Annual and batch fecundities of yellowfin sole, *Limanda aspera*, in the eastern Bering Sea

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Abstract—Annual and batch fecundities of yellowfin sole, *Limanda aspera*, in the eastern Bering Sea were determined. Most individuals had a determinate, group-synchronous mode of oocyte development as evidenced by a distinctly separate distribution of fully yolked oocytes in more advanced ovaries. The spawning of batches by an individual female occurs in uninterrupted succession, as indicated by the presence of oocytes with migratory-stage nuclei in nearly all females undergoing oocyte hydration. Total fecundity ranged from 295,615 to 3,635,108 oocytes per female and is described by $3.3225 \times TL^{3.6312}$, where T = total fish length (cm). The length-fecundity relationship was found to be the same in both southeast and northwest areas of the eastern Bering Sea, despite known growth differences between the two areas. Individual females spawn from 8 to 11 batches. The first batch spawned is generally smaller in number than succeeding batches. After spawning begins, fish remain in the nearshore spawning area (<30 m bottom depth) until spent. The presence of residual chorion tissue from unspawned ova in the ovary lumen of some maturing females indicates that at least some females are capable of spawning more than one series of batches within one reproductive season. The annual fecundity, therefore, for such individuals is consequently considered indeterminate

Manuscript accepted 10 August 2000.
Fish. Bull. 99:108–122 (2001).

Yellowfin sole, *Limanda aspera*,[1] have historically been among the more abundant fishes in the eastern Bering Sea, where biomass estimates have exceeded 2 million metric tons (t) annually since 1980[2] (Wilderbuer et al., 1992; Nichol, 1998). Yellowfin sole has been an important commercial trawl species with annual catches averaging 135,630 t from1991 to 1998.[2] Yellowfin sole spawn from May through August in nearshore waters of Bristol Bay northward to at least Nunivak Island (Fadeev, 1970; Nichol, 1995) at depths less than 30 m (Nichol, 1995). Yellowfin sole, like many other flatfishes, are batch spawners (Nichol, 1995). They spawn pelagic eggs that have been observed in the plankton with diameters of approximately 0.76–0.85 mm (Waldron, 1981; Matarese et al., 1989). Adult yellowfin sole generally undergo long migrations from wintering grounds near the shelf-slope break to spring-summer grounds at bottom depths less than 50 m (Wakabayashi, 1989; Nichol, 1998).

Annual fecundity has been used as a measure of reproductive output for many species; its use as a parameter in fishery population models makes it relevant to stock assessment. Annual fecundity is defined as the total number of eggs spawned by a female in a single year. Batch fecundity, defined as the number of eggs released at one time, can be estimated for any female from counts of hydrated oocytes as long as the female is not ovulating or spawning. Directly estimating annual fecundity from counts of advance-stage oocytes is feasible only if the number of eggs to be spawned is determinate or fixed prior to spawning (Hunter et al., 1985, Hunter et al., 1992). Females with a determinate fecundity, just prior to spawning, will have a fixed number of advanced-yolked oocytes that are separated from the other less developed oocytes by a distinct gap in size; these can either be spawned in batches or all at once. In contrast, species whose ovaries are characterized by continuous oocyte size distributions may be able to develop unyolked oocytes continually and add them to the stock of advanced-yolked oocytes even after spawning begins. These species will typically develop multiple groups of oocytes with size distributions that overlap. The method to estimate annual fecundity in such species with the least error uses batch fecundity, spawning frequency, and spawning season duration (Yamamoto, 1956; Hunter and Macewicz, 1985a). Prior to estimating annual fecundity, we examined oocyte size distributions to determine which mode of oocyte development yellowfin sole undergoes.

Assuming that yellowfin sole females have a determinate fecundity, two potential problems associated with estimating annual fecundity must be addressed. First, because yellowfin sole spawn eggs in batches, annual fecundity may be underestimated if partially spawned fish are included in estimates.

[1] Scientific name follows Cooper and Chapleau (1998).

[2] Wilderbuer, T. K., and D. Nichol. 1998. Yellowfin sole. Section 3 *in* Stock assessment and fishery evaluation report for the groundfish resources of the Bering Sea/Aleutian Islands regions. North Pacific Fishery Management Council, 605 West 4th Ave, Suite 306, Anchorage, AK 99501.

Identifying partially spawned ovaries can be difficult with unaided macroscopic observation. With microscopic observation, however, identification of postovulatory follicles (POFs) within an ovary verifies that at least one batch has been spawned (Hunter and Macewitz, 1985a; Hunter et al., 1992). Histological analysis of collected ovaries was employed in our study in part to identify POFs. Second, annual fecundity may be overestimated if the eventual loss of oocytes due to atresia (oocyte resorption) is not taken into account. Oocyte atresia can occur in varying degrees throughout the spawning season, depending on the species and environmental conditions (Hunter and Macewicz, 1985b; Macewicz and Hunter, 1994; Walker et al., 1994; McFarlane and Saunders, 1997). This bias can be minimized if ovaries chosen for fecundity estimates are well developed and near spawning condition.

Understanding the spawning characteristics along with other life-history parameters may help determine how fish abundance varies with changing environmental or fishing conditions. Moreover, knowledge of the fecundity and the spawning characteristics can help define how species, such as yellowfin sole, relate to other species from a phylogenetic perspective. In our study, we evaluate the annual and batch fecundities of yellowfin sole with reference to its spawning habits.

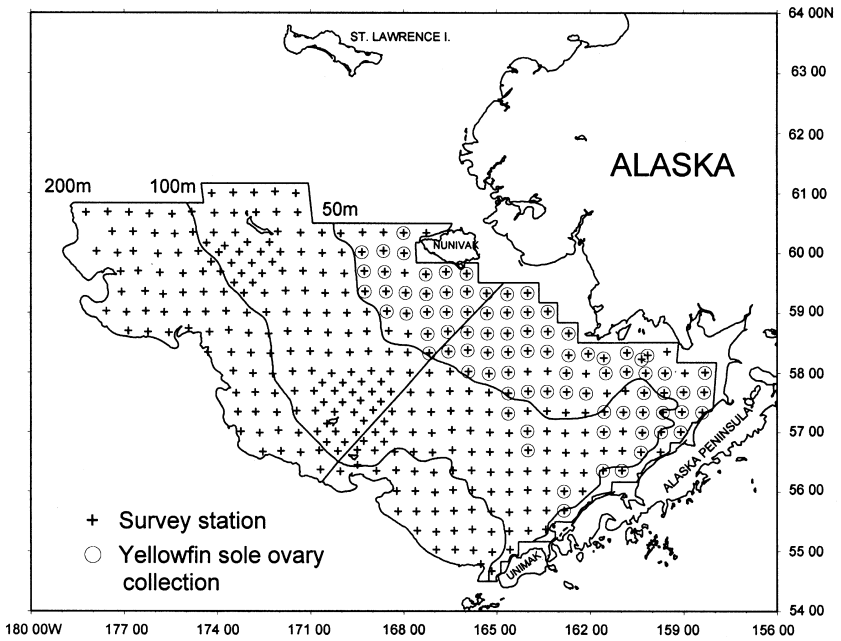

Figure 1

Location of yellowfin sole (*Limanda aspera*) ovary collections within the eastern Bering Sea trawl survey area, 1993. Stations where yellowfin sole ovaries were collected are circled. The diagonal line separates the northwest from the southeast sampling areas.

Materials and methods

Summary of collections

A total of 767 ovary pairs were collected in June and July of 1993 during a groundfish trawl survey in the eastern Bering Sea, conducted by the Alaska Fisheries Science Center (Nichol, 1995). Collections were made at 83 stations at depths shallower than 50 m (Fig. 1). Whole ovaries were extracted from approximately 10 females per station and then preserved in 10% formalin (3.7% formaldehyde) buffered with 19 g/liter sodium acetate-trihydrate. Females were selectively chosen by size: 2 females 25–30 cm total length (TL), 4 females 31–35 cm TL, and 4 females >35 cm TL. All females less than 25 cm TL were immature and therefore were not collected. Each preserved ovary lobe was weighed to the nearest milligram. Ovaries were assigned a maturity code based on a 5-point maturity classification scale for macroscopic examination (Table 1). These assignments were verified with histological evaluation.

Histological evaluation of ovaries

Histological cross sections were prepared from the middle portion of one ovary from each fish. Most sections (93%) were taken from the blind side; however, sections were occasionally taken from the eyed-side if fixation was not complete. Ovary tissues were embedded in paraffin, sectioned at 6 µm, then stained with hematoxylin and eosin.

Each ovary section was examined for the following oocyte stages: early perinuclear, late-perinuclear, partially yolked (PY), advanced-yolk (AY), migratory-nucleus (MN), unovulated hydrated (HY), and ova (ovulated, hydrated) (Howell,1983). We also noted the presence of postovulatory follicles (POF), atretic oocytes, and residual chorion tissue.

The maximum diameter of AY through MN oocytes were measured with an ocular micrometer. Oocyte diameters were measured from five of the largest spherical nonatretic oocytes with a centrally located nucleus. The average maximum oocyte diameters were then computed for each fish.

Examination of oocyte atresia

Occurrence of alpha (α) stage atresia (Hunter and Macewicz, 1985b) among advanced vitellogenic oocytes (AY, MN, and HY) and PY oocytes was recorded for 75 females by using histological ovary cross sections. Samples included 28 maturing (maturity-code 2) females with AY-stage oocytes and no evidence of POFs, 13 fish with AY and HY oocytes and no POFs, 23 fish that had spawned at least one batch (POFs present), and 11 fish with evidence of residual chorion tissue in the ovary lumen and no other evidence of batch spawning (no HY, ova, POFs). A 2 × 2 mm grid was used to count atretic and nonatretic PY oocytes, and AY through HY oocytes. One ovary section

was examined for each female. Grid counts were repeated 4 to 12 times at different locations within each ovary section, until counts totaled approximately 180 oocytes.

Testing for homogeneity within the ovary

Prior to subsampling for total fecundity, we tested (two-way ANOVA; *t*-tests) for differences in oocyte density (number of oocytes per gram of ovary tissue) and mean oocyte diameter between eyed-side and blind-side ovarian lobes and among three ovary positions (anterior, middle, posterior). Twenty ovaries histologically identified with AY oocytes (maturity-code 2) and no evidence of prior batch spawnings (i.e. no POFs) were selected from fish over a broad length range. AY oocytes were defined as those with yolk filling more than half the volume of the oocyte. Tissue samples averaging 10.5 mg (SD=2.9559) and 267 oocytes (SD=90.0) were taken from anterior, middle, and posterior positions along the long axis of each ovarian lobe (six subsamples per fish). All AY through MN stage oocytes from each tissue sample were counted manually with the aid of a dissecting microscope. Fifty of these oocytes per tissue sample were randomly selected for oocyte area measurements. Oocyte areas were measured with a microscopic image analysis system with Optimas 5.0 software (BioScan, Inc., 1992). Black and white images were generated with a video camera attached to a dissecting microscope (transmitted light) and were viewed on a 13-inch (diagonal) color monitor. The resolution was set to 640 × 480 pixels, corresponding to 4.149 µm/pixel at 25× magnification. Oocyte diameter was calculated from oocyte area by

$$Diameter = 2 \cdot \sqrt{\frac{Area}{\pi}}. \quad (1)$$

Oocyte size distributions

Oocyte areas were measured to determine whether there was a hiatus between distributions of AY oocytes and less advanced oocytes. Areas of oocytes in partially yolked (PY), unyolked, and AY stages were measured by using preserved tissue (as above), and calculated diameters were plotted for 75 of the 324 females examined for fecundity. These were the same females used to examine ooctye atresia, thus representing prespawning through partially spawned females, as well as those with residual chorion material present. PY-stage oocytes were considered as those with yolk that filled less than half the volume of the oocyte. Subsamples were taken from the anterior or middle portion of one ovary and weighed to the nearest 0.001 g. All PY and AY oocytes were counted separately. For the purpose of oocyte counts and measurements, MN oocytes were not distinguished from AY oocytes. No attempt was made to count unyolked oocytes or measure unyolked oocytes less than approximately 0.05 mm. Random oocyte area measurements by image analysis (at 25×) included 50 AY oocytes, 50 PY oocytes (if they existed), and 50 unyolked oocytes. The three oocyte diameter distributions were then plotted for each fish as PY and AY oocyte distributions in terms of number of oocytes per gram of ovary tissue and unyolked oocytes in terms of percent frequency of the 50 measured.

Total fecundity and batch fecundity estimation

Because of findings from the testing of homogeneity within ovaries (see "Results" section), two tissue subsamples were taken from the ovaries of each fish: one from the posterior third of either ovary, and one from either the middle or anterior third of either ovary. To estimate total fecundity, defined as the standing stock of AY through HY oocytes, only ovaries with no evidence of prior batch spawnings (no ova, no POFs, nor residual chorion material) were used. To eliminate less developed ovaries that contained many PY oocytes, we also limited fecundity samples to those with maximum oocyte diameters ≥0.35 mm as measured from histological slides. Area measurements of AY through MN stage oocytes with image analysis and counts were conducted in the same manner as the above test for homogeneity.

To determine the proportional mass of each ovary section (WF_p, WF_m, and WF_a), one of the paired ovaries from each of the 20 fish tested for oocyte homogeneity was cut into thirds, mid-way between anterior-middle and mid-way between middle-posterior tissue positions. Each section was weighed to the nearest 0.001 g. The proportional mass (section wt/sum of section wts) of anterior, middle, and posterior sections averaged respectively 0.536 (SE=0.0095), 0.311 (SE=0.0086) and 0.153 (SE=0.0059) of the total ovary mass.

Total fecundity was computed as

$$Total\ fecundity = \left[\frac{no_p}{wt_p}(WF_p) + \frac{no_{am}}{wt_{am}}(WF_{am})\right] POW, \quad (2)$$

where no_p = number of AY-HY oocytes in tissue sample from posterior position of either ovary;
no_{am} = number of AY-HY oocytes in tissue sample from either anterior or middle positions of either ovary;
wt_p = weight of tissue sample from posterior position of either ovary;
wt_{am} = weight of tissue sample (g) from either middle or anterior position of either ovary;
WF_p = weighting factor computed as the average proportional mass of the posterior third of either ovary; 0.153 g (n=20);
WF_{am} = weighting factor computed as the average proportional mass of anterior and middle ovary sections combined; 0.536 g + 0.311 g = 0.837 g (n=20); and
POW = paired ovary weight (g).

Batch fecundity was estimated from those ovaries containing HY oocytes (maturity-code 3). Subsample weights averaged 52 mg. Both HY oocytes (batch oocytes) and AY oocytes (remaining oocytes) were counted. Batch fecundity was computed as above (Eq. 2), substituting no_p and no_{am} with

Table 1

Maturity code criteria for yellowfin sole (*Limanda aspera*) ovaries based on macroscopic examination. Corresponding histological descriptions are included. LP = late perinucleus stage oocyte; PY = partially yolked oocyte; AY = advanced yolked oocyte; MN = oocyte with migratory nucleus; HY = unovulated hydrated oocyte. POFs = postovulatory follicles. PY is defined as an oocyte with yolk globules that filled less than half the volume of the oocyte.

Maturity code	Condition	Macroscopic examination	Histological examination
1	immature	Ovary clear to slightly pink or grey-pink. No distinct oocytes. Ovarian wall thin and taut around ovary interior.	LP is the most advanced oocyte stage. Ovarian wall diameter thin (generally <2 µm).
2	maturing	Ovary usually opaque with distinct vitellogenic oocytes. A network of veins covers the ovary.	PY or AY oocytes present (yolk globules present). MN oocytes may be present. POF may be present.
3	hydrated	As in code 2, but some portion of oocytes are translucent (hydrated-unovulated). Hydrated oocytes are larger than the opaque oocytes and are randomly scattered about the ovary.	HY oocytes (yolk coalesced) present, each surrounded by a follicle. AY oocytes present if prior to last batch. MN oocytes usually present if prior to last batch. POF may be present.
4	spawning	Hydrated (translucent) oocytes in lumen of ovary (ovulated). A continuous band of hydrated oocytes may also be visible from the ovary sides. Eggs may run with slight pressure. If all oocytes are translucent, they represent the last batch of eggs to be spawned in the season.	Ova present. AY oocytes present if prior to last batch. POFs present. MN oocytes usually present if prior to last batch.
5	spent	Deflated ovary, often with blood. Ovary wall thick and often flaccid around ovary interior.	LP to PY oocytes present. Ovarian wall diameter thick (generally >3 µm).

numbers of HY oocytes in the respective subsample. Ovaries were categorized by stages in the batch spawning succession: a first batch was recognized by the presence of HY and AY oocytes, and absence of POFs. A middle batch was recognized by the presence of HY oocytes, AY oocytes, and POFs. A final batch was recognized by the presence of HY oocytes and the absence of remaining AY or MN oocytes.

Fecundity-total length relationships were computed for total and batch fecundity by using Gauss-Newton nonlinear least squares regression (SAS Institute, 1989). The number of batches spawned from a female for a given fish length was then estimated as the estimated total fecundity divided by the estimated batch fecundity.

Results

Histological evaluation

Histological evaluation of 767 ovary pairs, in most cases (93%), verified the general ovary codes that were assigned macroscopically (Table 1). Resulting groupings are shown in Table 2. We note here that maturing (maturity-code 2) ovaries included females that had spawned one or more batches (POF present) but contained no hydrated oocytes (HY) or ova; these ovaries were indistinguishable macroscopically from advancing ovaries that had not yet spawned a batch. Early perinucleus stage oocytes were present in all ovaries examined. Late perinucleus stage oocytes were present in all but one of the mature fish ovaries (n=665; maturity-codes 2–5).

Migratory nucleus stage (MN) oocytes, vitellogenic oocytes that are precursors to hydrated oocytes, were present in 96% of the females undergoing oocyte hydration and 91% of spawning females. The high occurrence of MN oocytes among fish about to spawn a batch suggests that fish do not wait extended periods between batch spawnings.

Postovulatory follicles were observed in 121 of the ovaries examined. POFs were present in 50 of 75 females undergoing hydration, indicating for these fish that at least one batch was previously spawned. For the other 25 females with hydrated ovaries containing no POFs, HY oocytes represented the first batch of a series of batches. We could not distinguish more than one apparent age of POF among the 50 fish that had begun spawning. This indicates that yellowfin sole either resorb POFs before a succeeding batch is ovulated or that POFs of different ages (from different batches) are present but are indistinguishable.

Evidence of more than one series of batch spawnings

A total of 16 females with maturing ovaries (maturity-code 2) contained residual chorion tissue within the ovary lumen (Table 2; Fig. 2). The chorion tissue in these cases was sufficiently large to conclude that they were unspawned ova from a previous spawning. The ovaries ranged from those in early stages of yolk accumulation

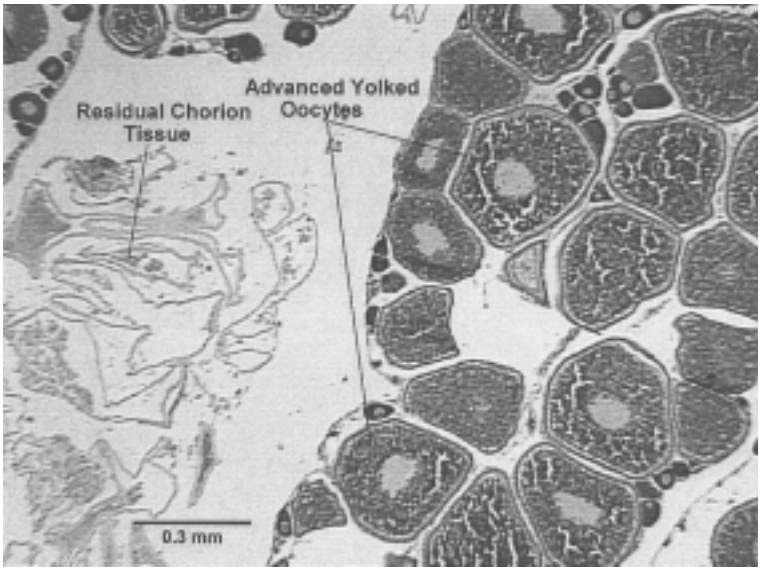

Figure 2

Histological section of a yellowfin sole (*Limanda aspera*) ovary with advancing yolked oocytes and remnants of chorion tissue leftover from previous spawning. The 38-cm-TL female was captured 17 June 1993 at a bottom depth of 27 m. The yolked oocytes averaged 0.31 mm in diameter, well below the mean diameter of yolked oocytes from spawning individuals (>0.44 mm).

Table 2

Occurrence of oocyte stages, postovulatory follicles, and other postspawning remnants within immature, maturing, hydrated, spawning, and spent yellowfin sole (*Limanda aspera*) ovaries. Histological examination of ovary cross sections.

Oocyte stage or intra-ovarian structure	Ovary maturity code					Total fish
	Immature (1)	Maturing (2)	Hydrated (3)	Spawning (4)	Spent (5)	
Early perinucleus	102	415	75	23	152	
Late perinucleus	58	415	75	23	151	
Partially yolked	8	349	17	7	82	
Advanced-yolked	0	409	72	23	0	
Migratory nucleus	0	63	72	21	0	
Hydrated-unovulated (HY)	0	0	75	3	0	
Ova	0	0	0	23	0	
Postovulatory follicles	0	13	50	19	40	
Atretic-HY	0	0	0	0	21	
Atretic ova	0	7	9	1	52	
Residual chorion tissue	0	15	1	0	29	
Number of fish	102	415	75	23	152	767

(mean AY diameters=0.27 mm), to those that contained AY oocytes near maximum size (mean AY diameter=0.43 mm). These ovaries did not contain POFs or MN stage oocytes; therefore ovaries were not advanced enough for there to be recent spawning from the existing AY standing stock.

It is possible that these fish had already spawned at least one series of batches, were spent, and were readying

Table 3

Two-way analysis of variance results comparing differences of oocyte density (top), and mean oocyte diameter (bottom) between blind and eyed-side ovaries and among anterior, middle, and posterior tissue subsampling positions in yellowfin sole, *Limanda aspera*. Paired *t*-tests (H_0=d_{post}–d_{ant}; H_0=d_{post}–d_{mid}) among ovary positions indicate significantly (P<0.05) greater oocyte densities (d) in posterior tissue samples compared with either anterior or middle positions. SS = sum of squares; MSE = mean square error.

Source	df	SS	MSE	*F*	*P*-value
Oocyte density (no. oocytes/g ovary tissue)					
Fish	19	3,391,989,272	178,525,751	62.32	0.0001
Ovary	1	3,466,212	3,466,212	1.21	0.2708
Position	2	25,951,981	12,951,981	4.53	0.0125
Ovary × position	2	9,505,128	4,752,564	1.68	0.1914
Error	95	268,371,656	2,824,965		
Corrected total	119	3,699,284,249			
Mean oocyte diameter					
Fish	19	5.7136	0.3007	183.25	0.0001
Ovary	1	0.0003	0.0003	0.19	0.6655
Position	2	0.0034	0.0017	1.02	0.3600
Ovary × position	2	0.0022	0.0011	0.68	0.5044
Error	5975	9.8053	0.0016		
Corrected total	5999[1]	15.5248			

[1] n = 6000; 2-ovary × 3-ovary positions × 20-fish × 50-oocytes/fish.

another standing stock of oocytes for spawning within the same reproductive season.

Homegeneity of oocytes between and within ovaries

Two-way ANOVA on mean oocyte diameters indicated that the means were not significantly different between ovaries or among the anterior, middle, and posterior ovary positions (Table 3). Additionally, our analysis revealed that oocytes were slightly more concentrated (number of oocytes/g ovary tissue) in posterior tissue samples compared with middle and anterior samples (paired *t*-tests, H_0: d_{post}–d_{ant}=0 and H_0: d_{post}–d_{mid}=0; n=20; P-values <0.05; Table 3). Comparison of oocyte density between middle and anterior tissue samples and between eyed-side and blind-side ovary lobes revealed no significant differences (paired *t*-test; P-value >0.05; Table 3). These results prompted us to take fecundity subsamples from two ovary locations (posterior and middle-anterior position from either ovary lobe) and to incorporate weighting factors (WF; Eq. 2) for all calculations of total fecundity.

The evidence for greater posterior-end oocyte densities that was found in 20 test fish prior to fecundity subsampling, was also present after all ovaries were subsampled. Oocyte densities were significantly greater in the posterior ovary end versus the anterior-middle positions among all ovaries sampled for fecundity (paired *t*-test, H_0: d_{post}–$d_{ant/mid}$=0; t=2.59; n=323; P=0.0100). The density of hydrated (HY) oocytes within maturity-code-3 ovaries, used for batch fecundity estimates, was also greater in subsamples taken from the posterior ovary end (paired *t*-test, H_0: d_{post}–$d_{ant/mid}$=0; t=3.40; n=75; P=0.0011). Computation of batch fecundity, therefore, incorporated the same weighting factors described for computation of total fecundity.

Oocyte size distributions

Oocyte diameter plots indicated a hiatus in distribution between AY oocytes and PY oocytes for ovaries with mean AY diameters ≥0.38 mm (Fig. 3). This separation of AY oocytes from other oocyte stages in more advanced ovaries (closer to spawning) is indicative of a determinate mode of oocyte development. In prespawning fish (maturity-code 2, no POFs), oocyte size distributions overlapped for fish with mean AY diameters less than 0.38 mm. PY oocytes, however, were a relatively minor portion in terms of oocyte density of the overall distribution for ovaries with mean AY diameters greater than 0.38 mm (Fig. 3). Oocyte distributions in maturing (maturity-code 2) fish with residual chorion tissue present in the ovary lumen exhibited the same hiatus between PY and AY oocytes where mean AY diameters were ≥0.38 mm (Fig. 3).

The size distribution of AY oocytes for those fish that were either spawning their first batch (maturity-code 4, no POFs; n=13) or had begun spawning (maturity-code 2 or 3, POFs present; n=23) was separated from PY and non-yolked oocyte distributions in 33 of the 36 fish examined. PY oocytes were either absent or were a very small fraction of the number of AY oocytes present. From the histological analysis, we found that 68 of the 86 fish that had begun spawning (maturity-codes 2 and 3 with POFs, and maturity-code 4) did not contain any PY oocytes, further indicating that only one stock of oocytes is advanced prior to the spent ovary condition.

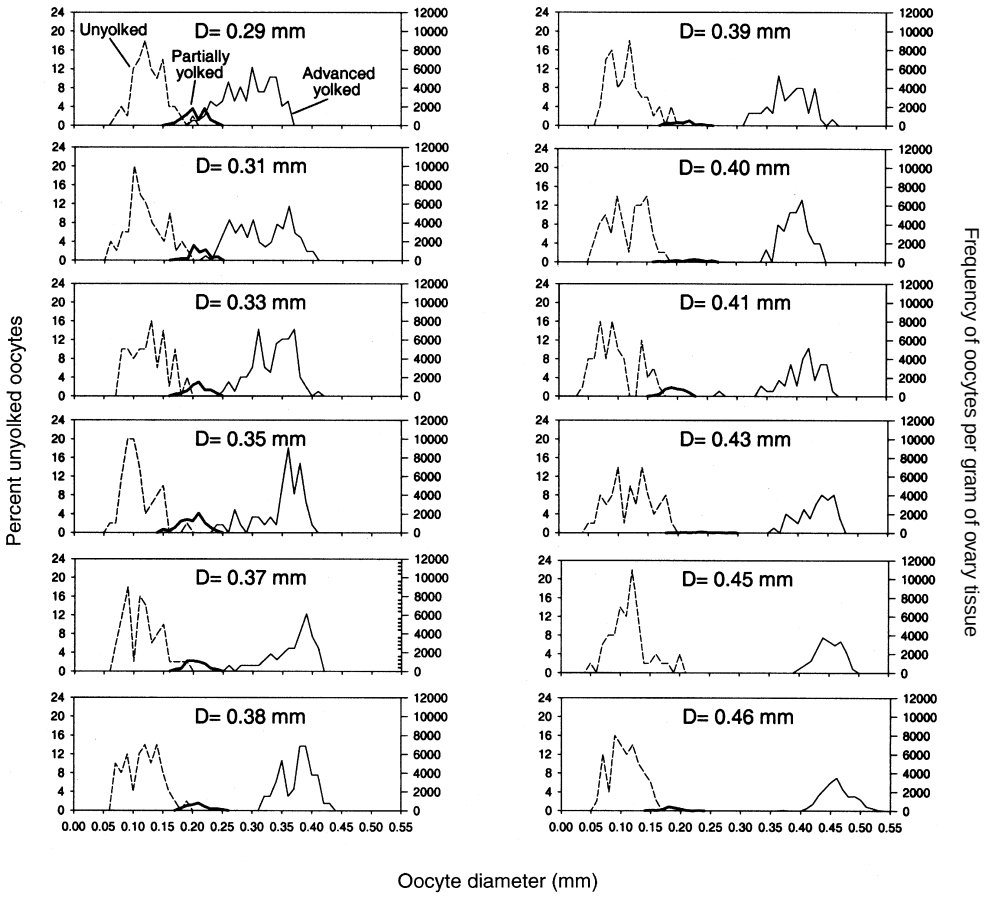

Figure 3

Size distributions for unyolked, partially yolked, and advanced-yolked oocytes for 12 yellowfin sole (*Limanda aspera*) females. Advanced-yolked and partially yolked oocyte diameters are plotted in terms of oocyte density (no. oocytes/g ovary tissue) and unyolked oocytes are plotted in terms of percent frequency. Note that frequencies of unyolked oocytes less than approximately 0.05 mm were not measured. Mean diameters (D) for advanced-yolked oocytes are noted.

Mean oocyte diameters of yolked oocytes (AY through MN) were generally larger among fish that had begun spawning compared with those that had not released a batch (Fig. 4). Ovaries that contained POFs had mean yolked oocyte diameters that on average were greater than 0.44 mm. Yolked oocytes in advancing ovaries with no evidence of recent spawning (no POFs) averaged less than 0.44 mm in diameter. Again, most of the ovaries with residual chorion material were significantly less developed than those with evidence of recent spawning (Fig. 4).

Occurrence of oocyte atresia

Of the 75 females examined histologically for the occurrence of atresia, only 15 (20%) had ovaries containing α-atretic AY, MN, or HY oocytes (Table 4). Within each of these 15 females, the average proportion of α-atretic AY-HY oocytes among all AY-HY oocytes was 0.034. Thus, among all females examined including those with no atresia (n=75), the relative frequency of α-atretic AY-HY oocytes among normal AY-HY oocytes was less than 1%. The occurrence of atretic AY-HY oocytes as well as atretic PY oocytes was higher among females that were either close to spawning or partially spawned compared with those in a prespawning condition (Table 4). As shown with the oocyte distribution plots, normal PY oocytes were more common among females that were in a prespawning condition. Lower frequencies of normal PY oocytes, but higher proportions of atretic PY oocytes among females that were partially spawned or close to spawning, indicated that many PY oocytes do not develop after spawning is initiated. We observed no cases of major atresia (>50% atretic) among advancing oocytes for all ovaries examined histologically. Given the low occurrence of oocyte atresia, we assumed a negligible effect of atresia on estimates of annual fecundity.

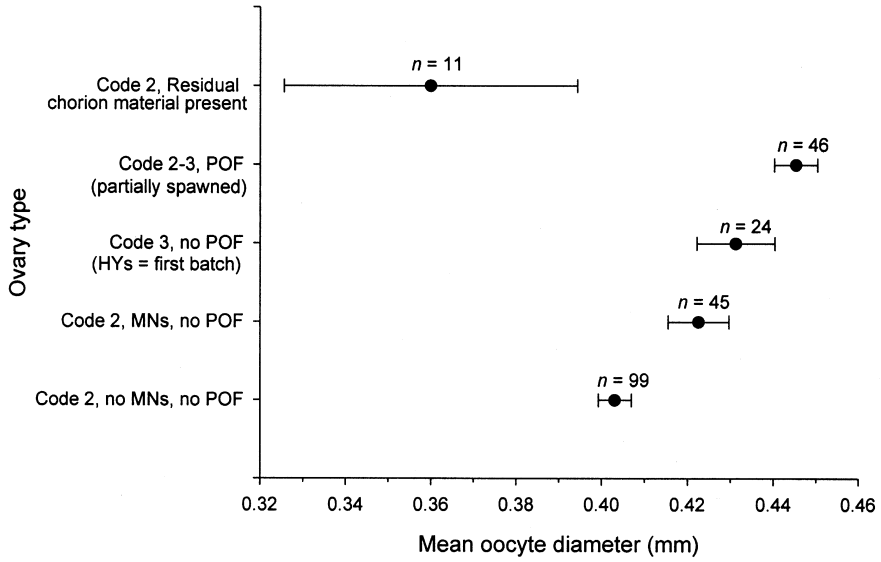

Figure 4

Comparison of mean yolked oocyte diameters among ovaries at different levels of development, from maturing (maturity-code 2) ovaries with no migratory nucleus stage (MN) oocytes (≥0.38 mm) to maturity-code 3 ovaries with postovulatory follicles (POFs) present. Error bars indicate 95% confidence intervals. See Table 1 for description of ovary maturity codes.

Table 4

Occurrence of alpha (α) atretic oocytes among advanced vitellogenic (AY through HY) and partially-yolked (PY) oocytes within yellowfin sole *(Limanda aspera*) ovaries (*n*=75 females). AY = advanced-yolked; HY = unovulated hydrated.

Maturity code	No. of females sampled	No. of females with α-atretic AY-HY oocytes	Proportion of α-atretic among all AY-HY (min.-max.)	No. of females with PY oocytes	No. of females with α-atretic PY oocytes
Code 2, no POFs (prespawning)	28	2	0.01–0.025	24	3
Code 3, no POFs (first batch)	13	5	0.004–0.058	4	3
Codes 2 and 3, POFs present (partially spawned)	23	6	0.005–0.037	6	3
Code 2, residual chorion tissue present	11	2	0.061–0.134	9	2

Total fecundity

In choosing ovaries to be used to estimate total fecundity, we selected ovaries that were advanced enough that the advancing stock (AY to MN) could be discriminated from less advanced oocytes (PY), yet were not advanced enough for there to have been potential spawning. First, we eliminated ovaries with mean oocyte diameters <0.38 mm due to the overlap in AY and PY distributions. Secondly, we eliminated ovaries with mean oocyte diameters greater than 0.44 mm (*n*=20) in an attempt to eliminate partially spawned ovaries that could not be identified with histological evaluation; POFs were not found in these ovaries; however, because the level of oocyte advancement (mean AY diameter) was similar to ovaries that did contain POFs (Fig. 4), the occurrence of recent batch spawning was possible.

Inclusion of ovaries with mean AY-oocyte diameters <0.38 mm as well as those >0.44 mm can potentially bias estimates of total fecundity. Estimates of total fecundity, measured from fish where distributions of PY and AY oocytes overlapped (Fig. 3), were higher than estimates from ovaries with more advanced oocytes (Fig. 5; Table 5). We compared yellowfin sole length-fecundity relationships of fish with ovaries that had mean AY-oocyte diameters ≥0.38 mm and ≤0.44 (*n*=148) to those with mean diameters <0.38 mm (*n*=80). Linear comparisons of the log(*length*)-log(*fecundity*) relationships between the two data sets indicated similar slopes (F=0.08; P=0.7725; df=1,

Table 5

Yellowfin sole (*Limanda aspera*) length-fecundity coefficients for nonlinear least-squares fit using equation $F = aL^b$, where F = fecundity and L = fish length (cm). MOD = mean oocyte diameter of advanced yolked oocytes. SE = standard error of estimate. Confidence intervals (CI) indicate approximate 95% bounds for predicted values of the mean (SAS Institute, 1989).

	Constants						
	a		*b*				
Fecundity type	Estimate	SE	Estimate	SE	*n*	r^2	Fecundity estimate for 35-cm female (Value ±95% CI)
Total							
MOD ≥ 0.38–0.44 mm[1]	3.322	2.909	3.631	0.243	148	0.60	1,343,807 ±64,406
MOD < 0.38 mm	4.947	5.564	3.550	0.311	80	0.64	1,496,401 ±105,108
All data (MOD ≤0.44 mm)	2.988	2.074	3.672	0.192	248	0.62	1,397,492 ±56,054
Batch	1.648	3.138	3.188	0.528	75	0.32	137,862 ±17,111

[1] Ovaries with mean AY through MN oocyte diameters ≥0.38 mm and ≤0.44 mm were considered the most appropriate for use in estimating total fecundity.

221) but different intercepts (F=6.77; P=0.01; df =1, 222). We also tested whether the inclusion of ovaries with mean oocyte diameters >0.44 mm would have a significant effect on the fish-length–fecundity relationship (Table 6). When ovaries with mean oocyte diameters >0.44 mm were included, estimates of total fecundity at length were significantly reduced. No such effect was apparent when the data were limited to ovaries with mean oocyte diameters ≤0.44 mm (Table 6).

Total fecundity as a function of fish length for yellowfin sole was estimated as

$$F = 3.3225 \times TL^{3.6312},$$

where F = standing stock of AYs; and
TL = total fish length in centimeters (Table 5).

Total fecundity ranged from 295,615 oocytes in a 29-cm-TL fish to 3,635,108 oocytes in a 39-cm-TL fish (Fig. 6).

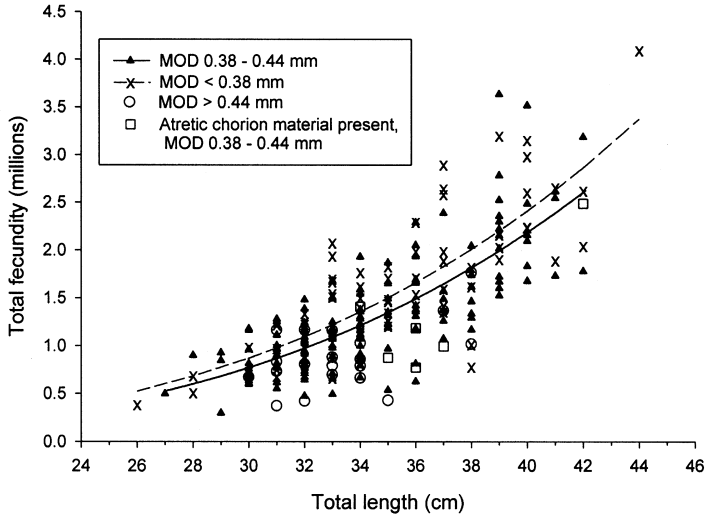

Figure 5

Total fecundity as a function total length (cm). Data for yellowfin sole (*Limanda aspera*) ovaries with mean AY diameters (MOD) 0.38 mm to 0.44 mm (n=148) were compared with ovaries with MOD <0.38 mm (n=80), ovaries with MOD >0.44 mm (n=20), and ovaries with residual chorion material present (n=7). Yellowfin sole ovaries with MOD 0.38 mm to 0.44 mm were considered most appropriate for use in total fecundity. Curves indicate predicated values from nonlinear regression. MOD = mean oocyte diameter of AY through MN oocytes.

Batch fecundity

Batch fecundity was estimated for 75 females and ranged from 2,400 to 408,000 oocytes and larger fish generally had larger batches (Figs. 6 and 7). The number of oocytes in the first batch was in most cases lower than in succeeding batches, although the variability of the first batch for a given fish length was quite high (Fig. 7). Twenty-five of the fish examined contained ovaries with unovulated hydrated (HY) oocytes and no evidence of prior batch spawnings, thus representing the first batch. Three fish contained ovaries with only one hydrated batch remaining (no AYs left), thus representing the last batch. The remaining "middle batch" fish (n=47) possessed ovaries containing unovulated hydrated oocytes and POFs, indicating that at least one batch had been previously spawned.

Batch fecundity, irrespective of batch order, is described in terms of fish length by

$$B = 1.6481 \times TL^{3.1879},$$

Table 6

Linear regression results from the model $\log(F) = \log(a) + b\log(L) + \log(c)$; the log-transformation of model $F = aL^bc$, where F = total fecundity, L = fish length (cm), and a, b, c are coefficients. Coefficient c represents the interaction of mean oocyte diameter on F. A series of regressions were run, first by using all data where the mean yolked oocyte diameter was ≥0.38, then with data sets that excluded ovaries with high mean oocyte diameters (i.e. ovaries with mean oocyte diameters >0.46 mm, >0.45 mm, >0.44 mm).

Mean oocyte diameter range of ovaries used in analysis	Estimate			*P*-value of H_0: log(*c*) = 0	*n*
	Log(*a*)	*b*	Log(*c*)		
≥ 0.38 mm	6.40	3.43	–1.22	0.003	168
0.38–0.46 mm	6.35	3.44	–1.22	0.006	165
0.38–0.45 mm	5.84	3.42	–1.06	0.026	160
0.38–0.44 mm[1]	3.07	3.44	–0.33	0.525	148

[1] This data set, which excluded ovaries with mean oocyte diameters > 0.44 mm, indicated no significant effect of mean oocyte diameter on the estimate of total fecundity.

where B = batch fecundity; and
TL = total fish length in centimeters (Table 5).

Number of batches

The number of batches that a female of a given length spawns was estimated as F/B (above). Yellowfin sole are estimated to spawn an average of 8 to 11 batches prior to the spent ovary condition. The frequency of batches appears to be slightly higher for larger fish.

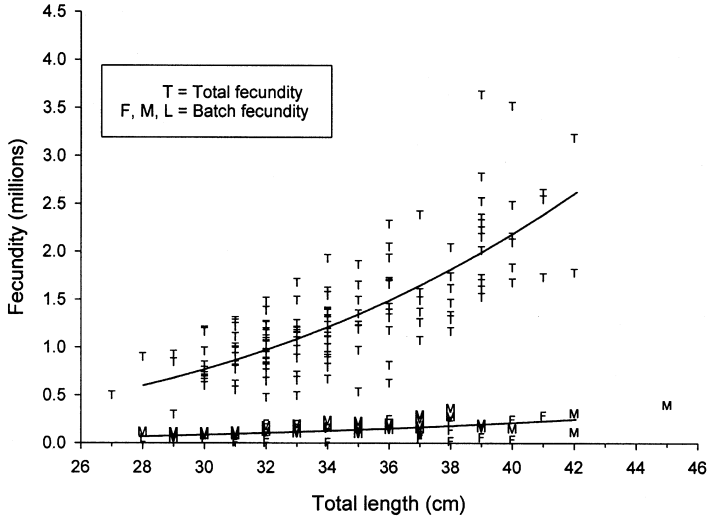

Figure 6

Total and batch fecundity by fish length for yellowfin sole (*Limanda aspera*) in the eastern Bering Sea. Batch fecundity symbols F, M, and L correspond respectively to first, middle, and last batch fecundity estimates.

Discussion

Determinate or indeterminate fecundity?

Fish with determinate fecundity are defined as those with ovaries whose advancing stock of oocytes represent the entire number of eggs to be spawned that year (Hunter et al., 1989; Horwood and Walker, 1990; Hunter et al., 1992). Fish with indeterminate fecundity, in contrast, are defined as those whose ovaries continuously mature yolked oocytes from unyolked oocytes; thus the "standing stock" of advanced oocytes does not represent the total number of eggs to be spawned that year (Hunter et al., 1989). Oocyte size frequencies of various stage oocytes (i.e. advanced-yolked, partially yolked, unyolked) have been used as criteria to determine if a fish has determinate fecundity (Hunter et al., 1989; Hunter et al., 1992; Horwood and Walker, 1990). If a break or "hiatus" has occurred between the advanced-yolked distribution and the less advanced ones, then the advanced-yolked distribution could be considered the determinate stock. This break in oocyte distributions was observed for yellowfin sole, and it is clear that batches are spawned from the advanced-yolked mode. A determinate mode of oocyte development in yellowfin sole is further indicated by the fact that total fecundity was substantially lower in fish that had spawned at least one batch (Fig. 8)—an indication that there is no oocyte recruitment to the advanced oocyte stock once spawning begins. Hence, although yellowfin sole spawns eggs intermittently in batches, they undergo a group synchronous mode of oocyte development.

In contrast to other fish with determinate fecundity, yellowfin sole fecundity estimates were higher among individuals with less-developed ovaries where PY and AY oocyte distributions overlapped (Fig. 5). Hunter et al. (1992) indicated the opposite for Dover sole; they found that fecundity among individuals where the advanced-stock size

distribution was not well separated from less developed oocytes was lower because oocyte recruitment to the advanced stock was not complete. We suggest two reasons for this difference between the two species. First, the discrimination between PY and AY oocytes and the criteria used to separate them were likely different for the two studies. Exact discrimination between oocytes that will not develop and those that are viable cannot occur until the distributions are completely separate. Second, rates of oocyte atresia between the two species may be different. Higher rates of PY and AY atresia may account for a decrease in fecundity as the AY distribution advances. As Hunter et al. (1992) noted, the fate of PY oocytes is uncertain; perhaps some individuals retain them for an additional series of batch spawnings.

Although multiple groups of oocytes are not continuously developed as are those observed for indeterminate fishes, such as the northern anchovy, *Engraulis mordax* (Hunter and Leong, 1981), yellowfin sole appear to have the potential to recover spent ovaries and spawn another series of batches. Remnants of chorions from hydrated oocytes in the lumen of ovaries containing a unimodal stock of advancing yolked oocytes with diameters significantly less than those of spawning fish (Fig. 4) suggest that at least some individuals can produce more than one series of batches in a single year. Annual fecundity for each of these individuals would be significantly greater than the estimated total fecundity. Although yellowfin sole exhibit a determinate group-synchronous mode of oocyte development, some individuals may spawn more than one series of batches; therefore, annual fecundity must be considered indeterminate.

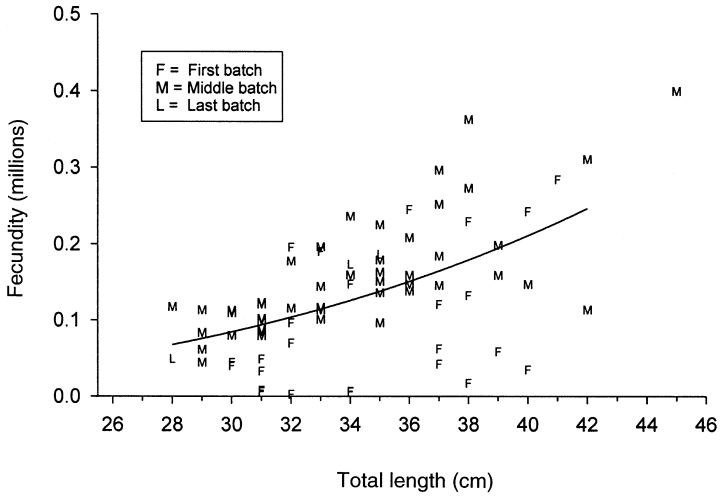

Figure 7

Batch fecundity as a function of fish total length for yellowfin sole (*Limanda aspera*) in the eastern Bering Sea (n=75). First, middle, and last batches are indicated. The curve represents the nonlinear least squares regression for all the batches.

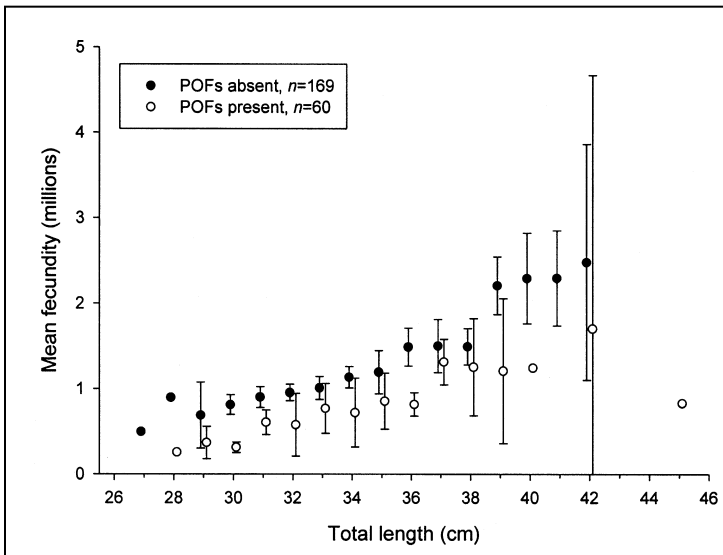

Figure 8

Comparison of mean total fecundity (no POF and mean oocyte diameter ≥0.38 mm) at length and the mean fecundity observed in yellowfin sole (*Limanda aspera*) that had already spawned at least one batch (POFs present).

Comparison of total fecundity between southeast and northwest areas

Total fecundity for yellowfin sole was compared for the northwest and southeast areas of the eastern Bering Sea. Although Nichol (1997) found that yellowfin sole growth and size at maturity were greater in the northeast area of the eastern Bering Sea compared with the southeast area (Fig. 1), we found no differences in fecundity between areas. Neither slopes (ANCOVA: F=0.09; P=0.77; df =1, 144) nor intercepts (ANCOVA: F=0.56; P>0.10; df =1, 145) were different for the log-transformed (linear) length-fecundity relationships.

Comparison of results with those from other authors

With the exception of fecundity data presented by Fadeev (1970), the relationship between yellowfin sole fecundity and fish length appears similar between east and west sides of the Bering Sea and among years (Fig. 9). Ivankov and Ivankova (1974), who reported that yellowfin sole in the northwestern Sea of Japan spawn up to five batches, presented slightly lower values of total fecundity compared with our results. Tikhonov (1977) presented similar length-fecundity relationships for yellowfin sole off

the west coast of Kamchatka for five different years, 1963–69. Because methods (i.e. selection criteria for ovaries) likely varied among studies, critical interpretation of these comparisons is difficult.

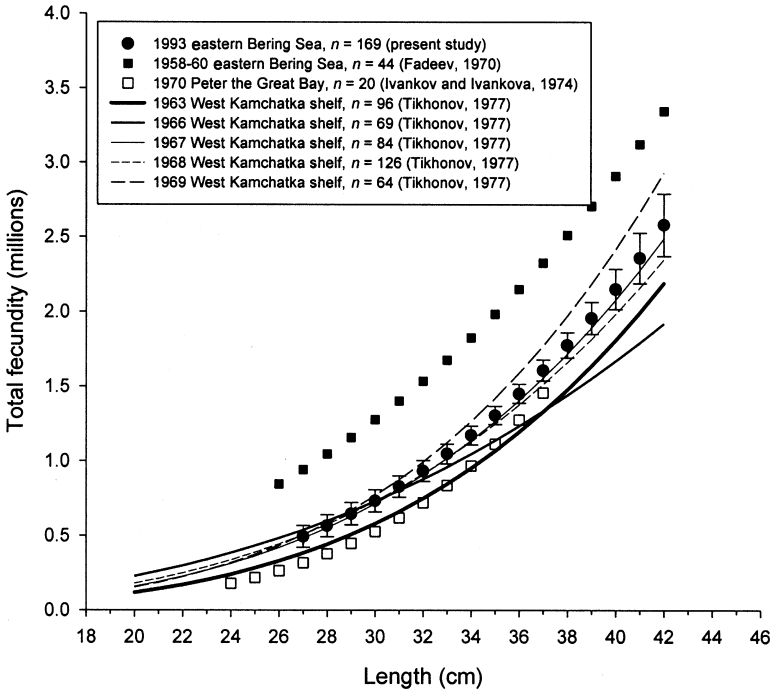

Figure 9

Comparison of predicted values of total fecundity as a function of fish length for yellowfin sole (*Limanda aspera*), as presented by various authors. Error bars presented for the present study indicate 95% confidence intervals for the mean.

Comparison of yellowfin sole with other species

Yellowfin sole is more fecund and spawns smaller eggs than other flatfish species in the eastern Bering Sea (Table 7). Most flatfishes in the eastern Bering Sea, with the exception of northern rock sole (*Lepidopsetta polyxystra*, Orr and Matarese, 2000), spawn pelagic eggs intermittently (in batches). Longhead dabs, also within the genus *Limanda* (*proboscidea*), have similar reproductive characteristics to yellowfin sole in respect to their high fecundity at length, small diameter of eggs, shallow spawning location, and spring-summer spawning season (Table 7).

Yellowfin sole are most closely related to yellowtail flounder, *Limanda ferruginea* (Cooper and Chapleau, 1998), a western Atlantic species ranging from the Gulf of St. Lawrence to Chesapeake Bay (Howell, 1983; Zamarro, 1992). Although only morphological characters were used to determine the phylogenetic relationships of these two species among pleuronectids (Cooper and Chapleau, 1998), yellowfin sole and yellowtail flounder also share very similar life history characteristics. Fecundity ranges, egg diameter, egg type, spawning interval, and spawning seasons are very similar between the two species (Table 7). Like yellowfin sole females, yellowtail flounder females develop oocytes in a group-synchronous manner (Howell, 1983). In addition, they have MN oocytes present in their ovaries that contain hydrated oocytes, indicating that spawning of batches is similarly continuous (Zamarro, 1992). Yellowtail flounder spawn approximately 7 batches compared with 8–11 for yellowfin sole in the eastern Bering Sea. In short, closely related species share more than just morphological similarities; reproductive characteristics also reflect a shared evolutionary history.

Spawning habits

Yellowfin sole in the eastern Bering Sea have been observed from prespawning to spawning conditions from mid-May through August (Fadeev, 1970; Nichol, 1995). Observations of eggs and early-stage larvae in ichthyoplankton surveys conducted in the eastern Bering Sea (Musienko, 1963; Waldron, 1981) indicate that spawning may not completely end until September. Given that the spawning season is protracted and that spawning of a series of batches is fairly rapid, individuals may have the potential to recover spent ovaries and spawn more than one series of batches within a single year. The possibility that residual chorion tissue is left over from the previous year's spawning seems unlikely given that it would have been retained within the ovary for more than 8 months (Sep–May).

Yellowfin sole remain in the spawning area (<30 m bottom depth) until a series of batches have been spawned. The absence of partially spawned fish, those with ovaries containing POFs and AY oocytes, found outside the spawning area (>30 m) indicate that after spawning begins (first batch) fish remain in the spawning area until spent. Again, the presence of MN oocytes in most ovaries undergoing oocyte hydration indicates that there is very little lag period between batch spawnings. This evidence refutes an earlier assertion by Nichol (1995) that yellowfin sole may migrate in and out of the spawning area between batch spawnings. However, some females do migrate out of the spawning area after a series of batches has been completely spawned; both spent and maturing (maturity-code 2) females with evidence of completed batch spawnings (i.e. with residual chorion tissue) were observed in spawning (<30 m) and nonspawning (>30 m) waters.

Acknowledgments

Claire Armistead, Jan Haaga, Mark Conrad, and Gary Walters aided with tissue collections. Frank Morado, Lisa

Table 7

Fecundity and spawning habits of nine species of flatfishes found in the eastern Bering Sea and yellowtail flounder *(Limanda ferruginea*) from the Atlantic coast of North America. Spawning interval refers to whether eggs are spawned intermittently (batch) or all at once (synchronous). Numbers in parentheses are the range of fish lengths used for the respective fecundity estimates. All estimates are for the eastern Bering Sea except where noted.

Species	Fecundity range	Egg diameter in plankton	Egg type	Spawning interval	Spawning location (bottom depth)	Spawning season
Yellowfin sole (*Limanda aspera*)	295,615–3,635,108[1] (27–42 cm)	0.76–0.85 mm[2]	pelagic[2, 3]	batch[4, 5]	< 30 m[4]	May–Sep[4, 6]
Alaska plaice (*Pleuronectes quadrituberculatus*)	56,300–312,600[5] (28–50 cm)	1.67–2.21 mm[2]	pelagic[2, 3]	batch[5]	75–150 m[7]	Apr–Jun[5]
Arrowtooth flounder (*Atheresthes evermanni*)	246,000–2,224,000[8] (48–83 cm)	~ 3 mm[2]	mesopelagic[2]	batch[9]	108–360 m[10]	Dec–Mar[11]
Flathead sole (*Hippoglossoides elassodon*)	51,600–160,100[5] (22–42 cm)	2.75–3.75 mm[2, 7]	pelagic[2, 3, 7]	batch[5]	50–150m[7]	Feb–May[5]
Greenland turbot (*Reinhardtius hippoglossoides*)	15,000–215,000[12] (73–106 cm)	4.00–4.50 mm[2, 7]	bathypelagic[7]	—	> 100 m[2]	Oct.–Dec[11]
Longhead dab (*Limanda proboscidea*)	78,000–841,200[5] (14–26 cm)	0.72–0.87 mm[2]	pelagic[7]	batch[13]	26–35 m[7]	July–Aug[5, 13]
Pacific halibut (*Hippoglossus stenolepis*)	200,000–4,000,000[14] (83–200 cm)	2.90–3.80 mm[2, 7]	pelagic[2, 3]	batch[15]	300–500 m[15]	Nov–Mar[7]
Northern rock sole (*Lepidopsetta polyxystra*)	150,000–400,000[5] (22–42 cm)	0.87–1.00 mm[5]	demersal[2, 16]	synch.	70–140 m[15]	Mar–Jun[16]
Starry flounder (*Platichthys stellatus*)	913,4005–11,000,000[17] (38–56 cm)	0.88–1.28 mm[2]	pelagic[2]	batch[5]	11–75 m[7]	May–Jun[5]
Yellowtail flounder (*Limanda ferruginea*)	333,500–4,215,000[18, 19] (28–54 cm)	0.75–0.90 mm[20]	pelagic[20]	batch[21]	—	May–Sep[22, 23]

[1] Present study.
[2] Matarese et al. (1989).
[3] Waldron (1981).
[4] Nichol (1995).
[5] Fadeev (1965); Fecundity range represents the average fecundity at 2-cm minimum and 2-cm maximum fish lengths.
[6] Musienko (1963).
[7] Musienko (1970).
[8] Zimmermann (1997).
[9] Rickey (1995).
[10] Hirshberger and Smith (1983); from Gulf of Alaska.
[11] Pertseva-Ostroumova (1961).
[12] Lear (1970); Estimated from *Reinhartius hippoglossoides* from the Newfoundland area.
[13] Nichol; personal obs., 1999.
[14] Schmitt and Skud (1978); from Gulf of Alaska.
[15] St. Pierre (1984).
[16] Shubnikov and Lisovenko (1964).
[17] Orcutt (1950); fish was 56.5 cm standard length; from Monterey Bay, California.
[18] Pitt (1971); from Grand Banks, off Newfoundland.
[19] Howell and Kesler (1977); from off southern New England.
[20] Yevseyenko and Nevinskiy (1981); from Northwest Atlantic.
[21] Zamarro (1992); from Grand Banks, off Newfoundland.
[22] Pitt (1970); from Northwest Atlantic, off Newfoundland.
[23] Walsh (1992); from Grand Banks, off Newfoundland.

Mooney, and personnel at East-side Medical Laboratory, Inc. performed most of the histological processing. Beverly Macewicz provided knowledgeable suggestions that improved both the analyses and the text. We also thank Dave Somerton, Jay Orr, Gary Walters, Gary Duker, and James Lee for helpful reviews prior to the submission to this journal. Two anonymous reviewers improved final versions of the manuscript.

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