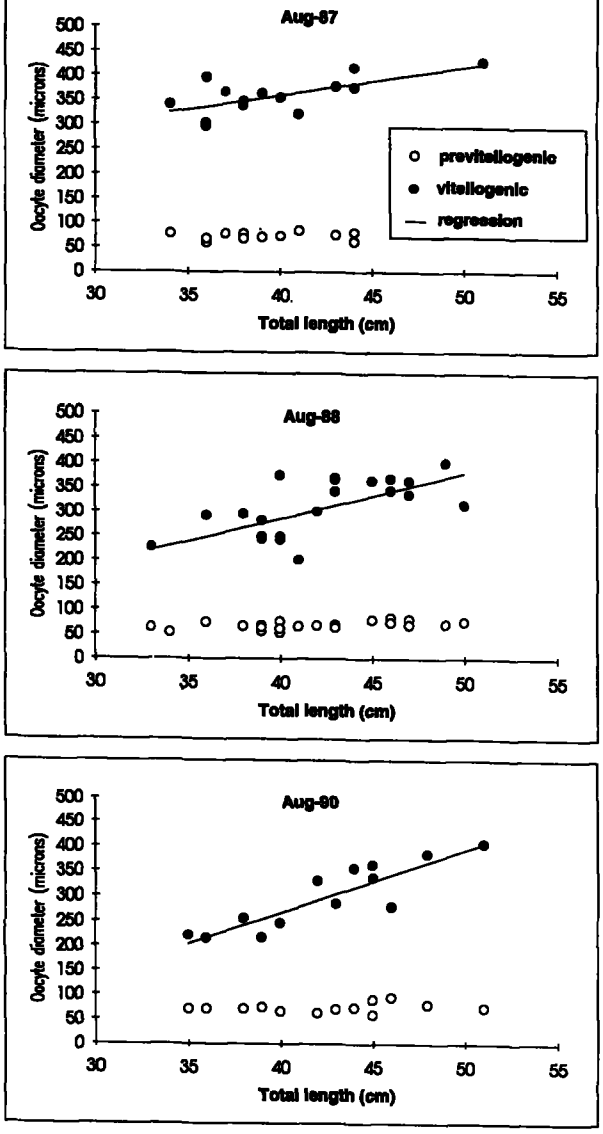

Figure 4

Mean oocyte diameter vs fish length determined from ovary samples collected from Hecate Strait English sole (*Pleuronectes vetulus*) during the month of August, 1987, 1988, and 1990.

We also found no trend in the mean size of previtellogenic oocytes among months within years, contrary to results reported by Dunn and Tyler (1969). One explanation for this is that the recruitment of small immature (previtellogenic) oocytes from the germinal epithelium is a continual process for Hecate Strait English sole. Alternatively, there may be a short time period, following spawning for example, during which previtellogenic oocytes recruit and quickly grow to a size of around 80 μ. Additional work is needed to resolve these possibilities.

Table 3

Results of two sample *t*-tests of mean diameters of previtellogenic and vitellogenic oocytes for English sole (*Pleuronectes vetulus*) determined from samples collected during the same month in 1987 and 1988.

Month and year	*n*	mean diameter (microns)	*P*
previtellogenic			
January 1987	6,264	69.0	
January 1988	1,001	69.4	>0.1
March 1987	1,603	59.2	
March 1988	1,737	59.8	>0.1
June 1987	1,389	72.4	
June 1988	1,132	72.9	>0.1
August 1987	1,812	66.7	
August 1988	2,071	65.8	>0.1
vitellogenic			
June 1988	953	219.1	
June 1988	1,029	203.3	<0.0001
August 1987	1,774	362.1	
August 1988	3,584	318.1	<0.0001

Spawning

In general larger fish produced yolk earlier and spawned earlier than smaller fish. Most of the spawning fish were obtained from samples collected in October and November but there was also evidence of spring (March) spawning for smaller fish. Egg size at the time of spawning did not appear to be dependent on fish length. However, there is some evidence from this study to suggest a possible minimum size limit for eggs at the time of spawning. That is, the difference in the mean diameter of vitellogenic oocytes between smaller and larger fish decreased over time until there was no apparent difference at the time of spawning. Observations made during this study indicate that atresia was not as prevalent for Hecate Strait English sole as that reported for English sole in Puget Sound by Johnson et al. (1991).

Marine fish species show wide variability in the reproductive process, which enables them to mitigate the uncertain conditions in the marine environment (Murphy, 1968; Roff, 1981). English sole demonstrate considerable phenotypic plasticity with regard to spawning. In Hecate Strait the spawning season extends from early fall through the follow-

Table 4

Results of two sample t-tests of the mean diameter (μ) of previtellogenic oocytes in English sole (*Pleuronectes vetulus*) among months for samples collected in 1987 and 1988.

Year and Month	January	March	June	August	November
1987					
January (n=6264, $\bar{x}$=69.0μ)	—	P<0.0001	P<0.0001	P=0.0004	P<0.0001
March (n=1603, $\bar{x}$=59.2μ)	—	—	P<0.0001	P<0.0001	P<0.0001
June (n=1389, $\bar{x}$=72.4μ)	—	—	—	P<0.0001	P<0.0001
August (n=1812, $\bar{x}$=66.7μ)	—	—	—	—	P<0.0001
November (n=4205, $\bar{x}$=63.0μ)	—	—	—	—	—

Year and Month	January	March	May	June	August	October
1988						
January (n=1001, $\bar{x}$=69.4μ)	—	P=0.0009	P<0.0001	P=0.0009	P<0.0001	P<0.0001
March (n=1737, $\bar{x}$=59.8μ)	—	—	P<0.0001	P<0.0001	P<0.0001	P<0.0001
May (n=1609, $\bar{x}$=76.2μ)	—	—	—	P=0.003	P<0.0001	P<0.0001
June (n=1132, $\bar{x}$=72.9μ)	—	—	—	—	P<0.0001	P<0.0001
August (n=2071, $\bar{x}$=65.8μ)	—	—	—	—	—	P<0.0001
October (n=1500, $\bar{x}$=56.9μ)	—	—	—	—	—	—

Table 5

Results of two sample t-tests of the mean diameter (μ) of vitellogenic oocytes in English sole (*Pleuronectes vetulus*) among months for samples collected in 1987 and 1988.

Year and month	June	August	November
1987			
June (n= 953, $\bar{x}$=219.1μ)	—	<0.0001	<0.0001
August (n=1774, $\bar{x}$=362.1μ)	—	—	<0.0001
November (n= 488, $\bar{x}$=413.7μ)	—	—	—

Year and month	May	June	August	October
1988				
May (n=191, $\bar{x}$=201.4μ)	—	>0.1	<0.0001	<0.0001
June (n=1029, $\bar{x}$=203.3μ)	—	—	<0.0001	<0.0001
August (n=3584, $\bar{x}$=318.1μ)	—	—	<0.0001	<0.0001
October (n=710, $\bar{x}$=342.1μ)	—	—	—	—

ing spring. Johnson et al. (1991) reported a similar spawning period for Puget Sound English sole as did Kruse and Tyler (1989) in their study of English sole off the Oregon coast. This reproductive strategy may increase the probability of encountering favorable conditions for larval survival by spreading the reproductive effort over the longest possible time span.

Based on our results it is unlikely that cohort-specific spawning occurs as in Pacific herring, *Clupea pallasi* (Ware and Tanasichuk, 1989), and Norwegian Atlantic herring, *Clupea harengus* (Lambert, 1990). However, in view of the relation between oocyte maturation and fish length and the duration of the spawning period, it is possible that first time

spawners spawn at a different time than the rest of the stock. We can suggest no mechanism to account for this and more data are required to corroborate these results.

There is also evidence of interannual variability in oocyte maturation and this process appears to be size-related. Smaller fish matured later and spawned later than larger fish. Our results indicate that the time of peak spawning and the duration of the spawning season are variable from year to year. The results from this study provide baseline information for an investigation of the recruitment biology of this stock.

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Literature cited

Dunn, R. S.
1970. Further evidence for a three year oocyte maturation time in the winter flounder (*Pseudopleuronectes americanus*). J. Fish. Res. Board Canada. 27:957–960

Dunn, R. S., and A. V. Tyler.
1969. Aspects of the anatomy of the winter flounder (*Pseudopleuronectes americanus*) with hypotheses on oocyte maturation time. J. Fish. Res. Board Canada 26:1943–1947.

Fargo, J.
1993. Flatfish. *In* B. M. Leaman and M. Stocker (ed.), Groundfish stock assessments for the west coast of Canada in 1992 and recommended yield options for 1993. Can. Tech. Rep. Fish. Aquat. Sci. 1919:95–131.

Fargo, J, R. P. Foucher, S. C. Schields, and D. Ross.
1984. English sole tagging in Hecate Strait, R/V G.B. REED, June 6–24, 1983. Can. Data Rep. Fish. Aquat. Sci. 427, 49 p.

Foucher, R. P., and R. J. Beamish.
1980. Production of nonviable oocytes by Pacific hake (*Merluccius productus*). Can. J. Fish. Aquat. Sci. 37:41–47.

Hart, J. L.
1973. Pacific fishes of Canada. Fish. Res. Board Can. Bull. 180, 740 p.

Johnson, L. L, E. Casillas, M. S. Myers, L. D. Rhodes and O. P. Olson.
1991. Patterns of oocyte development and related changes in plasma 17–B estradiol, vitellogenin and plasma chemistry in English sole *Parophrys vetulus* Girard. J. Exp. Mar. Biol. Ecol. 152: 161–185.

Ketchen, K. S.
1956. Factors influencing the survival of the lemon sole (*Parophrys vetulus*) in Hecate Strait, British Columbia. J. Fish. Res. Board Canada, 13(5): 647–694.

Kruse, G. H., and A. V. Tyler.
1989. Exploratory simulation of English Sole (*Parophrys vetulus*) recruitment mechanisms. Trans. Am. Fish. Soc. 118:101–118.

Lambert, T. C.
1990. The effect of population structure on recruitment in herring. J. Cons. int. Explor. Mer 47:249-255.

Murphy, G. I.
1968. Pattern in life history and the environment. Am. Nat. 102:391–403.

Roff, D. A.
1981. Reproductive uncertainty and the evolution of iteroparity: why don't flatfish put all their eggs in one basket? Can. J. Fish. Aquat. Sci. 38:968–977.

Ware, D. M., and R. Tanasichuk.
1989. Biological basis of maturation and spawning waves in Pacific herring (*Clupea harengus pallasi*). Can. J. Fish. Aquat. Sci. 46(10):1776–1784.

Yasutake, W. T., and J. H. Wales.
1983. Microscopic anatomy of salmonids: an atlas. Fish. Wild. Ser. U.S. Dep. Int. Res. Pub. 150, 189 p.