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Batch Fecundity and Spawning Frequency of Yellowtail Flounder (*Limanda ferruginea*) on the Grand Bank

Javier Zamarro
Instituto de Investigaciones Marinas, Muelle de Bouzas
Vigo (Pontevedra), Spain

Abstract

The spawning frequency of yellowtail flounder (*Limanda ferruginea*) on the Grand Bank of Newfoundland was studied through analysis of 1,892 mature females from 35 different samples. Batch fecundity was determined using the "hydrated oocytes" method and a value of 200,000 ± 20,000 eggs was obtained. Histological analysis of 103 ovaries showed that the maturation process is continuous. When a batch of eggs is spawned the oocytes of the following batch have already gone through the stage of migration of the nucleus.

Based on the percentages of maturity stages through the hours of the day and assuming a hydration process which lasts the same as in other species (12 hr), a daily spawning frequency is proposed for yellowtail flounder.

Introduction

Yellowtail flounder (*Limanda ferruginea*) is distributed along the North American Atlantic coast, from Chesapeake Bay (USA) to the Strait of Belle Isle (Labrador). Its highest abundance is found between depths 20 and 40 fm (Leim and Scott, 1966). The spawning season varies with latitude, occurring earlier in the southern part of its distribution area. On the Grand Bank spawning has been reported to occur from May to July (Pitt, 1970). Total fecundity in this species has been studied in relation to size, age and ovary weight (Pitt, 1971; Howell and Kesler, 1977).

Yellowtail flounder is known to be a batch (serial) spawner, with the total number of eggs to be spawned in one season determined before the onset of the spawning season (Howell, 1983). Several groups of yolked oocytes begin their final maturation at the same time; this can be seen by the migration of the nucleus to the animal pole, which is followed by hydration and ovulation (Wallace and Selman, 1981). The eggs remain for some time in the ovary lumen before they are expelled.

The purpose of this paper is to analyze the spawning process in yellowtail flounder on the Grand Bank, from the point of view of final maturation of the fully yolked oocytes, batch fecundity, relative fecundity and time of spawning, using macroscopic and microscopic characteristics of the ovary.

Materials and Methods

The samples were collected on board a commercial freezer trawler in the southern part of the Grand Bank (NAFO Div. 3N), during June and July 1987. Each trawl lasted 4 hr. The reference time for samples was set at 2 hr before hauling.

A total of 1,892 mature females (37-53 cm length) from 35 different samples were analyzed. For every individual, total length was taken and a maturity stage assigned according to Table 1. A sample of 103 ovaries was preserved in 4% buffered formalin (Hunter, 1985) for histological analysis. In those individuals, total length and weight of the fish with the ovary removed, were recorded. The weight of the preserved ovaries was determined in the laboratory. For histological analysis, two pieces of ovary from the anterior and posterior extreme parts were embedded in Paraplast, sectioned at 6μm, and stained using Harris' haematoxylin and Eosin-Phloxine B.

The "hydrated oocyte" method (Hunter *et al.*, 1985) was used to calculate batch fecundity (number of

TABLE 1. Macroscopic characteristics of the different maturity stages in yellowtail flounder (Stages from Howell, 1983).

Stage I.	Ovaries small (2-6 cm), conical, pinkish and generally translucent. No oocytes visible to the naked eye.
Stage II.	Ovaries relatively small (6-12 cm), reddish and translucent. Ovarian wall thick.
Stage III.	Ovaries larger in size (>12 cm) and occupying most of ovarian cavity. Visible oocytes large, yellowish in colour and opaque. Ovarian wall thin, translucent.
Stage IV.	Ovaries very large. Some oocytes yellowish and opaque, others transparent (hydrated).
Stage V.	Ovaries very large. Some oocytes yellowish and opaque, others transparent (hydrated). Ova run from the vent upon slight pressure.
Stage VI.	Ovaries flaccid, bloodshot.

oocytes released per spawning event). In ovaries where recent post-ovulatory follicles (type A) were not observed or the nuclear migration had progressed far enough, three samples of ovarian tissue, between 400 and 500 mg were removed from the anterior, central and posterior positions of each ovary. They were placed on microscope slides in a drop of glycerine and the number of hydrated oocytes in each sample was determined. Hydrated oocytes are easily identified by their much larger size and their translucent appearance. Batch fecundity was calculated based on the average of the three samples, and relative fecundity was determined by dividing batch fecundity by ovary-free female weight (Hunter and Goldberg, 1980).

The number of remaining fully yolked oocytes was calculated from the average of the three samples using between 200 and 250 mg of ovarian tissue.

Histological Classification

To estimate the reproductive state of different females, the maturity stage was determined microscopically by classifying the most developed oocytes as shown in Table 2, and describing the degree of degeneration of the postovulatory follicles. Hunter and Goldberg (1980) developed criteria for ageing postovulatory follicles in northern anchovy (*Engraulis mordax*), by establishing different stages of degeneration. Further observations in other species indicate that this degeneration is a process occurring in most teleosts with small variations in the form and duration of each step (Hunter and Macewicz, 1985). Following these general criteria, the postovulatory follicles were classified into three groups of degeneration for this study:

TABLE 2. Classification of the last stages of the oocyte development in yellowtail flounder.

Yolked oocytes. In the last phase of vitelogenesis, the cytoplasm is completely full of yolk globules and the nucleus is central, the diameter from 290 to 430 m (Fig. 4 and 6).
Oocytes ending the nuclear migration. The nucleus is irregularly shaped and located at the animal pole. Yolk globules have begun to fuse, forming yolk plates (Fig. 4).
Hydrated oocytes. The nucleus is not visible. In early stages, the yolk globules are fused into plates. At conclusion of this stage, the interior of the oocyte shows homogeneity (Fig. 5 and 6).

Postovulatory Follicles A (Fig. 1). Follicles with no signs of degeneration. The lumen is spacious, the granulosa epithelial cell layer of the follicle appears as an irregularly looped cord of cuboidal cells with prominent healthy nuclei linearly arranged. The granulosa appears only loosely attached to the thecal connective tissue layer.

Postovulatory Follicles B (Fig. 2). The granulosa is folded and the lumen is narrow. The nuclei are linearly arranged and are not pycnotic, i.e. they are smaller with strong pigmentation and sometimes irregular in form.

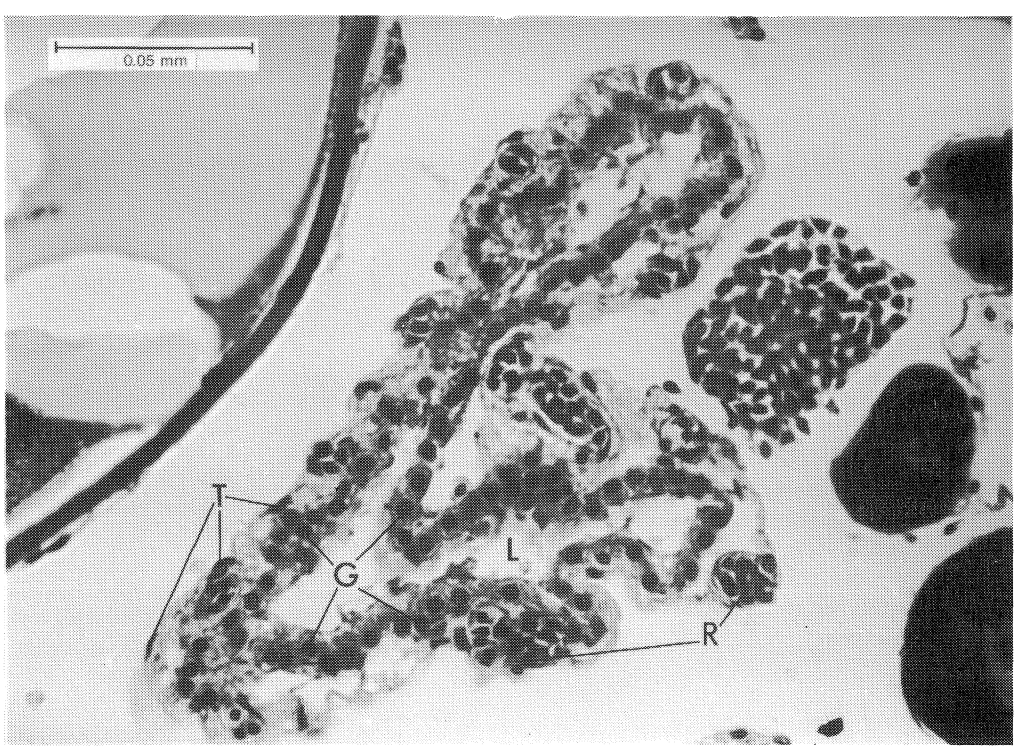

Fig. 1. Photomicrograph of yellowtail flounder ovary showing postovulatory follicle A. G = granulosa epithelial cell layer, L = lumen of follicle, T = thecal connective cell layer, R = red blood cells.

Postovulatory Follicles C (Fig. 3). Follicle is much smaller and shows pronounced signs of degeneration. The granulosa cells do not have the nuclei linearly arranged and some nuclei are pycnotic. The granulosa is attached to the thecal connective tissue layer. The lumen is much reduced or absent.

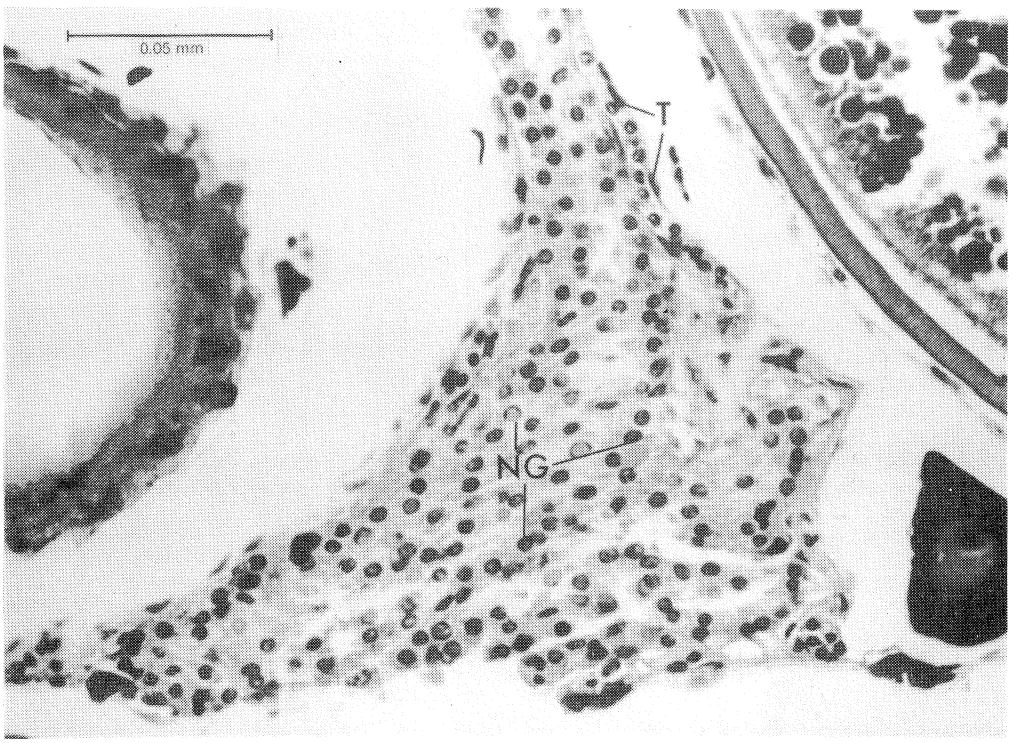

Fig. 2. Photomicrograph of yellowtail flounder ovary showing postovulatory follicle B. NG = nuclei of the granulosa epithelial cells, T = thecal connective cells.

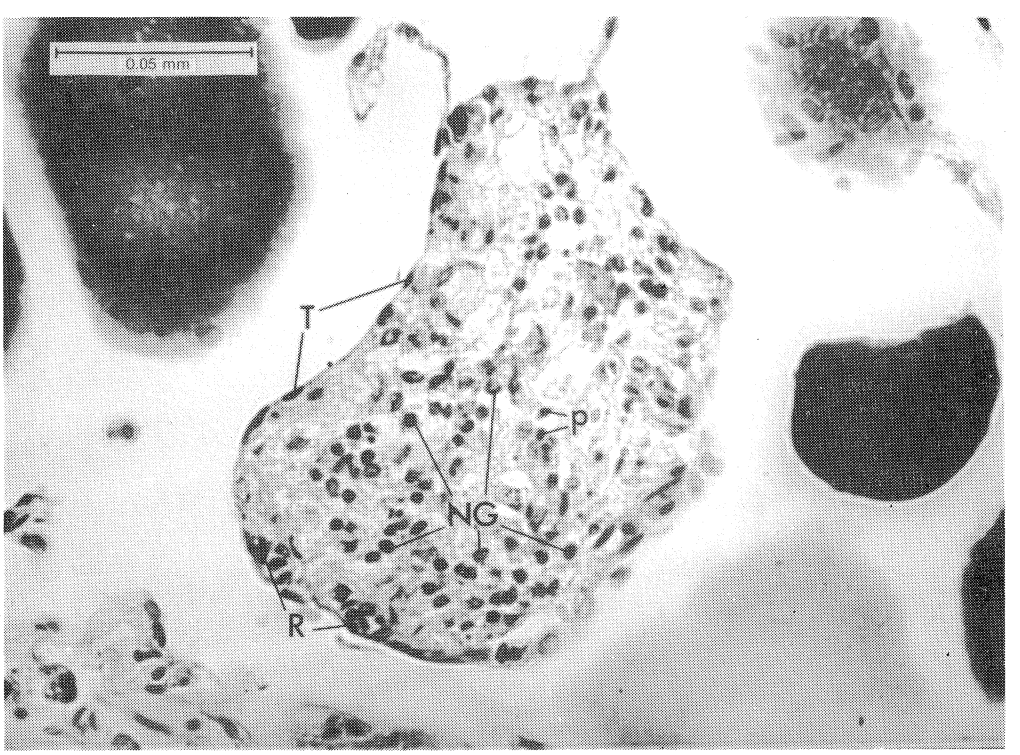

Fig. 3. Photomicrograph of yellowtail flounder ovary showing postovulatory follicle C. NG = nuclei of the epithelial granulosa cells with some picnotics (p), R = red blood cells, T = thecal connective cells.

Results

Table 3 shows the observed frequency of microscopic structures at different stages of maturity. They correspond to the following reproductive stages:

Stage III. Ovaries contained yolked oocytes but without signs of final maturation (nuclear migration and hydration). There were no postovulatory follicles. Spawning had not begun.

Stage IV. Distinguished by the presence of oocytes in final maturation (nuclear migration and hydration) (Fig. 4, 5 and 6). These ovaries were forming the next batch. Postovulatory follicles were present in those where previous spawning had occurred.

Stage V. Ovaries had completely hydrated oocytes and eggs were present in the lumen. In the most advanced cases, all the hydrated oocytes had ovulated and the next batch was ending the nuclear migration, thus there were at the same time, eggs in the lumen, postovulatory follicles A and oocytes with nuclear migration (Fig. 4).

The presence of postovulatory follicles A at Stage V and some at Stage IV in some but not all the ovaries could be due to the different lengths of time the eggs remain in the ovary lumen. The ovaries at Stage V were in ovulation or ready for the next release as eggs.

Stage VI. Postovulatory follicles were in an advanced state of reabsorption. The ovaries had fin-

TABLE 3. Microscopic characteristics of the different maturity stages in yellowtail flounder.

Maturity stage	No. of ovaries sampled	% of ovaries with yolked oocytes	% of ovaries with oocytes ending the nuclear migration	% of ovaries with hydrated oocytes	% of ovaries with postovulatory follicles A	% of ovaries with postovulatory follicles B	% of ovaries with postovulatory follicles C
III	20	100	—	—	—	—	—
IV	42	88	26	78	31	74	86
V	16	94	31	100	81	87	100
VI	25	—	4	—	4	4	100

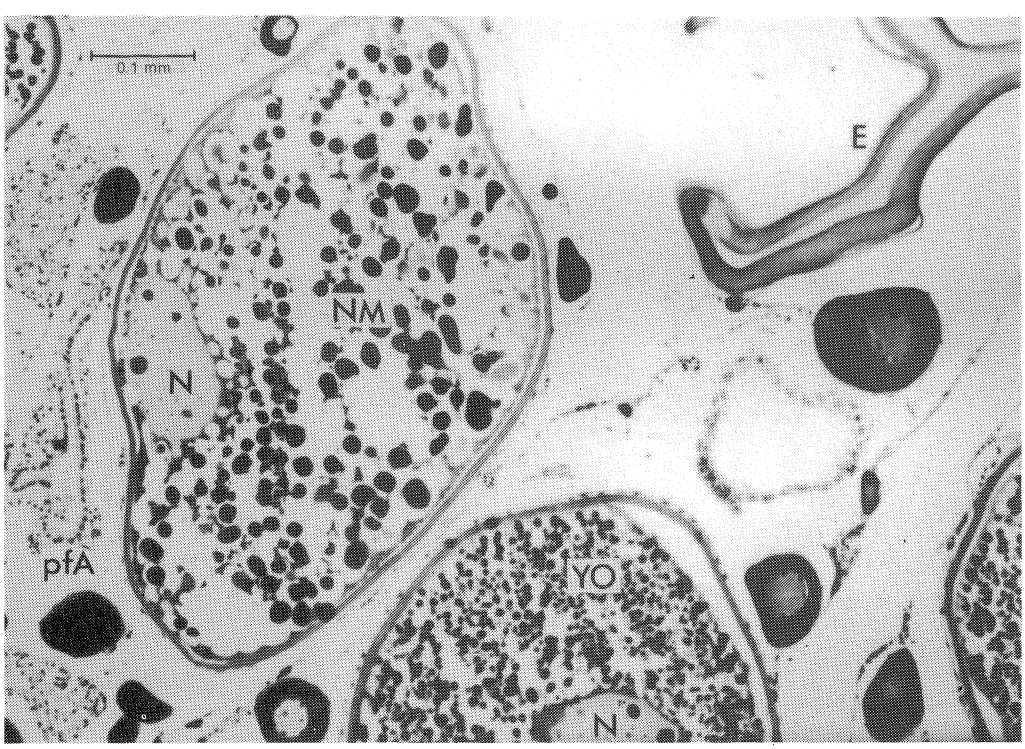

Fig. 4. Photomicrograph of ovary of yellowtail flounder showing three different batches at the same time. E = egg in the ovary lumen, NM = oocyte with nuclear migration, N = nuclei, pfa = new postovulatory follicle (type A), YO = yolked oocyte.

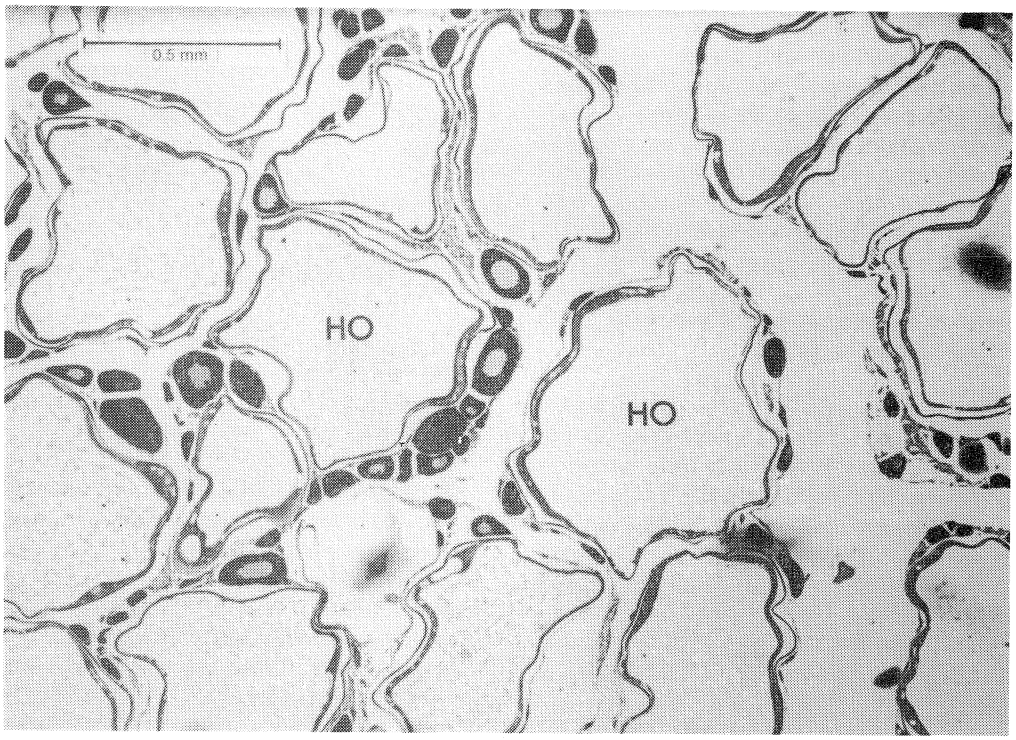

Fig. 5. Photomicrograph of ovary of yellowtail flounder in late spawning, showing all the yolked oocytes are hydrated. HO = hydrated oocyte.

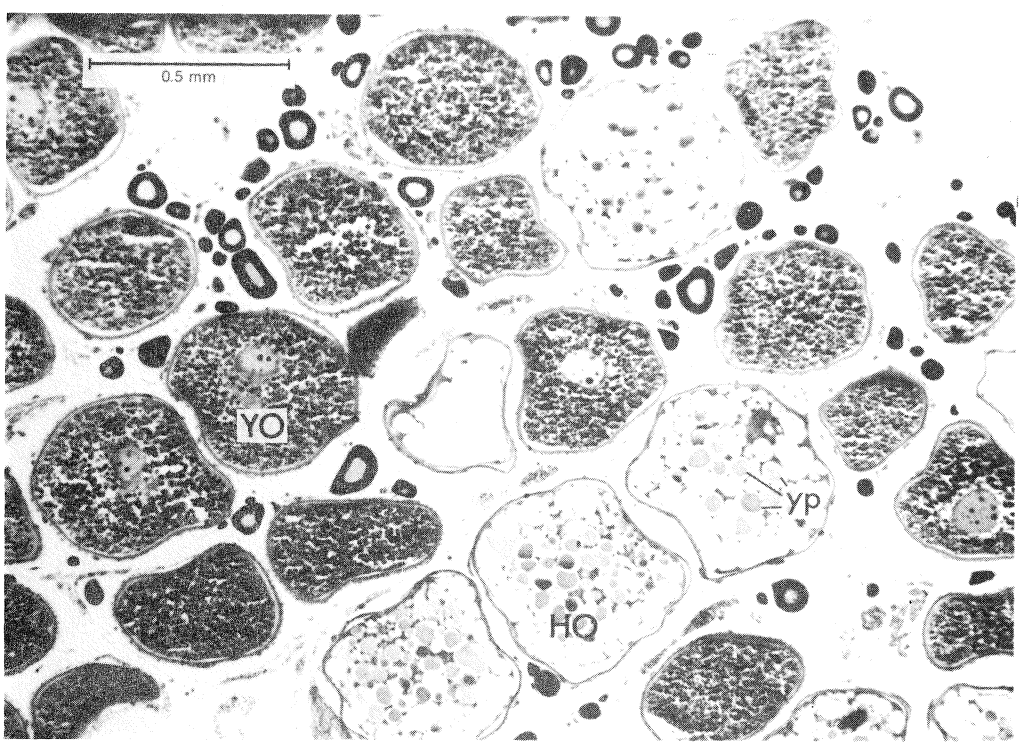

Fig. 6. Photomicrograph of ovary of yellowtail flounder with a batch in an early stage of hydration, showing the yolk globules fused in plates. HO = oocyte in an early stage of hydration (yp = yolk plates), YO = yolked oocyte.

ished spawning and neither yolked oocytes nor atretic oocytes were present. A special note should be made that one of the ovaries classified under Stage VI in Table 3, contained a small batch of oocytes showing nuclear migration and new postovulatory follicles. This ovary had not finished with spawning, and should have been classified in Stage IV.

Table 4 shows the overall classification of 1,892 ovaries into macroscopic stages.

In order to estimate the time of spawning of yellowtail flounder on the Grand Bank, the females in the spawning period (Stages IV and V) were grouped according to the sampling hour (Table 5). The percentage of females with eggs in the lumen (Stage V) were similar at the different sampling times, a chi-square contingency test resulted in no significant differences at 99% level of confidence. The percentages of spawning females throughout the sampling period are presented in Fig. 7. The highest values were during June and they gradually dropped to zero by the end of July. The overall mean of the females that had begun the spawning period and had eggs in the ovary lumen was 44.5%.

TABLE 5. Incidence of ovaries at the spawning stages (Stages IV and V) in yellowtail flounder caught at different time periods of the day.

Time period (hr)	No. of samples	No. of ovaries in Stages IV & V	% of ovaries in Stage V
0600–1100	24	415	43.9
1400–1500	3	62	48.4
1900–2300	5	101	44.6

Among the ovaries studied, 22 showed no postovulatory follicles A or their nuclear migration had progressed far enough to enable the calculation of batch fecundity. These results are given in Table 6. The mean value was 200,000 ± 20,000 eggs-per-batch. The relative fecundity was 300 ± 30 eggs-per-g of ovary-free female weight. There was no significant relationship

TABLE 4. Maturity stages determined macroscopically found through the sampling period.

Sample date (1987)	Sampling time (hr)	No. sampled	Maturity stage (%) II	III	IV	V	VI
21 Jun	1930	34	2.9	11.7	35.3	14.7	35.3
22 Jun	0930	40	5.0	12.5	37.5	10.0	35.0
23 Jun	2330	52	5.7	3.8	38.5	25.0	26.9
24 Jun	1430	45	8.9	17.8	35.5	24.4	13.3
25 Jun	1000	54	3.7	25.9	37.0	12.9	20.4
27 Jun	0700	82	4.9	13.4	23.2	12.2	46.3
27 Jun	1030	68	1.5	17.6	22.1	25.0	47.1
27 Jun	1530	50	8.0	18.0	16.0	30.0	28.0
28 Jun	1030	90	3.3	18.9	17.8	20.0	40.0
30 Jun	1000	34	2.9	8.8	23.5	23.5	41.2
30 Jun	1030	58	5.2	3.5	29.3	25.8	36.2
30 Jun	2030	67	11.9	7.5	26.9	28.4	25.4
1 Jul	1000	78	5.1	17.9	15.4	14.1	7.4
2 Jul	1045	60	—	16.7	25.0	15.0	38.3
3 Jul	1000	54	3.7	9.3	25.9	14.8	46.3
3 Jul	2030	66	7.6	4.5	16.7	18.2	53.0
4 Jul	1030	41	4.9	14.6	17.1	17.1	46.3
7 Jul	2030	50	4.0	6.0	18.0	12.0	60.0
7 Jul	1000	45	11.1	4.4	22.2	15.6	46.7
8 Jul	1000	61	9.2	3.3	8.2	6.6	73.8
9 Jul	0800	69	—	2.9	2.9	10.1	84.0
9 Jul	1030	57	5.3	5.3	8.8	14.0	66.7
12 Jul	1530	32	6.3	3.1	25.0	12.5	53.1
13 Jul	0630	39	20.5	—	17.9	10.3	51.3
14 Jul	1000	69	6.8	1.2	7.3	2.9	82.6
15 Jul	1000	38	13.2	—	15.8	2.6	68.4
16 Jul	1030	62	11.3	—	1.6	11.3	75.8
19 Jul	0930	42	7.1	—	16.7	11.9	64.3
20 Jul	1030	38	2.6	2.6	7.9	7.9	78.9
22 Jul	1030	42	9.5	—	2.4	4.8	83.3
23 Jul	2130	47	2.1	—	12.8	6.4	78.7
23 Jul	1030	52	9.6	—	5.8	9.6	75.0
27 Jul	2000	72	30.3	—	—	4.5	65.2
28 Jul	1400	72	40.2	—	—	—	59.7
29 Jul	0730	32	46.8	—	—	—	53.1

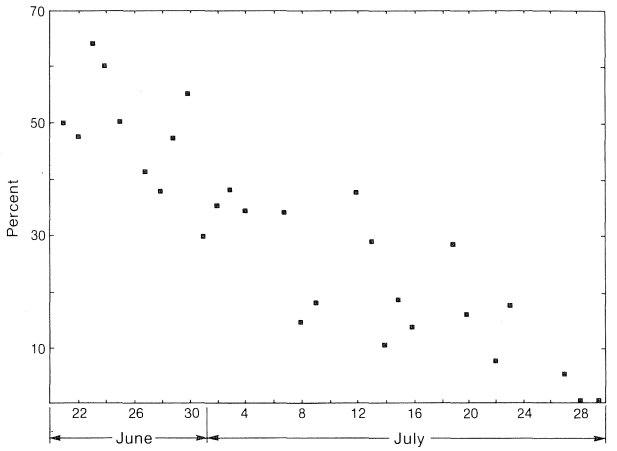

Fig. 7. Percentage of females in spawning condition (Stages IV and V) during the sampling period (June-July).

between batch fecundity and fish length or ovary-free body weight. Similarly, there was no relationship with the relative fecundity. The values of the correlation coefficient of the regression analysis are given in Table 7.

In order to see if the eggs-per-batch were related to the number of oocytes that remained in the ovary, the proportion of oocytes remaing in the ovary was calculated adding the number of yolked oocytes in the ovary to the batch fecundity and dividing by the total fecundity. The total fecundity was obtained from Pitt (1971). The values obtained (Table 6), show they do not have a significant relationship with the batch and or relative fecundity (Table 7).

Incidence of oocyte atresia was very scarce. Only some oocytes in alpha atresia were found in ovaries at Stage III, in numbers lower than .001% of the yolked oocytes. In ovaries at Stage VI (postspawning) some hydrated oocytes were observed in atresia, but they were also in very small quantities.

Discussion

The oocytes of yellowtail flounder show a development described as "group synchronous" by Howell (1983); who also found the number of atretic oocytes was small. This seems to support that all the fully yolked oocytes reach the egg phase and are expelled.

The yellowtail flounder is a batch spawner since during the spawning period the ovaries present one group of fully yolked oocytes while another group is in the process of maturation (nuclear migration and hydration); and the latter will be spawned in the next batch.

At Stage V, the ovaries with nuclear migration (Table 4) had eggs in the lumen and postovulatory follicles A. This was indicative of a continuous maturation. Thus, when ovulation of one batch has finished, the next one is ending the nuclear migration stage. In

TABLE 6. Yellowtail flounder batch fecundity, relative fecundity and proportion of oocytes remaining in the ovary (batch fecundity and yolked oocytes/total fecundity (Pitt, 1971)) calculated from observations on 22 females.

Fish length (cm)	Fish weight (g)	Batch fecundity	Relative fecundity	No. yolked oocytes	Proportion of oocytes remaining
44	674	243,337	361	757,429	0.55
43	684	176,518	258	1,250,105	0.88
42	622	200,599	322	—	0.13
41	564	183,455	325	681,158	0.66
47	824	292,208	355	801,171	0.44
46	842	148,507	176	1,253,884	0.63
39	496	153,603	310	572,247	0.71
39	524	153,759	293	465,267	0.60
41	690	192,652	279	676,559	0.67
40	564	259,616	460	977,769	1.00
44	622	169,459	272	312,598	0.27
46	1,008	303,308	301	1,449,256	0.79
40	522	166,474	319	211,809	0.33
39	542	235,643	435	119,297	0.34
41	638	180,680	283	—	0.14
43	660	190,147	288	862,906	0.65
41	644	175,680	273	595,139	0.59
45	878	178,535	203	—	0.09
44	722	165,074	229	1,092,181	0.69
44	714	275,049	385	1,347,555	0.90
42	672	176,956	263	—	0.12
41	598	103,864	174	—	0.07

TABLE 7. Correlation coefficient values in the regression analysis of the batch fecundity (number of ovaries used 22).

	Log. weight	Ovary free weight	Proportion of oocytes remaining
Log. batch fecundity	.347	—	—
Log. weight	.895	—	—
Batch fecundity	—	.423	.383
Relative fecundity	—	.326	.355

this continuous maturation, it is possible to identify macroscopically the females in the spawning period (Stages IV and V) by the presence of some hydrated oocytes in the ovary.

Batch fecundity is directly related to the weight (ovary free) and size of the female (De Martini and Fountain, 1981; Hunter and Macewicz, 1980; Alheit and Alegre, MS 1986; Alheit *et al.*, MS 1987) and can have variations during the spawning season (Alheit and Alegre, MS 1986; Alheit, 1988). Urban (MS 1988) analyzed the batch fecundity of two Pleuronectidae, *Pleuronectes platessa*, with a similar "group synchronous" development of the oocytes and the *Solea solea* which has an "asynchronous" development. In the first case studied with 17 females, the relationship between the batch fecundity and the weight (ovary-free) was good ($r = 0.90$); in the second one analyzed with 47 females, the relationship was not significant ($r = 0.12$). In the 22 ovaries of yellowtail flounder studied, the relationship between batch fecundity and weight (ovary free) or size of the female, was not significant. The stage at which the female is in the spawning season does not explain the changes observed in the batch fecundity either. It is possible however, that the samples were not large enough.

The number of oocytes maturing at the same time (batch) was $200{,}000 \pm 20{,}000$. This means that a female of 42 cm length with a total fecundity of 1,456,000 eggs (Pitt, 1971), would spawn 7 ± 1 times during the spawning season.

The proportion of individuals in the spawning period with eggs in the lumen was 44.5%, and the next maturing batch was 55.5%. The values obtained by sampling at different hours of the day did not show any significant difference, thus to maintain this proportion it would be necessary that there were females spawning throughout the whole day. These results seem to support a lack of synchronism noted above.

Two methods are currently used to calculate the frequency of spawning in fish populations. One of them is the "hydrated oocytes" method (De Martini and Fountain, 1981) and the other the "postovulatory follicles" (Hunter and Goldberg, 1980). The former is based on the percentage of females with hydrated oocytes and requires that there is synchronism in the process; the latter is based on the percentage of females showing postovulatory follicles and requires that the age of the follicles is known. Therefore, it was not possible to use either of them in this study.

Fulton (1898) described the process of hydration in the fish ovaries which produce pelagic eggs. The duration of the process has been studied in many different species: *Oryzias latipes* (Poeciliidae) (Yamamoto and Yoshioka, 1964), *Seriphus politus* (Sciaenidae) (De Martini and Fountain, 1981), *Engraulis mordax* (Engraulidae) (Hunter and Macewicz, 1980), *Engraulis ringens* (Alheit *et al.*, 1984), *Sardina pilchardus* (Clupeidae) (Perez and Cal., 1988). The spawning temperatures ranged from 12° to 13.5° C in *Sardina pilchardus* off the northwest of Spain (Nelida Perez, pers. comm.) to 13° to 18° C in *Engraulis mordax* (Brewer, 1978) and 17° to 19° C in *Seriphus politus* (De Martini and Fountain, 1981) off California. The process of hydration lasted about 12 hr in the species investigated.

If the process was similar in yellowtail flounder, and taking into account that the percentage of individuals in Stage V is constant in all the samples examined, Stage V would be expected to last 12 hr and the frequency of spawning to be daily. However, the yellowtail flounder is a cooler water species and different to those species studied; the mean bottom water temperature in the south part of the Grand Bank is 2° to 3° C during spring and summer (Borovkov and Tevs, MS 1988). It is therefore not certain whether the pattern would be similar.

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