Chapter 8
Fecundity and optimal sperm density for fertilization in the ormer (*Haliotis tuberculata* L.)

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ABSTRACT: The potential and instantaneous fecundity of *Haliotis tuberculata* L. was studied in the vicinity of St Malo (northern Britanny). A linear relationship is found between potential fecundity of males or females and weight of individuals but the total quantity of sperm and ova shed during laboratory-induced spawning (instantaneous fecundity) is generally lower than expected from this correlation. Incubations of ova with increasing concentrations of sperm reveal zero or very low fertilization rates for sperm densities less than 10^5 cells ml^{-1}, and a maximal rate at between 10^5 and 10^6 cells ml^{-1}. During spawning, 2×10^9 to 3×10^9 sperm are released at 30- to 45-second intervals. In natural grounds, this gamete concentration may be diluted by water movement and sperm concentration may be lower than the threshold of 10^3 cells ml^{-1}. *Haliotis tuberculata* is sedentary even during the reproductive period and good reproductive success may be ineffective on beds with low ormer densities.

RESUMEN: Se estudia la fecundación instantánea y absoluta de *H. tuberculata* L. en la vencindad de St Malo (norte de la Bretaña). La relación entre la fecundidad absoluta de los machos o de las hembras con el peso es lineal, pero la cantidad de esperma y de huevos emitidos durante el desove provocado en el laboratorio es generalmente menor que tal correlación deja suponer. La incubación de los huevos con concentración creciente de esperma revela tasas de fertilización nulas o muy bajas para densidades de espermatozoides inferiores a $10^3 ml^{-1}$ y tasa máximas para densidades de 10^5 a $10^6 ml^{-1}$. Durante el desove, 2×10^9 a 3×10^9 espermatozoides fueron emitidos cada 30 a 40 segundos. En el medio natural de vida, esa 'unidad de fecundación' puede sufrir una dilución por los movimientos del agua y la concentración de espermatozoides puede diminuir debajo de $10^3 ml^{-1}$. *Haliotis tuberculata* estando sedentario incluso durante el período de reproducción, se supone que la fecundación podría ser ineficaz cuando la densidad de abulones queda baja.

INTRODUCTION

The ormer (*Haliotis tuberculata* L.) lives along the Atlantic coast of Europe from the English Channel to Africa. It occurs in some abundance off the north coast of Brittany and the Channel Islands where it is regarded as a desirable shellfish delicacy. Nowadays, diving for ormers is not authorized in Europe and shore gathering is the only legal fishing method (Chapter 33, this volume).

The first accounts of ormer reproduction were published by Stephenson (1924) and Crofts (1929). Since then, an abundant literature has been devoted to the reproductive biology of *H. tuberculata* (Girard, 1972; Cochard, 1980; Hayashi, 1980). *Haliotis tuberculata* is dioecious with an equal sex ratio. Maturation of the gonad is mainly related to both photoperiod and temperature; spawning occurs during summer (July–September). The early development of *H. tuberculata* has been described (Koike, 1978) and the technology for mass production of juveniles is controlled (Flassch & Aveline, 1984).

Fecundity, representing the total number of oocytes in the ovary, is usually involved in models of population dynamics. However, for sedentary species like

H. tuberculata, other factors such as spawning behaviour, the sperm density required and fertilization are also important.

In the present study, measurements of the number of gametes shed during induced spawning, observations on spawning behaviour and fertilization experiments for *H. tuberculata* were undertaken. The implications for fishery management are discussed.

MATERIALS AND METHODS

Haliotis tuberculata were collected from the northern coast of Britanny, in the vicinity of Saint-Malo (48°40'N–2°00'W) during June 1984, just prior to the spawning season. The total number of mature oocytes contained in the ovaries of *H. tuberculata* was estimated. After formalin fixation, each gonad was carefully dissected, drained on filter paper and weighed. Subsamples were taken from near the base, mid and apical parts of the ovary and weighed to 0.0001 g. Oocytes were loosened from their follicles by tearing the tissues with glass needles and their number was counted under a dissecting microscope. Estimates of the number of oocytes per whole ovary were then calculated. Because some oocytes may not be released during spawning and may be resorbed, the total number of oocytes is referred to as 'potential fecundity'.

The total number of gametes shed during spawning was estimated by the use of induced-spawning techniques. Mature *H. tuberculata* were selected according to the swelling of their gonad and induced to spawn. They were first left out of water for one hour (Genade *et al.*, 1988) and then isolated in containers filled with exactly 5 l filtered seawater irradiated with UV light (Kikuchi & Uki, 1974a) and heated 3° above ambient temperature to give them a temperature shock (Imai, 1967). Following spawning, ormers were removed and the number of eggs in each container was calculated by counting 10 samples of 1 ml. Sperm concentration was determined by haemocytometer readings on 10 successive samples. The number of ova shed during induced spawning is referred to as 'instantaneous fecundity'.

Fertilizations trials were conducted by combining gamete stocks collected according to the above method. A range of sperm densities was obtained by progressive dilution of a sample collected after spawning. Sperm density in each dilution was measured with a haemocytometer; 10 ml of each sperm suspension was added to an equal volume of water containing 100 to 200 ova spawned synchronously with sperm shedding or less than 30 minutes after sperm. Percentage fertilization was estimated by direct counts of cleaving eggs after 3 hours at ambient temperature (19°C). Spawning behaviour including frequency of pulses of gametes through shell perforation was noted during these experiments.

RESULTS

The number of ripe oocytes in the ovaries (potential fecundity) ranged from 4×10^5 for 20 g *H. tuberculata* to 3.8×10^6 for 160 g (Fig. 8.1). Potential fecundity (NO) of *H. tuberculata* is given by:

$$NO = 2.35\ 10^4\ W - 1.855\ 10^5$$

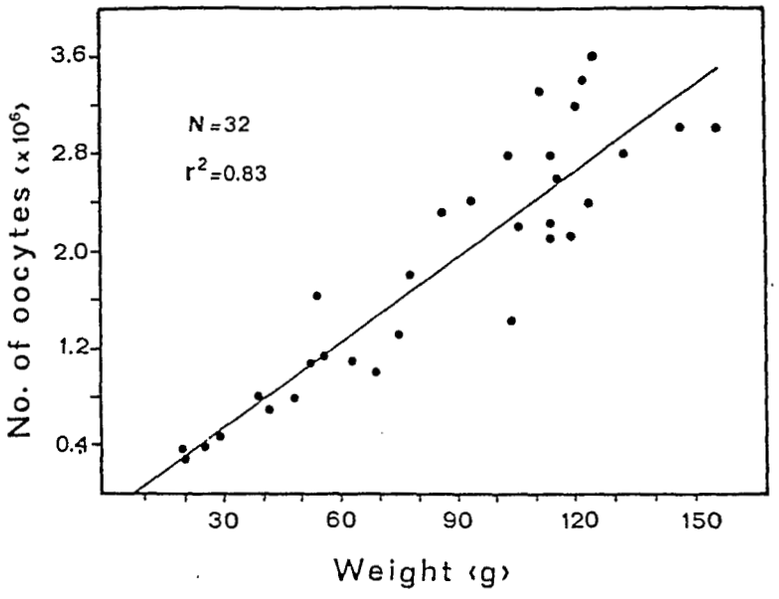

Fig. 8.1 Relationship between the number of oocytes in the ovary and total weight. *N* is the number of observations and r is the correlation coefficient.

where W is the total weight of *H. tuberculata* in g. From this relationship the number of eggs is nil for an individual weight of 8 g corresponding to a shell length of about 40 mm and an age of 3 years (Clavier & Richard, 1986).

The number of eggs shed during induced spawning (instantaneous fecundity) ranged from 2×10^5 to 1.6×10^6 (Fig. 8.2(A)). The values are generally lower than would have been expected from a full ovary. As pointed out by Hayashi (1980), this may be a result of a partial release of the ripe eggs in the ovary. In fact, the potential fecundity line drawn on Fig. 8.2(A) is the upper limit of induced spawning figures.

The relationship between the number of sperm released during induced spawning and the weight of *H. tuberculata* is given in Fig. 8.2(B). The general disposition of experimental points is similar to Fig. 8.2(A) and the number of sperm varies widely for a given body weight. By analogy with females, we should assume that potential fecundity of males is linear with individual weight and corresponds to the upper limit of the induced-spawning values. The total number of sperm in the gonad (NS) may be estimated by:

$$NS = 2.56\ 10^9\ W - 2.3\ 10^{10}$$

where W is the total weight of *H. tuberculata* in g.

During the experiments, the total spawning time varied from 40 to 80 minutes. The frequency of sperm pulses shows a fairly constant pattern for observed *H. tuberculata* (Fig. 8.3). After a short initial phase, sperm were released every 30 to 45 seconds. This frequency decreases progressively at the end of the process and spawning was completed after 30 to 70 pulses according to shell length. As a

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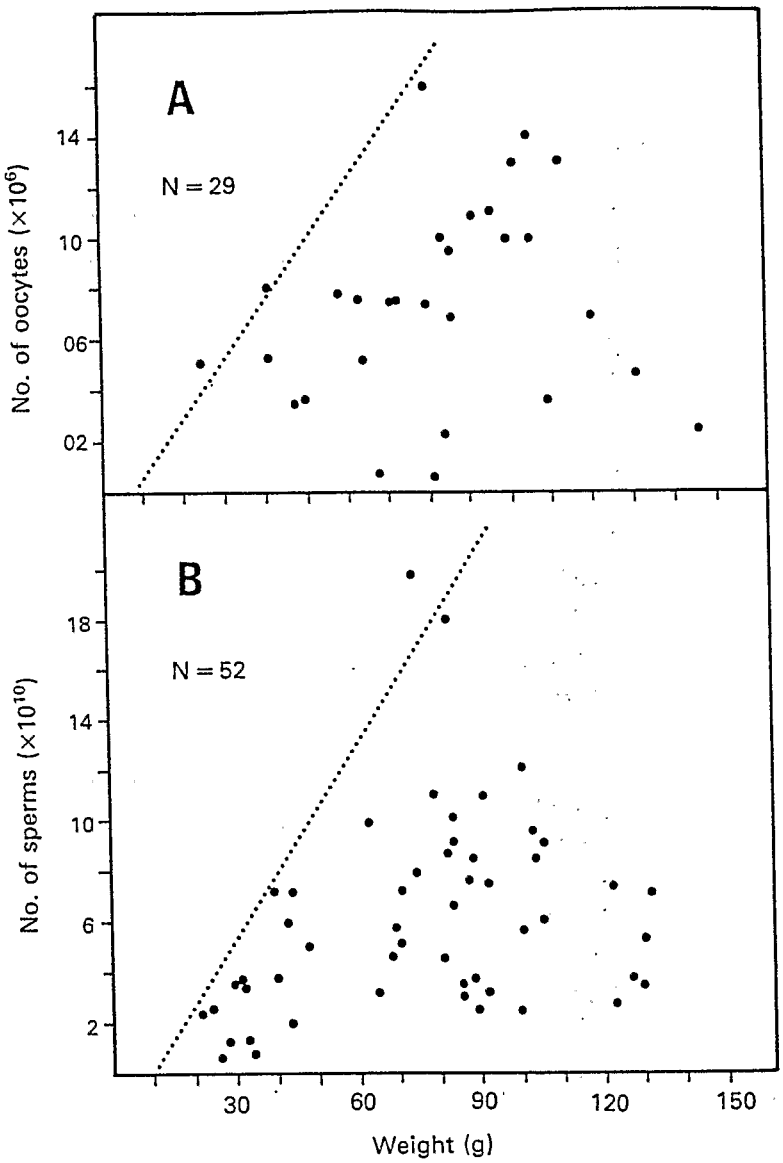

Fig. 8.2 Relationship between numbers of ova (A) and sperm (B) induced to spawn and total weight. Dotted lines represent relationships between the total number of gametes in reproductive glands calculated for females (A) in Fig. 8.1 and assumed for males (B), and the total weight. *N* is the number of observations.

general rule, male *H. tuberculata* release 2 to 3×10^9 spermatozoa every 30 to 45 seconds during a period of about one hour.

The effect of sperm concentration on fertilization was studied on six different male–female pairs (Fig. 8.4). No cleaving eggs were observed at sperm concentrations lower than 1000 cells ml^{-1}. Fertilization rates increased progressively with increasing sperm concentration, but replicate test runs disclosed wide variations.

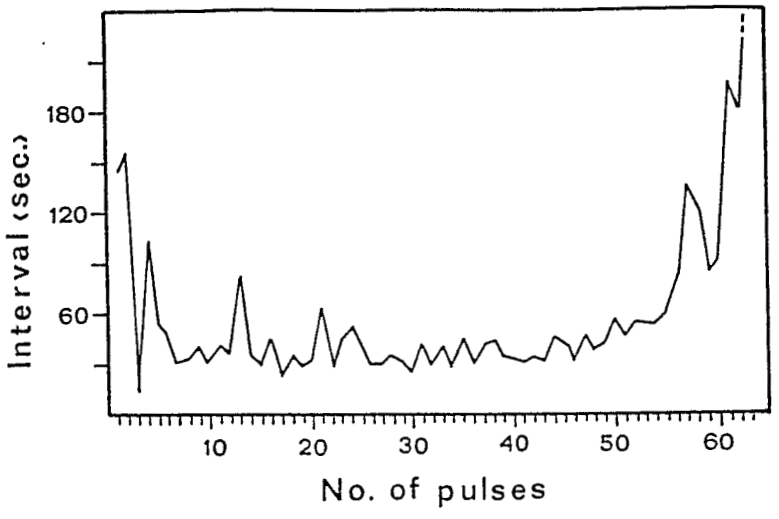

Fig. 8.3 Plot of the time interval between sperm pulses versus number of pulses ordered sequentially during the spawning of an 87 mm *Haliotis tuberculata*.

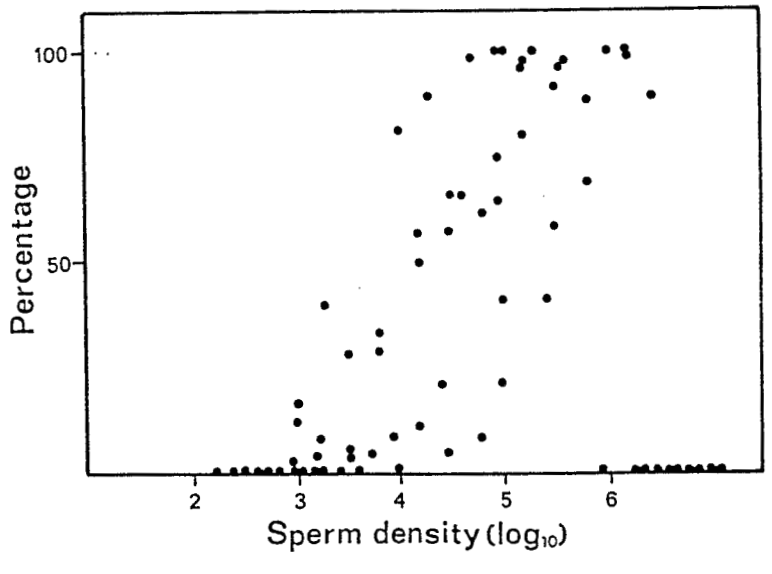

Fig. 8.4 Relation between sperm density and percentage fertilization rate in six male–female pairs.

Fertilization rates of 100% were obtained with concentrations of 10^5 sperm ml^{-1}, although results were more reliable at 10^6 sperm ml^{-1}. Concentrations greater than these levels caused lysis of the vitelline layer with destruction of the ova or abnormal development of embryos.

DISCUSSION

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DISCUSSION

First maturity of *H. tuberculata* at a length of 40 mm is consistent with the observations of Hayashi (1980) on Guernsey populations. A linear relationship between the number of mature eggs and body weight has been reported for other *Haliotis* species (Newman, 1967; Poore, 1973; Kikuchi & Uki, 1975). It corresponds to a power relationship between the number of ripe eggs and the length of the shell (Girard, 1972; Hayashi, 1980). This result may have practical significance in stock management. For example, when potential fecundity is linearly related to biomass, a similar reproductive output may be provided by a low number of old, slow-growing individuals or by a greater number of relatively young specimens with high production. In areas with high recruitment, preservation of old *H. tuberculata* to maintain the propagation of the species (Girard, 1972) is therefore useless from the theoretical point of view.

Fertilization is not effective at all sperm concentrations. In the course of laboratory experiments, concentrations of 10^3 to 10^6 sperm ml^{-1} were required for fertilization and the sperm densities yielding maximum fertilization were between 10^5 and 10^6 sperm ml^{-1}. Similar results have been found on the Japanese abalone *H. discus hannai* Ino by Kikuchi & Uki (1974b). Moreover, a sperm density of 10^6 cells ml^{-1} yielded maximal fertilization among several species of *Haliotis* from the California coast (Leighton & Lewis, 1982).

Like most other abalone, *H. tuberculata* is sedentary and movement does not increase during the spawning season (Clavier & Richard, 1984). This contrasts with the studies of Breen & Atkins (1980) on *H. kamtschatkana* Jonas and of Shepherd (1986) on *H. laevigata* Donovan, who recorded aggregative behaviour of the two species for spawning. If the author's laboratory observations could be transposed to natural grounds, male ormer would release 2 or 3×10^9 sperm every 30 to 45 seconds. Tidal currents are typically strong along the northern coast of Britanny and dilution of this 'fertilization unit' below 10^3 sperm ml^{-1} would occur quickly and at a relatively short distance from the spawning male. Hence, fertilization may be ineffective on beds with low *H. tuberculata* densities. In contrast, on dense *H. tuberculata* grounds gametes from several males could raise the local concentration of sperm and increase the chances of fertilization.

The results of the present study suggest that, in the case of sedentary species like *H. tuberculata*, fecundity is related more to the sperm concentration at spawning than the number of eggs in the ovary. This has implications for stock management of abalone populations. It is generally assumed that the highest fishing mortality rates occur on *Haliotis* aggregations (Newman, 1969; Breen & Atkins, 1980; Shepherd, 1986). The removal of *H. tuberculata* aggregations is likely to have a drastic effect on fertilization and therefore to reduce recruitment (Shepherd, 1986). Management of the fishery of *H. tuberculata* should provide for maintenance of aggregations such that recruitment is not endangered.

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