Aspects of the reproductive biology of the bass, *Dicentrarchus labrax* L. II. Fecundity and pattern of oocyte development

J. Fish Biol. (1990) 36, 141–148

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(Received 31 May 1989, Accepted 7 August 1989)

The European bass, *Dicentrarchus labrax* L., in common with most temperate marine teleosts, exhibits a distinct seasonal reproductive cycle. Its reproductive strategy is characterized by a high absolute fecundity (2–25 x 10⁶), both absolute and relative fecundity increasing with size and age. The cyclic pattern of oocyte development has been determined by histology and from oocyte size-frequency analysis. Results show that the bass exhibits group-synchronous oocyte development and is a 'fractional spawner', i.e. it spawns a number (3–4) of discrete clutches in quick succession, successive clutches containing fewer oocytes. All oocytes which are recruited into the secondary growth phase (> 110 pm) are either spawned that season or become atretic, i.e. no secondary oocytes are held over for the subsequent reproductive season.

Key words: *Dicentrarchus labrax*; fecundity; spawning; oocyte development.

I. INTRODUCTION

In view of the recent extensive interest in the bass, *Dicentrarchus labrax* L., (Pawson & Pickett, 1987) it is surprising that so little information is available concerning its reproduction in the wild. In particular, little attention has been paid to the dynamic aspects of oocyte development from which considerable information on the seasonal cyclic changes in ovarian development can be gained. These are species-specific and are modified in a variety of ways to ensure a successful reproductive strategy within those environments to which a teleost species has become adapted.

The annual cyclic pattern of oocyte development and the mode of oocyte recruitment in teleosts can be determined from a series of ovary samples by histological examination and by plotting successive oocyte size-frequency histograms (review: de Vlaming, 1983). Further, a knowledge of the relative fecundity (i.e. the number of eggs produced per unit body weight) of the bass can be of great benefit to fishery scientists in assessing the size of fish stocks from plankton survey results (Lockwood et al., 1981). To that end, the primary aim of the present study was to determine the dynamic aspects of oocyte development, including fecundity, in natural bass populations.

II. MATERIALS AND METHODS

Samples of adult bass, caught by means of gillnetting, were obtained from Carmarthen Bay in the northern Bristol Channel and from near the Eddystone Rocks off Plymouth in the western English Channel. Fish were aged by means of scale reading (Kelley, 1988).

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ESTIMATION OF FECUNDITY

The ovaries were removed from the fish, weighed, split open longitudinally and immersed in Gilson's fixative (Gatenby & Beam, 1950) in the proportion of one part ovary to two parts fixative (v/v). The ovaries were left in the fixative for 4–6 months, with frequent shaking to facilitate membrane breakdown and subsequent oocyte release. When this was completed, the oocytes were separated from the other tissues by suspending each sample in water, decanting the lighter debris and then pouring it through a series of sieves, the final sieve having a mesh size of 100 μm. The oocyte sample was further cleaned by a series of mixing and decanting processes and the oocytes were then sampled volumetrically with a 5-ml Stempel pipette to determine whether the concentration of debris was within an acceptable level (<1% of egg count). The cleaned samples (in distilled water) were then passed through an automated particle counter (APC) comprising a HIAC Criterion PC-320 particle size analyser interfaced with a pulse height analyser (Tracor Northern) which sized and counted the oocytes in 20-μm size intervals (for apparatus details, see Whittames & Greer Walker, 1987). The particle size analyser was calibrated to size and count only those oocytes <200 μm in diameter. Therefore, this method of estimating fecundity had the limitation of not being able to size and count those secondary oocytes <200 μm in diameter. For each ovary sample, both the relative (eggs g⁻¹ body weight) and absolute (eggs female⁻¹ year⁻¹) fecundity was determined.

SIZE–FREQUENCY DISTRIBUTION OF OOCYTES:

During this study the size–frequency distribution of growing oocytes was determined by two different methods:

Automated particle counter (APC)

The APC was also used to determine the size–frequency distribution of oocytes from ovary samples. Owing to the large number of oocytes counted (each sample contained a minimum of 10⁵ oocytes) this was undoubtedly the most accurate method employed in this study for determining the size–frequency distribution of oocytes >200 μm in diameter from an ovary sample.

Histological sections

In addition to providing histological descriptions of oocyte development (for maturity stage descriptions, see Mayer et al., 1988) oocyte size–frequency distributions were also determined from histological sections. This method was particularly important for determining the size–frequency distribution of oocytes from early maturity stage gonads which contain predominantly primary oocytes (<120 μm). For each ovary specimen, 300–400 oocytes were measured and recorded from 3-μm HistoResin sections. In order to obtain a true representative oocyte count with the minimum bias towards a particular oocyte size, counts were made of all oocytes within a number of ovigerous folds. Oocyte size was obtained by taking the mean of the maximum and minimum diameter of only those oocytes which had been sectioned through the nucleus. This procedure has been shown by Foucher & Beamish (1980) to be representative of the true oocyte diameter.

Shrinkage factor

In order to interrelate the results of the oocyte size–frequency counts determined by the two methods described above, the relative shrinkage factor for each method was determined. For this comparison, tissue from the same ovary (containing both granular and hyaline oocytes) was fixed and processed separately for each method. The histological method had a shrinkage factor of c. 8–12% (oocyte diameter), whilst the APC method had a shrinkage factor of 15–20%.

III. RESULTS

FECUNDITY

Values of absolute and relative fecundity determined from the APC are given in Table I. These data are plotted against fish size in Fig. 1, and the line of best fit
## Table I. Fecundity estimates for bass

<table>
<thead>
<tr>
<th>Area of capture</th>
<th>Date</th>
<th>Age (years)</th>
<th>Weight (g)</th>
<th>Absolute fecundity*</th>
<th>Relative fecundity* (eggs g(^{-1}))</th>
</tr>
</thead>
<tbody>
<tr>
<td>Plymouth</td>
<td>29/01/84</td>
<td>17</td>
<td>3800</td>
<td>2 043 126</td>
<td>538</td>
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<tr>
<td>~</td>
<td>15</td>
<td>2650</td>
<td>1 390 023</td>
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<td>~</td>
<td>11</td>
<td>2350</td>
<td>949 094</td>
<td>486</td>
<td></td>
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<tr>
<td>~</td>
<td>8</td>
<td>2000</td>
<td>971 933</td>
<td>367</td>
<td></td>
</tr>
<tr>
<td>~</td>
<td>9</td>
<td>2000</td>
<td>734 121</td>
<td>444</td>
<td></td>
</tr>
<tr>
<td>Gower</td>
<td>28/04/85</td>
<td>10</td>
<td>2250</td>
<td>1 049 027</td>
<td>466</td>
</tr>
<tr>
<td>28/04/85</td>
<td>9</td>
<td>1241</td>
<td>552 512</td>
<td>445</td>
<td></td>
</tr>
<tr>
<td>03/05/85</td>
<td>8</td>
<td>1000</td>
<td>412 789</td>
<td>413</td>
<td></td>
</tr>
<tr>
<td>04/04/86</td>
<td>9</td>
<td>1200</td>
<td>449 434</td>
<td>375</td>
<td></td>
</tr>
<tr>
<td>25/04/86</td>
<td>10</td>
<td>1225</td>
<td>559 513</td>
<td>457</td>
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<tr>
<td>~</td>
<td>9</td>
<td>1175</td>
<td>457 567</td>
<td>389</td>
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<td>9</td>
<td>1065</td>
<td>290 390</td>
<td>273</td>
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<td>9</td>
<td>1060</td>
<td>360 014</td>
<td>340</td>
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</tr>
<tr>
<td>03/05/86</td>
<td>10</td>
<td>1390</td>
<td>612 153</td>
<td>440</td>
<td></td>
</tr>
<tr>
<td>03/05/86</td>
<td>10</td>
<td>1320</td>
<td>585 000</td>
<td>443</td>
<td></td>
</tr>
</tbody>
</table>

*Absolute and relative fecundity estimated for oocytes only > 200 μm in diameter.

![Fig. 1. Relationship between fish weight and fecundity (oocytes > 200 μm) in *Dicentrarchus labrax*.](image)

- **Absolute fecundity**: ○
- **Relative fecundity**: ●

Line of best fit for absolute fecundity determined by linear regression analysis: \( y = 557.12x - 226,020, r = 0.962 \).
determined by regression analysis. This positive linear relationship shows that absolute fecundity is directly related to size and age, and that relative fecundity tended to be higher in larger, older fish.

These estimates show that the bass is a very fecund species, with absolute fecundity exceeding 2 million in the oldest fish (> 18 years). Assuming that the age of first maturity in females is 7 years (Mayer, 1987), from the regression equation the absolute fecundity of first-time spawners would be $c. 2 \times 10^5$. Relative fecundity varied between 273 and 538, somewhat higher than the range (293–358) determined by Kennedy & Fitzmaurice (1972) for Irish bass. Conversely, these estimates appear low when compared to the range of relative fecundity (492–955) calculated by Bou Ain (1977) for Mediterranean bass. Due to the differences in methods and criteria between the above authors it is difficult to determine whether or not these observed differences in relative fecundity are due to real geographical biological variations.

In the bass, oocytes are recruited into the secondary growth phase (vitellogenesis) at a size of 110–120 μm diameter (Mayer et al., 1988). Therefore, fecundity estimates in the present study are underestimated, as the APC (Hiac) can only size and count oocytes > 200 μm in diameter. Histological studies show that at the beginning of the spawning season (April–May) the ovaries of mature females contain a large proportion (c. 50% of total) of oocytes < 200 μm in diameter (Mayer, 1987). However, > 90% of these oocytes are small primary oocytes (< 120 μm in diameter) which do not appear to enter the secondary growth phase during the spawning period. Therefore, the present fecundity estimates using the APC are probably underestimated by < 10%.

**CYCLIC PATTERN OF OOCYTE DEVELOPMENT**

Figure 2 shows the oocyte size-frequency histograms determined from histological sections for adult bass between June and November. Figure 2(a) and (b) pertain to females sampled during the post-spawning period, and indicate that the ovaries, with the exception of a number (c. 4% total oocyte population) of atretic oocytes at various stages of degeneration, contain almost entirely small primary oocytes (< 120 μm). This is in agreement with previous studies which have shown that, in the bass, the peak period of both oogonial proliferation and oogenesis occurs during the immediate post-spawning period (Mayer et al., 1988). Thus, from the ovary maturity stages defined by Mayer et al. (1988), these histograms represent either stage VII (‘spent’) or stage IIR (‘recovering spent’) ovaries. Taken together with Fig. 2(c), it appears that over the period from June to early August oocyte development is minimal, with only a small number of primary oocytes having been recruited into the secondary growth phase (> 110 μm). This protracted period of slow oocyte development, viz. recruitment of primary oocytes into secondary (vitellogenic) growth, continues through August and September, by the end of which time the ovaries have reached maturity stage III [Fig. 2(d), (e)]. From mid-October, oocyte development starts to accelerate as more oocytes are recruited from the large population of primary oocytes into the secondary growth phase. This accelerated oocyte growth is indicated by the observed spread in the oocyte size-frequency distribution [Fig. 2(f), (g)] although no distinct clutch is yet distinguishable. By mid-November [Fig. 2(h)] the gonads have reached maturity stage IV, i.e. the large oocytes have attained the primary yolk granule stage (260–440 μm).
Oocyte development continues rapidly through December and January. By late January, oocyte size–frequency histograms [Fig. 3(a), (b)], determined by the APC, indicate that the ovaries have now reached maturity stage V, i.e. a high proportion of the secondary oocytes have attained a size (530–800 μm) corresponding to the tertiary yolk granule stage. These histograms show a clear bimodal oocyte size–frequency distribution pattern, with a relatively synchronous population of large ‘vitellogenic’ oocytes (defined as the first clutch) and a more heterogeneous population of smaller oocytes from which the first clutch had been recruited. This indicates that the bass shows group-synchronous oocyte development (Marza, 1938); at least two populations (‘clutches’) of oocytes can be distinguished in the ovary of an individual at some time during the reproductive cycle. Figure 3(a) and (b) shows that oocyte development is somewhat more advanced in the older fish, which is in agreement with the observation that older fish tend to spawn earlier in the season than younger fish.

Figure 3(c)–(i) shows oocyte size–frequency histograms for females sampled during the main spawning period (April–May). In order to determine more
accurately the sequence of events in oocyte development during this period, oocyte size–frequency histograms from two spawning seasons are used. Figure 3(a)–(c) suggests that minimal oocyte development has occurred between late January and just prior to the spawning period of early April when the ovaries are still at maturity stage V ('gravid'). Figure 3 (d)–(f) illustrates the sequence of dynamic events during maturation and subsequent ovulation of the first clutch of oocytes and indicates that the oocytes in the first clutch all undergo maturation in unison. The most prominent event during maturation is hydration, the postvitellogenic oocytes rapidly increasing in volume by about 250% until they reach the hyaline stage
BASS FECUNDITY AND SPAWNING

(1000–1100 μm); maturity stage VI (‘ running ’). It appears from Fig. 3(f) and (g) that, concomitant with maturation and ovulation of the first clutch, a second clutch of oocytes is recruited into the postvitellogenic stage. Thus, once spawning has started, successive clutches appear to be recruited in quick succession from the large heterogeneous population of smaller secondary oocytes. Figure 3(h) shows an oocyte size–frequency histogram from an ovary in which the penultimate clutch of oocytes is undergoing maturation, while Fig. 3(i) appears to show the final clutch of oocytes being recruited.

Analysis of the results from the APC showed that the first clutch contained 30–50% of the total number of secondary oocytes (> 200 μm) and that successive clutches contained relatively fewer oocytes. While it is difficult to determine accurately the total number of clutches spawned by a single female, the results suggest that females spawn three or four separate clutches. It is probable the older ‘ more fecund ’ females produce more clutches than younger fish, especially the first-time spawners.

The results from the oocyte size–frequency histograms indicate that the bass exhibits group-synchronous oocyte development and is a ‘ fractional spawner ’, i.e. it spawns a number of discrete clutches (3–4) in quick succession, successive clutches containing fewer oocytes. No secondary oocytes are ‘ held over ’ for the subsequent reproductive season, all oocytes recruited into the secondary growth phase either being spawned that season or becoming atretic.

IV. DISCUSSION

The fecundity estimates show that the bass has a reproductive strategy common to many temperate marine teleosts, i.e. it produces large numbers (up to 2 million) of small pelagic eggs (c. 1.2 mm diam). This inverse relationship between egg size and fecundity holds true for most teleosts so far studied (Blaxter, 1969), and is indicative of a species’ spawning strategy.

The dynamic aspects of the oocyte growth, viz. oocyte development and method of recruitment, have been determined from oocyte size–frequency analysis. Results show that the bass exhibits group-synchronous oocyte development, that is, at least two populations (clutches) can be distinguished at some time. This type of oocyte development is by far the most common strategy among teleosts (Wallace & Selman, 1981; de Vlaming, 1983) although a number of different recruitment tactics exist, e.g. recruitment may occur directly from oogonia, as in the stickleback Eucalia inconstans (Braekevelt & McMillan, 1967), or from primary oocytes, as in the herring Clupea harengus (Bowers & Holliday, 1961), or from secondary (vitellogenic) oocytes, as in the sticklebacks Gasterosteus aculeatus and Apeltes quadracus (Wallace & Selman, 1979). In the bass, recruitment of the successive clutches occurs directly from a large heterogeneous population of smaller oocytes at various stages of secondary growth, although the recruited clutches (more especially the first clutch) may be temporarily arrested at the postvitellogenic stage before being re-recruited into maturation.

The reproductive strategy of the bass is further characterized by being that of a ‘ fractional spawner ’. It spawns a number of discrete clutches in quick succession, successive clutches containing fewer oocytes. Whether being a fractional spawner offers a more effective reproductive strategy than one in which the female spawns
all the eggs at once is debatable. However, taking into account its high fecundity, the bass may have evolved into becoming a fractional spawner for purely logistical reasons, such as the ovary not being able to physically accommodate all the secondary oocytes hydrating (c. 250% increase in volume) at once.

This research was carried out while I.M. was in receipt of a NERC/CASE postgraduate studentship. We thank Dr Mike Pawson (MAFF, Lowestoft) for helpful discussions on the manuscript, and Mr K. Naylor for drawing the figures.

References


