

# FIELD AND LABORATORY ASSESSMENT OF PATTERNS IN FECUNDITY OF A MULTIPLE SPAWNING FISH: THE ATLANTIC SILVERSIDE *MENIDIA MENIDIA*<sup>1</sup>

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## ABSTRACT

Patterns in fecundity (i.e., spawning frequency, batch fecundity, annual egg production) of a multiple spawning fish, the Atlantic silverside, *Menidia menidia*, were assessed by 1) gonadal analysis of field specimens, 2) visual observations of spawning periodicity in the field, and 3) laboratory experiments. The gonadal analysis assumed that the difference between total number of eggs (recruitment + mature) per female just prior to the beginning of spawning, and recruitment egg retention per female at the end of the spawning season, represented annual egg production. Annual egg production estimated in this manner was  $893 \pm 197$  eggs/g ovary-free body weight ( $\pm 95\%$  C.L.). Batch fecundity (no. eggs in the most advanced size class/g ovary-free body weight,  $\pm 95\%$  C.L.) varied significantly during the breeding season, being lowest near the beginning ( $179 \pm 21$ ) and end ( $181 \pm 28$ ), and highest during the middle ( $266 \pm 34$  and  $267 \pm 23$ ) of the breeding season. Batch fecundity averaged over the entire breeding season, was about 225 eggs/g ovary-free body weight, indicating that each female must spawn about four times. The gonadal estimate was tested by inferring the actual spawning frequency from daily, visual observations of spawning in the field. These observations showed that spawning occurred on a fortnightly cycle coincidental with new and full moons, and that each female spawned at most once per semilunar period. There were about four semilunar spawning phases during the breeding season, indicating close correspondence with the results of gonadal analysis.

Laboratory observations demonstrated that female *M. menidia* are physiologically capable of spawning more frequently than in nature. Total egg output in the laboratory was about twice that in the field.

Accurate estimates of fecundity are important in describing the dynamics of fish populations. In some fishes, all eggs mature synchronously and are shed in a single batch over a relatively brief period of time each year (Bagenal 1967). Estimating fecundity in such species is a simple process of enumerating the number of ripening eggs per female. However, in many other fishes, ova mature in multiple batches that are spawned successively within one spawning season. These species have been termed multiple spawners, batch spawners, serial spawners, or fractional spawners by various authors (Bagenal and Braum 1971; Hempel 1979; DeMartini and Fountain 1981; Gale 1983; Snyder 1983). Little is known about the patterns in fecundity of multiple spawners, even though many marine and freshwater fishes from diverse taxonomic groups in both temperate and tropical regions produce eggs in this manner. Determination of annual egg production in multiple spawners is difficult and recent studies have in-

dicated that in some species, previous assessments may be in error by as much as an order of magnitude (Hunter and Goldberg 1980; Hunter and Leong 1981; DeMartini and Fountain 1981).

Frequency distributions of egg size (diameter) within ovaries of multiple spawning fishes are characteristically multimodal (Hempel 1979). In most multiple spawners, a synchronously maturing batch of eggs that is accumulating yolk sequentially arises from a much larger group of previtellogenic immature eggs, termed "recruitment" ova (Clark 1925; Bagenal and Braum 1971; Jones 1978; Hunter and Leong 1981). The problem in estimating fecundity has been to determine how many modes or batches of eggs are spawned annually. The conventional approach has been to count only the largest eggs or those above an arbitrary size (e.g., all yolked eggs) under the assumption that smaller eggs would be resorbed or spawned in later years. Whenever this assumption is incorrect, fecundity can be grossly underestimated. A second approach has been to infer the spawning frequency of adults from the proportion of field-collected females in ready-to-spawn condition (i.e., those containing hydrated eggs, e.g., Demartini and Fountain 1981) or from females showing evidence of having just spawned (i.e.,

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presence of 1-d-old postovulatory follicles, observed histologically, Hunter and Goldberg 1980). Spawning frequency is then multiplied by batch fecundity (number of eggs in the largest size class) to arrive at annual fecundity. Excellent examples of this methodology can be found in DeMartini and Fountain (1981), Hunter and Goldberg (1980), and Hunter and Macewicz (1980). A third technique for estimating fecundity in multiple spawners has been laboratory experiments where females are confined and allowed to spawn repeatedly (Gale and Gale 1977; Gale and Buynack 1978, 1982; Hislop et al. 1978; Gale 1983). The problem here is that spawning frequency and fecundity are dependent on the food supply (Wootton 1973, 1977, 1979; Townshend and Wootton 1984), so that it may be difficult to interpret laboratory data unless detailed studies of feeding rate and/or fecundity of fish in nature have been previously conducted (e.g., Hunter and Leong 1981).

The ovarian cycle of many fishes that breed during a restricted season involves two major, alternating phases of oocyte production and growth: 1) a previtellogenic phase during which new oocytes are produced, cell organelles form, and cytoplasmic growth occurs; and 2) a vitellogenic phase during which growth is faster and yolk accumulates in the ovum (Ball 1960; Jones 1978; Tokarz 1978; Baggerman 1980). The greatest production of new oocytes and phase one growth occurs during the postspawning season, with vitellogenic growth and maturation of eggs occurring just prior to and during the spawning season (this may not be true in tropical or other fishes that breed throughout most of the year, see reviews by Ball 1960; Jones 1978; Baggerman 1980). Hence, in multiple spawners having a restricted breeding season, the reservoir of recruitment eggs may be largely formed prior to the breeding season. If true, then the number of recruitment eggs per female should consistently decline as the breeding season progresses. The rate of decline in number of eggs per female would provide an estimate of seasonal egg production, and spawning frequency per female could be estimated from the total number of eggs shed divided by batch fecundity. The method could be tested by comparing the estimated spawning frequency with the actual spawning frequency determined independently in some other manner.

The purpose of this paper is to describe patterns of batch fecundity and annual egg production in the Atlantic silverside, *Menidia menidia*. The analysis employs the method described above: I show how the total number of eggs per female (recruitment + maturing) present at the beginning of the spawning season minus recruitment eggs per female retained

at the end of breeding can be used as an estimate of total egg production. The method is tested by showing that predicted spawning frequency is identical to the spawning frequency inferred from direct visual observations of spawning periodicity in a field population. Observations of spawning frequency and egg production under laboratory conditions are used to demonstrate that individual females are physiologically capable of maintaining the egg production rates and spawning frequency estimated from field populations.

The Atlantic silverside, *Menidia menidia*, (Pisces: Atherinidae) is a multiple spawning marine fish that inhabits coastal waters of eastern North America (Middaugh 1981; Conover and Kynard 1984). *Menidia menidia* is an annual fish: all individuals mature at age 1 and < 1% of breeding populations are 2 yr old. The ecological importance of *M. menidia* in terms of biomass transport from salt marsh to offshore communities and as forage for piscivorous fishes has been previously documented (Bayliff 1950; Conover and Ross 1982; Conover and Murawski 1982). The Atlantic silverside is an excellent species for studying patterns in fecundity because it is numerous and can be easily collected, spawning is easy to visually observe in the field, and it readily breeds in the laboratory.

## METHODS

### Gonadal Analysis

#### Field Sampling

Fish were sampled from the salt marsh region of Essex Bay, MA, with beach seines. Specimens were collected every 2 wk during 1977 as part of a general study of the population ecology of *M. menidia*. Additional specimens were collected intermittently in the spring during the breeding season. All collections were made in daylight within 1-2 h of low tide, and all specimens were immediately preserved in 10% buffered Formalin<sup>3</sup>. Detailed descriptions of Essex Bay and sampling methodology are available in Conover and Ross (1982).

#### Fecundity

Gonads were excised and weighed (nearest 0.01 g) from fish captured on 11 dates from October 1976 to July 1977. All fish were measured for total length

<sup>3</sup>Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

(nearest millimeter) and gonad-free body weight (nearest 0.1 g). The gonadosomatic index (GSI) was calculated by expressing gonad weight as a percentage of total weight (Snyder 1983).

Preliminary microscopic examination of ripe ovaries from collections during the breeding season revealed three general egg types that corresponded with modes found in frequency distributions of egg diameters from ripe females (see Figure 1 below). The three egg classifications were defined by both size and appearance of the ova as follows:

**Immature ova:** spherical, 0.05-0.60 mm in diameter.

The smaller ova in this group (0.05-0.15 mm) were primary oocytes with a clear cytoplasm and large nucleus. The larger ova (0.15-0.60 mm) were opaque and white. These ova formed one continuous mode in the frequency distribution so they were considered as one group (Fig. 1A, B).

**Maturing ova:** spherical, 0.6-1.0 mm in diameter, yellowish, and translucent.

**Ripe ova:** spherical, hydrated, 1.0-1.2 mm in diameter, hyaline and golden, with visible gelatinous threads coiled around the egg.

To confirm that these classifications represented distinct groups of synchronously maturing ova, I measured the diameter (random axis) of about 150 eggs, randomly subsampled from each of several females. In females captured during the breeding season, there were two distinct modes: the most advanced mode represented maturing eggs, and the other mode represented immature eggs (Fig. 1A). In females with ripe eggs, three modes in egg frequency were apparent: the most advanced group represented ripe eggs, the intermediate mode represented the next batch of maturing eggs, and the remaining mode consisted of immature eggs (Fig. 1B).

"Batch fecundity" was defined as the number of mature eggs in the most advanced size class, and presumably represented the number of eggs spawned at one time. As illustrated in Figure 1, the most advanced size class of maturing or ripe eggs was clearly distinguishable from, and did not overlap in size with, the immature ova. In ripe females, batch fecundity represented the number of hydrated eggs (e.g., the most advanced mode in Figure 1B). In nonripe females, batch fecundity represented the number of maturing eggs (e.g., the most advanced mode in Figure 1A). "Recruitment fecundity" was defined as the number of eggs smaller than the most advanced egg batch. Recruitment fecundity presumably represented the number of ova from which addi-

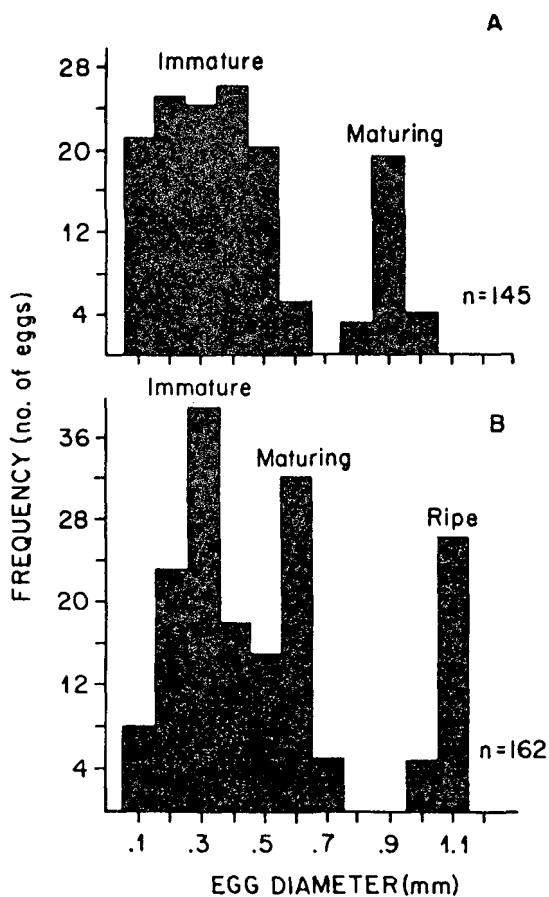


FIGURE 1.—Frequency vs. egg size (diameter in 0.1 mm intervals) for ova randomly sampled from two female *Menidia menidia* collected 6 June in Essex Bay, MA. A) A nonripe female in which there is a large number of immature eggs and a clearly definable mode of maturing eggs. B) A ripe female in which there is a large mode representing immature eggs, an intermediate mode of eggs beginning to mature, and an advanced mode of ripe eggs.

tional batches of mature eggs could potentially arise. In ripe fish containing three modes (e.g., Fig. 1B), the intermediate mode of eggs in early maturation was included with the immature eggs as part of the recruitment egg group because these overlapped in size with, and were difficult to separate from, immature ova. The minimum size of recruitment eggs was 0.05 mm in diameter. "Total fecundity" was defined as the sum of recruitment and batch fecundity.

Batch, recruitment, and total fecundity of individual females were estimated gravimetrically in the following manner. A cross section comprising 10-20% of the total ovarian weight was cut from a randomly chosen portion of one ovary. Both the sub-

sample and the remaining ovarian material were blotted on absorbent paper and weighed to the nearest milligram. The subsample was then placed in modified Gilson's fluid (Bagenal and Braum 1971), teased apart and vigorously shaken to separate ova, and stored for several weeks. All eggs in a subsample were counted and classified as belonging to either the recruitment pool or the mature batch of eggs. Batch and recruitment fecundities were then estimated for each female by multiplying the number of eggs in the subsample by an expansion factor (total ovarian weight/subsample weight). The mean diameter of the largest size class of eggs was also determined by measuring a random sample of about 20 mature eggs from each female. Shrinkage of eggs during preservation appeared to be minimal, so no correction for shrinkage was made. Fecundity was estimated for females collected on four occasions, from just before the beginning of the spawning season to its end. These dates were 6 May, 6 June, 22 June, and a pooled sample captured over the period 6-13 July.

To demonstrate whether estimates of fecundity were dependent on the location of the ovarian subsample, I compared these among replicate subsamples taken from the anterior and posterior sections of the right and left ovaries of six different females (i.e., four subsamples per female). Two-way ANOVA indicated that estimated fecundity was independent of subsample location ( $P > 0.10$ ) and the coefficient of variation was low ( $CV = 4.2\%$ ). The ratio of the number of batch eggs to recruitment eggs was also independent of subsample location ( $P > 0.5$ ). Moreover, I also directly counted the total number of batch eggs in four of the females used in the above analysis; in each case estimated batch fecundity was within 10% of the true value.

### Field Observations of Spawning Frequency

The frequency of spawning in a natural population of *Menidia menidia* was inferred from daily, direct field observations of mating. The Atlantic silverside spawns in large groups of fish that broadcast milt and eggs amongst vegetation in the upper intertidal zone of salt marshes within 1 or 2 h of the daylight high tide (Middaugh 1981; Middaugh et al. 1981; Conover and Kynard 1984). At such times, spawning can be easily observed. My observations were conducted at a major spawning site in Salem Harbor, MA. Daily assessments of spawning intensity were conducted throughout the spawning season by counting the number of aggregations of spawning fish

sighted during high tide. Methodological details are provided in Conover and Kynard (1984).

### Laboratory Observations of Spawning Frequency and Egg Production

Spawning frequency and egg production were also assessed by confining fish in laboratory tanks. A summary of the experimental procedure, described fully in Conover and Kynard (1984), follows. A large group of *M. menidia* were captured at Salem Harbor on 5 May 1979 and transported to the University of Massachusetts marine laboratory at Gloucester, MA. One female and two male fish were placed into each of the four 74 L tanks at room temperature on a natural photoperiod. Four males and four females were also placed into each of two circular plastic pools (diameter 1.5 m, depth 0.3 m). These pools were located outdoors. All fish were fed fresh, chopped seaworms (*Nereis*) and amphipods in excess of daily consumption. Spawning substrates consisted of a small tuft of synthetic aquarium filter floss, anchored to the bottom of each tank or pool. The floss was checked several times daily for the presence of eggs. When eggs were discovered, the floss was replaced. All eggs were preserved and enumerated later. Eggs from each female were usually deposited in a distinct clump on the floss, providing a means for determining the number of females that had spawned in the previous interval. The experiment was allowed to continue until spawning ceased (27 July). Length and weight of spawners was measured at the conclusion of testing.

## RESULTS AND DISCUSSION

### Gonadal Analyses

In late fall, just prior to the offshore winter migration (Conover and Murawski 1982), ovaries represented about 1% of total body weight (Fig. 2) and contained only small ( $< 0.1$  mm), clear, transparent eggs. Upon return of fish to the shore zone the following April, the ovarian GSI was about 4% and many opaque, white, immature ova ( $< 0.5$  mm) were present. Of the 25 females captured on 6 May, 92% contained numerous immature ova and a clearly definable batch of maturing ova. The first female carrying ripe eggs was collected on 12 May. The GSI peaked in both sexes on 25 May and declined thereafter until the end of July. The first fish in spent condition (no maturing egg class, recruitment eggs, if present, degenerating,  $GSI < 5\%$ ) was captured on 22 June. The proportion of spent fish was 23% on

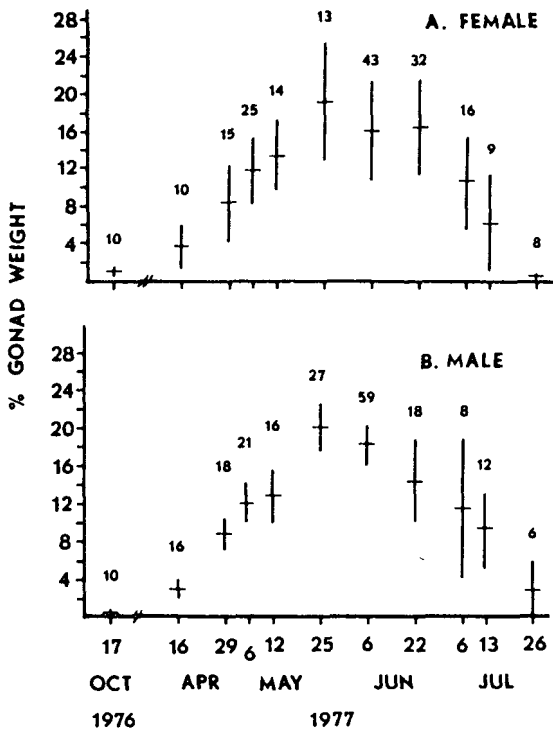


FIGURE 2.—Gonadosomatic index (gonad weight expressed as a percentage of total weight) for *Menidia menidia* collected during 1976-77 in Essex Bay, MA. The horizontal lines represent means, the vertical lines represent one standard deviation, and the sample size is given above the datum for each collection.

6-13 July and 100% on 26 July. Hence, the breeding season in Essex Bay began sometime after 6 May and was over by 26 July during 1977.

The potential annual fecundity of *M. menidia* may be represented by the total number of eggs (recruitment + maturing ova) within females just prior to the breeding season (i.e., 6 May), if additional immature eggs are not continually added to the recruitment pool as the spawning season progresses. If this premise is true, then there should be a continuous decline in recruitment fecundity and total fecundity during the breeding season (although not necessarily in batch fecundity).

Comparison of fecundities between sample dates was facilitated by the following observations. Total number of eggs per female was linearly related to ovary-free body weight (Fig. 3). Batch fecundity was also a simple linear function of ovary-free body weight (Fig. 4) and the rates of increase in batch fecundity, recruitment fecundity, and total fecundity with increase in female weight were generally similar among sample dates (i.e., regression slopes

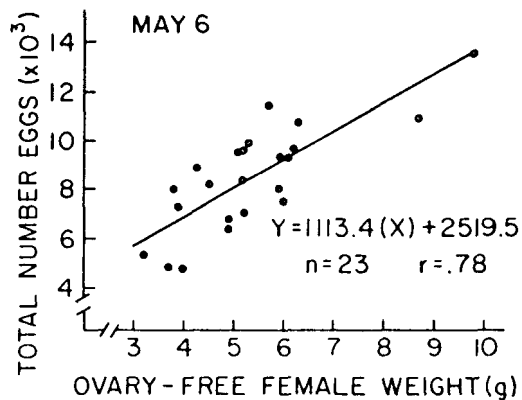


FIGURE 3.—Relation between total number of eggs (recruitment plus mature) and ovary-free female body weight for Atlantic silversides captured just prior to the beginning of the spawning season (6 May 1977) in Essex Bay, MA.

differed little, *t*-test,  $P > 0.05$ ). Correspondingly, relative batch fecundity, relative recruitment fecundity, and relative total fecundity (relative fecundity = no. eggs/g ovary-free body weight) were each independent of body weight in nearly all tests (linear correlation,  $P > 0.05$ ), suggesting that females of all sizes allocated about the same proportion of energy to reproduction. Hence, fecundity was adequately described and compared between dates if expressed as a proportion of ovary-free body weight, rather than as a function of weight.

Batch fecundity, recruitment fecundity, and total fecundity (no. eggs/g ovary-free body weight) during the spawning season are presented in Figure 5. Three patterns are evident. First, total fecundity and recruitment fecundity monotonically declined (Fig. 5A, B). Total fecundity was  $1,609 \pm 126$  (95% C.L.) on 6 May and declined to  $876 \pm 177$  by the second week of July (Fig. 5A) while recruitment fecundity was initially  $1,430 \pm 128$  on 6 May and declined to  $716 \pm 164$  in July (Fig. 5B). Second, batch fecundity differed significantly between sample dates, being maximal during the middle of the breeding season ( $266 \pm 34$  and  $267 \pm 23$  on 6 and 22 June, respectively) and minimal at the beginning and end of the breeding season ( $179 \pm 21$  and  $181 \pm 28$  on 6 May and 6-13 July, respectively; Fig. 5C). Third, many recruitment eggs remained in ovaries near the end of the spawning season (Fig. 5B) and most of these were probably resorbed soon thereafter because all females captured on 26 July contained only small ( $< 0.10$  mm), transparent oocytes. Two females from the 6-13 July collection contained only immature eggs that appeared to be in a state of resorption and had no maturing egg group.

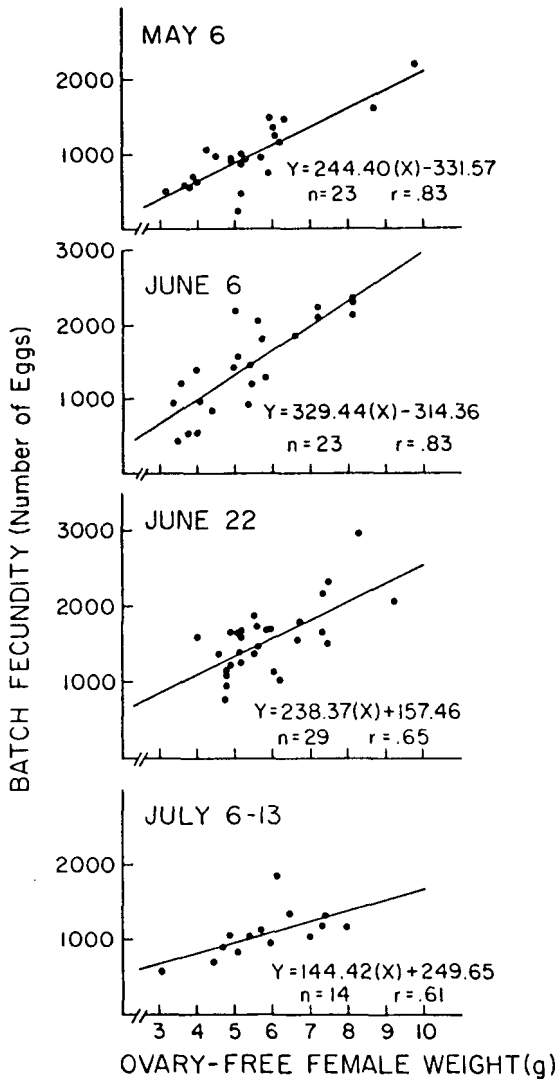


FIGURE 4.—Relation between batch fecundity (no. of eggs in the most advanced size class) and ovary-free female body weight for Atlantic silversides captured on four occasions during the 1977 breeding season in Essex Bay, MA.

Batch fecundity as estimated above assumes that the number of eggs in the most advanced mode is not reduced by atresia as they grow and are eventually shed. I noted few eggs which appeared to be atretic or in a process of resorption (except near the very end of the breeding season) and females which had recently spawned usually contained few, if any, residual ripe eggs. Similar observations were reported by Clark (1925) for the atherinid *Leuresthes tenuis*. Moreover, if some eggs cease growing and are resorbed before reaching maturity, there should

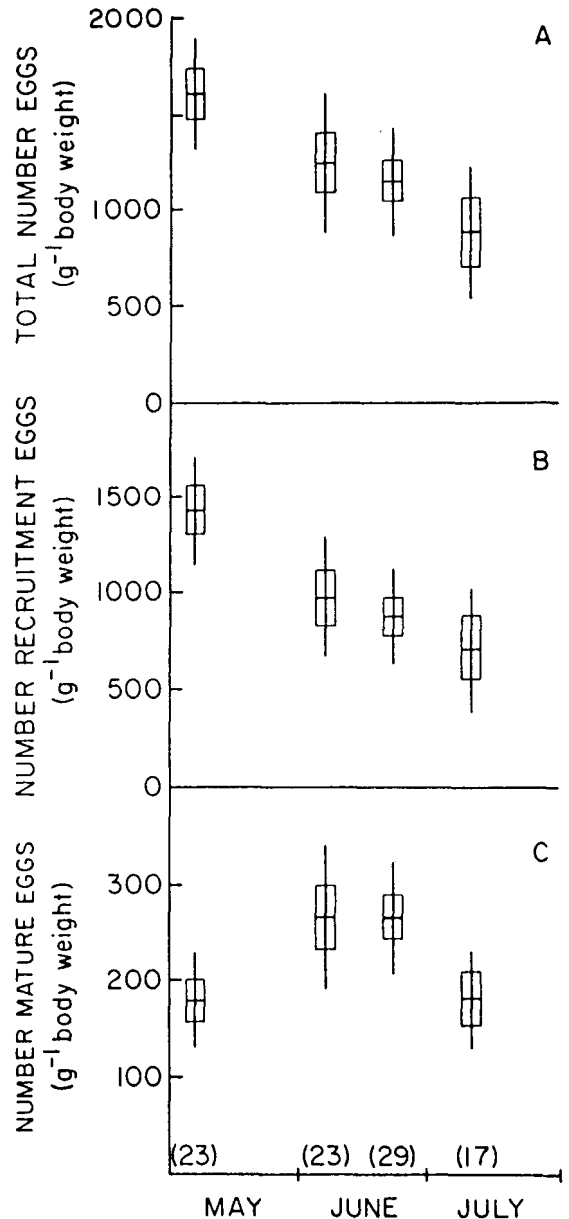


FIGURE 5.—Relative fecundity (no. eggs/g ovary-free female body weight) for Atlantic silversides captured on four occasions during the 1977 breeding season in Essex Bay, MA. The horizontal lines represent means, the vertical lines represent one standard deviation, and the rectangles represent 95% C.L. Sample sizes are in parentheses. All fish were spent on 26 July. A) Total number of eggs. B) Number of recruitment eggs (recruitment fecundity). C) Number of mature eggs (batch fecundity).

be a negative correlation between batch size and the mean diameter of eggs in the batch (i.e., no. batch eggs/g ovary-free body weight should generally be

lower in fish nearly ready to spawn than in fish where batch eggs are still maturing). Linear correlations of batch size and mean diameter of the maturing egg batch for each of the four dates on which fecundity was measured were nonsignificant ( $P > 0.05$ ), suggesting that the number of eggs in a batch does not decline much as the oocytes grow to maturity.

Assuming that the recruitment pool of immature eggs is fully formed prior to the breeding season, an estimate of the actual number of eggs produced annually can be derived from the above data. Because recruitment eggs remain at the season's end, actual egg production is best represented by the total number of eggs present just prior to the beginning of the spawning season minus the number of recruitment eggs retained when the spawning season ends. For the above data, this provides a value of  $(1,609 \pm 126) - (716 \pm 164) = 893 \pm 197$  eggs/g ovary-free body weight ( $\pm 95\%$  C.L.). The mean body weight of females during the breeding season was 5.6 g so that the average female would have spawned about 5,001 eggs in a season. The mean batch fecundity over the spawning season was 223 eggs/g ovary-free body weight or about 1,249 eggs/female. Hence, if the initial assumption is correct, the average female must spawn about four times during the breeding season.

### Frequency of Spawning in Nature

To test the prediction of spawning frequency derived above, spawning periodicity was determined from direct, visual observation of breeding events in the field. In 1978, I discovered a large spawning site in Salem Harbor, MA, where numerous eggs of *M. menidia* were deposited amongst mats of filamentous algae in the upper intertidal zone. Salem Harbor is located 20 km southwest of Essex Bay; however, individuals in each area are likely members of the same population because extensive mixing occurs during the offshore winter migration (Conover and Murawski 1982). Electrophoretic studies of geogra-

phic variation in *M. menidia* also support this contention (Johnson 1975).

Daily observations of the number of spawning aggregations sighted during high tide at Salem Harbor in 1979 showed that populations of Atlantic silver-sides breed on a semilunar periodicity coinciding with new and full moons (see figure 2 in Conover and Kynard 1984). Middaugh (1981) has reported similar observations based on a 3-yr study of populations in South Carolina. Within each semilunar spawning period of 1979 in Salem Harbor, the majority of spawning (40-90%) occurred on a single day, suggesting that females spawn, at most, once per semilunar cycle. This conclusion is further supported by the observation that sex ratios in spawning aggregations were highly male biased, whereas during non-spawning intervals, the sex ratio was near unity (Conover 1984). The sex ratio data is explained if females spawn, at most, once per cycle, while males spawn each day of a spawning period.

During 1979 in Salem Harbor, there were five semilunar spawning periods, although the first in late April was very light. In Essex Bay during 1977, there were four semilunar phases during the period defined as the breeding season. Hence, estimated spawning frequency based on gonadal analysis and direct observations of spawning fish agreed closely.

### Spawning Frequency and Egg Production in the Laboratory

Females held in laboratory tanks, whether housed individually indoors or outdoors in groups where natural day and night illumination was present, did not maintain a fortnightly spawning periodicity. Instead, spawning occurred much more frequently; the interval between spawnings averaged about 4 d/female (Table 1; see also figure 4 in Conover and Kynard 1984). Batch fecundity averaged 99-187 eggs/g ovary-free body weight among different tanks. Total egg production averaged 1,425-3,375 eggs/g ovary-free body weight. Hence, the experi-

TABLE 1.—Egg production by *Menidia menidia* on unlimited food rations in the laboratory. Field data are also provided for comparison.

	No. of females	Mean ♀ body weight (g)	Days from 1st to last spawning	No. of egg batches per ♀	Days between spawn per ♀	No. eggs/g ♀ body weight per egg batch	Total eggs per ♀ (no.)	Total eggs/g ♀ body weight (no.)
Pool 1	4	6.32	63	15.25	3.9	99.0	9,551	1,511
Pool 2	4	5.82	51	11.75	3.7	121.2	8,299	1,426
♀ A	1	3.9	72	20.0	3.6	169.5	13,218	3,389
♀ C	1	3.6	128	17.0	4.0	187.0	14,710	11,308
Field	—	—	60-75	4.0	14-15	180-266	5,000	893 ± 197

<sup>1</sup>Low values reflect the fact that ♀ C died before the conclusion of the experiment.

mental fish responded to laboratory conditions by reducing batch fecundity somewhat, but spawning more frequently, and thereby producing about twice the number of eggs as in nature (Table 1). The daily rate of egg production was 24-47 eggs/g female body weight per d in the laboratory, but averaged about 14 eggs/g female body weight per d in the field.

At the termination of the experiment, four of the eight females in the outdoor pools were spent, three contained only recruitment eggs, and one had both recruitment and maturing eggs. Female A died of unknown causes after its last spawning on 22 July. Female C also died (9 June) before cessation of spawning by jumping out of the tank.

The total weight specific egg production for the experimental fish was generally within the range of total eggs available prior to the beginning of the breeding season. The one exception was female A which produced about twice the total number of eggs that a fish of its size should have had available at the beginning of the spawning season (see Figure 3). Hence, under certain laboratory conditions, females may be capable of producing new oocytes from oogonia during the breeding season, as recruitment eggs become depleted. These laboratory observations show that the reproductive patterns of egg maturation and spawning which are highly synchronized with and influenced by environmental factors in the field, easily become disrupted when individuals are removed from their natural habitat.

## CONCLUSIONS

This study indicates that annual fecundity in *Menidia menidia*, and perhaps certain other fishes, can be estimated from the difference between total number of eggs (recruitment plus maturing) prior to the breeding season and recruitment egg retention near the end of the breeding season. Dividing the estimated total number of eggs shed per female by mean batch fecundity provided an estimate of spawning frequency. The accuracy of this value for spawning frequency was tested and found to agree closely with the spawning frequency inferred from direct field observations of breeding fish. Previous estimates of the fecundity of *M. menidia* were about 3-10 times less than that reported here because spawning frequency was not determined (Bayliff 1950; Jessop 1983). The studies of Hunter and his coworkers on northern anchovy, *Engraulis mordax* (Hunter and Goldberg 1980; Hunter and Macewicz 1980; Hunter and Leong 1981), and DeMartini and Fountain (1981) on queenfish, *Seriphus politus*, have amply demonstrated that estimates of annual fecun-

dity can be in error by over an order of magnitude when multiple spawning is ignored.

The estimation of fecundity from the difference between total prespawning fecundity and recruitment egg retention is dependent on the assumption that new oocytes are not simultaneously produced from oogonia and added to the reservoir of recruitment eggs as mature eggs are spawned. Agreement between predicted and observed spawning frequency suggests that this may be true in *M. menidia*. Many more recruitment eggs were present in ovaries at the beginning of the spawning season than were actually spawned in nature. Evidently, the recruitment egg pool is largely formed before the breeding season in *Menidia*, as is believed for some other seasonal spawners (Tokarz 1978; Jones 1978; Baggerman 1980). However, the generality of this pattern in other multiple spawning temperate or tropical fishes is not clear. Clark (1925) noted that the relative abundance of mature, intermediate, and immature eggs in *Leuresthes tenuis* was relatively constant during the breeding season and concluded from this that new oocytes must be continuously produced to replenish those spawned. Taylor and DiMichele (1980) reached a similar conclusion based on the relative abundance of different developmental stages of oocytes during the semilunar spawning cycle of *Fundulus heteroclitus*. However, analyses based on relative proportions do not take into account that gonad weight (GSI) generally declines as the season progresses (e.g., Fig. 2) and that number of eggs in the most advanced mode is not necessarily constant during the breeding season. Comparison of the relative abundance of egg sizes from sections of an ovary may not reflect changes in absolute number. For example, the relative abundance of recruitment eggs in *M. menidia* during 1977 was 0.88 on 6 May, 0.78 on 6 June, 0.76 on 22 June, and 0.79 during 6-13 July. Hence, the relative proportion of recruitment eggs did not consistently decline during the breeding season even though the absolute number of eggs declined by a factor of 2.4. In any event, too little is known about patterns of oocyte growth in fishes to recommend that the annual fecundity of multiple spawners can generally be determined by monitoring the decline in the standing stock of ova as was done here. For instance, in tropical species that breed most of the year recruitment eggs may be produced continuously. Whenever possible, the results of several different approaches to estimating fecundity should be compared.

The results of the laboratory study demonstrated that *M. menidia* is physiologically capable of spawning much more frequently and over a shorter interval



than normally occurs in the field. The reasons for the higher spawning frequency and cumulative egg production for fish in captivity are probably several. Fecundity may have been increased because ration size was unlimited. Fecundity is dependent on the food supply in many species (Wootton 1979). In the stickleback, *Gasterosteus aculeatus*, (Wootton 1977) and the convict cichlid, *Cichlasoma nigrofasciatum*, (Townsend and Wootton 1984) experimental studies have demonstrated that the number of spawnings was positively related to food ration and the interval between spawnings was inversely related to ration.

In my experiments on *M. menidia*, spawning frequency may also have been increased beyond that in nature due to the continuous availability of appropriate spawning substrates and lack of tidal spawning cues in the laboratory. Conover and Kynard (1984) noted that both marine and freshwater populations of *Menidia* spp. tend to spawn during midmorning, and speculated that spawning in nature may be restricted by the fact that suitable spawning substrates are covered by high tide during midmorning only at fortnightly intervals. Correspondingly, a lacustrine population of *M. beryllina* spawns daily at midmorning (Hubbs 1976). Hence, in the laboratory where tidal cues are removed, spawning substrates are continuously available, and food is abundant, *M. menidia* responded by spawning more frequently. The high egg production of female A also suggests that if the supply of recruitment eggs is exhausted, new recruitment eggs can be formed. It is clear that estimates of fecundity in natural populations of multiple spawners based on laboratory studies alone should be interpreted with caution.

Many aspects of the fecundity and spawning periodicity of *M. menidia* are paralleled in a west coast atherinid, *Leuresthes tenuis*. The California grunion has a well-known semilunar spawning cycle (Walker 1952). Clark (1925) conducted a detailed study of egg diameter frequencies in ovaries of *L. tenuis* and concluded that each female spawns once about every 15 d. Batch fecundity was very similar to that reported here for *M. menidia*. Although Clark measured batch fecundity in only a few individuals, a 118 mm grunion contained 1,613 ova. I calculate that a 118 mm Atlantic silverside would be expected to have 1,704 ripening eggs during the middle of the breeding season. Clark also found retention of recruitment eggs at the end of the breeding season and presented histological evidence that retained eggs were being resorbed.

Based on my estimate of the average annual fecundity of *M. menidia* ( $893 \pm 197$  eggs/g ovary-free body weight) and the wet weight of ripe eggs (0.8

g/1,000 eggs), an Atlantic silverside produces nearly 0.7 of its body weight in eggs during the breeding season in nature. In the laboratory, females produced 1.1-2.7 times their body weight in eggs. Studies of other multiple spawners have yielded similar results. DeMartini and Fountain (1981) estimated that the queenfish could spawn about 114% of its body weight in a year. Experiments on several species of cyprinids indicate that they are capable of spawning 0.7 to 6.8 times the volume of the female in eggs, at least in the laboratory (Gale and Gale 1977; Gale and Buynak 1978, 1982; Gale 1983). Hubbs (1976) estimated that a freshwater population of *Menidia beryllina* spawned 6-8 times female weight in eggs, although his assumption that each female spawns daily throughout the length of the breeding season needs further documentation.

Subseasonal trends in batch fecundity among multiple spawners have been examined by few investigators. If trends in batch fecundity within the breeding season are the adaptive result of natural selection, then periods of maximum batch fecundity should reflect the period when the probability of offspring survival is greatest. On the other hand, trends in batch fecundity could simply result from varying food conditions for adults. Three general relationships between the batch fecundity and the time of the breeding season have emerged from field studies with which I am familiar. These include 1) constant batch fecundity during the breeding season (Fig. 6, curve A), 2) a concave downward relation between batch fecundity and the breeding season (Fig. 6, curve B), and 3) a constant decline in batch fecundity during the breeding season (Fig. 6, curve C). Constant fecundity (curve A) might be expected where the optimal environmental conditions for reproduction and offspring survival are constant or vary unpredictably during the breeding season. This pattern has been found in the queenfish (DeMartini and Fountain 1981), a pelagic spawner of the western North American coast where aperiodic upwelling events produce unpredictable variations in plankton productivity and potential larval survival (Lasker 1978). When seasonal environmental conditions change in a predictable manner, there may be an optimal period for reproduction that occurs at roughly the same time each year, and batch fecundity would be expected to be maximal at that time (curve B). In *M. menidia*, the relation between batch fecundity and the breeding season was concave downward, suggesting that reproductive success is maximal during the middle of the breeding season. There is some independent evidence to support this hypothesis. Winter mortality during the offshore migration is

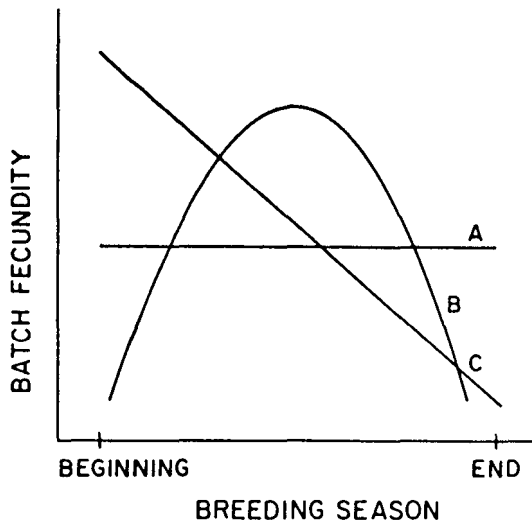


FIGURE 6. — Three hypothetical relationships between batch fecundity and time of the breeding season that have empirical support in the literature. A) Constant batch fecundity. B) Batch fecundity maximal during the middle of the breeding season. C) Batch fecundity maximal at the beginning of the breeding season and declining continuously thereafter.

strongly size-selective in *M. menidia* (Conover and Ross 1982; Conover 1984): the largest young-of-the-year have the highest probability of surviving. Hence, there should be selection pressure to breed as early in the spring as physical conditions (such as temperature) permit, and perhaps before conditions are optimal. Any offspring that managed to survive early in the breeding season will ultimately benefit from having a longer growing season. Conversely, towards the end of the breeding season, energy placed into reproduction becomes wasted because these offspring will have almost no chance of growing to a size that will permit winter survival. It follows that somewhere in the middle of the breeding season will be the optimal period for reproduction. Declining batch fecundity during the breeding season (curve C) has been reported for a population of the common mummichog, *Fundulus heteroclitus*, where batch fecundity was greatest at the beginning of the breeding season and became progressively less thereafter (Kneib and Stiven 1978). A continuous decline in batch fecundity may evolve when the value of putting energy into current reproduction, as opposed to somatic growth, declines continuously as the breeding season progresses. Although few data are now available for comparing the subseasonal patterns of batch fecundity in multiple spawning fishes, such information may eventually prove useful in

understanding the general reproductive strategies of fishes.

## ACKNOWLEDGMENTS

I thank the staff of the University of Massachusetts Marine Station for logistic support. D. Chevalier assisted in maintaining the laboratory fish and in counting eggs. F. Sutter helped with field sampling. The comments of two anonymous reviewers improved the clarity of the manuscript. During part of this study, I received support from the Massachusetts Cooperative Fishery Research Unit, which is jointly funded by the Massachusetts Division of Marine Fisheries, the Massachusetts Division of Fish and Wildlife, the University of Massachusetts, and the U.S. Fish and Wildlife Service.

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