REPRINT FROM
Calif. Fish and Game, 63(2) : 80-94. 1977.

A STUDY OF THE REPRODUCTIVE BIOLOGY OF THE RED ABALONE, *HALIOTIS RUFESCENS* SWAINSON, NEAR MENDOCINO, CALIFORNIA [1]

ALBERT E. GIORGI [2]
Humboldt State University
Arcata, California 95521

JOHN D. DEMARTINI
Department of Biology
Humboldt State University
Arcata, California 95521

The reproductive cycles of two subtidal populations of the red abalone, *Haliotis rufescens,* were studied at Point Cabrillo Lighthouse Station and Van Damme State Park near Mendocino, California. From June 1972, through March 1974, gametogenesis was monitored histologically. Both populations spawned during spring and early summer. Not all members of either population spawned during a season. Fecundity was estaimated for females ranging in shell lengths 134.00 to 198.5 mm (5.3 to 7.8 inches). The lowest and highest estimates were 619,000 and 12,575,000 ripe oocytes per ovary. The minimum size at sexual maturity was investigated. The smallest male was 84.5 mm (3.3 inches) and the smallest female was 39.5 mm (1.6 inches). Females matured at a smaller size than males. A possible mode of gamete resorption was noted.

INTRODUCTION

The purpose of our study was to determine minimum size at sexual maturity, to measure fecundity, and to monitor histologically the reproductive cycle of two populations of the red abalone, *Haliotis rufescens* Swainson, for 2 years near Mendocino, California.

Early investigators believed that the red abalone spawned during late winter and early spring (Heath 1925, Bonnot 1930, and Croker 1931). Boolootian, Farmanfarmaian and Giese (1962) used a gonad index to detect spawning in a red abalone population at Pacific Grove, California. Their gonad index is the ratio of the cross-sectional area of the gonad, at a fixed location, to the shell length times 100. The index allows for detection of reduction in gonad size during spawning. No definite spawning cycle was detected and ripe gametes were present the year round. Young and DeMartini (1970) detected the presence of mature gametes throughout the year in red abalones near Fort Bragg, California. Additionally, they found necrotic oocytes in females. Shibui (1971) studied red abalone imported to Japan from California and found gonadal maturation optimal at temperatures ranging from 14 to 20 C (57 to 68 F).

Leighton (1974) noted that southern California red abalones spawned in the laboratory every month of the year. Price (1974), using a gonadal bulk index to monitor a natural population of red abalones in southern California, found that spawning occurred in April, with possible minor spawnings in January and September.

---

[1] Accepted October 1976.

[2] Present address: College of Fisheries, Univ. of Washington, Seattle, WA 98195.

Giese (1959) noted that periodic histological examination of gonads over several years is an excellent method for determining the time and duration of reproductive cycles in many marine invertebrates.

METHODS AND MATERIALS

From June 1972 through April 1973, 10 red abalones were collected monthly from a subtidal population at the Point Cabrillo Lighthouse Station, Mendocino, California. In April 1973, sampling of a second population was initiated at Van Damme State Park, Mendocino, California. Subsequently, these two populations will be referred to, respectively, as the Point Cabrillo and Van Damme popula-

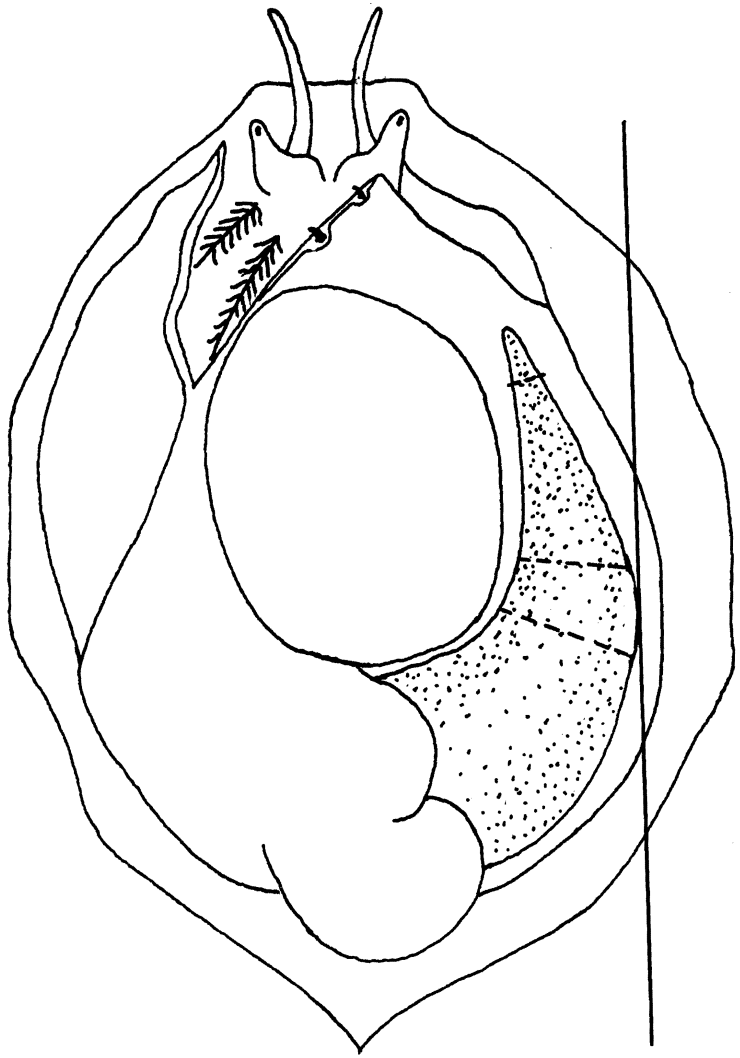

FIGURE 1. *Haliotis rufescens* with shell removed, showing conical appendage (stippled) and sampled areas of conical appendage (broken lines). From Young and DeMartini (1970).

tions. Sampling continued through April 1974. In May 1973, the sample was increased from 10 to 15 abalones per population. Monthly sampling was often interrupted by adverse conditions, especially during winter. Abalones were procured using scuba at depths between 7.5 and 15 m (25 and 50 ft). We collected 321 specimens during this study.

Shell length in millimeters, total weight, shell weight, and shucked body weight in grams, sex, and remarks concerning macroscopic features were recorded for each specimen. From each specimen, two pieces of conical appendage, consisting of digestive gland and surrounding gonad, were excised from the tip and the midportion. The latter section was determined by locating the tangent of the conical appendage parallel to the longitudinal axis of the abalone as done by Young and DeMartini (1970) (Figure 1). Excised pieces were fixed and stored in a mixture of formalin, ethanol, and glacial acetic acid (FAA). Tissue was processed in an Autotechnicon. At least three slides were processed for each piece of gonad and examined histologically.

Ninety-nine animals were collected at Point Cabrillo Lighthouse Station during summer 1974 to determine minimum size at sexual maturity. Shell length, total weight, and shucked weight were recorded for each specimen. The sex was recorded for those specimens displaying gonadal pigmentation, the ovaries green and the testes cream-colored. Shell lengths ranged from 21.5 to 204.5 mm (0.8 to 8.1 inches). The entire conical appendage was removed and fixed for specimens up to approximately 120 mm (4.7 inches). Apical and lateral pieces of gonad were excised from larger specimens and tissues were prepared as previously mentioned. Slides were examined then to assess gametogenic activity.

Thirty-three females were collected at Point Cabrillo for fecundity estimates on December 3, 1973. Twenty-five specimens, a minimum of 134.0 mm (5.3 inches), were used for counting oocytes because smaller specimens had thin ovaries which were not readily separated from the digestive glands. The entire conical appendage was excised and fixed in F.A.A., and subsequently split longitudinally and slashed every few centimeters to assure thorough fixation. After a few days, the F.A.A. was replaced by 70% ethanol. Later, the ovary was dissected from the digestive gland and weighed to the nearest 0.1 g. One piece, weighing approximately 0.03 to 0.06 g, was excised from each of three portions of the gonad, the tip, midportion and base. This method is similar to Newman's (1967). Oocytes were then teased from the trabeculae of each piece with a small coarse paint brush. Next, oocytes from each piece were dispersed into 100 ml of tap water, a procedure similar to Poore's (1973). The beaker and its contents were placed on a magnetic stirring plate. Subsamples of 2 ml were pipetted from the beaker while the liquid was agitated. The subsample was placed in a watch glass and larger oocytes (160 to 250 microns in diameter) were counted using a dissecting microscope. The subsample was then returned to the beaker and two more subsamples were drawn and counted, yielding three counts per piece of excised ovary. Because the variation about the mean for the subsamples was slight, the means were used to calculate the total number of large oocytes in each ovary.

RESULTS AND DISCUSSION

Reproductive Cycle

Histological examination of specimens collected during summer 1972 indicated that part of the Point Cabrillo population spawned during the preceding spring and early summer. Some specimens contained only early gametogenic stages, while others were full of apparently mature gametes. Still other specimens contained both early stages and ripe, residual gametes.

During autumn 1972, some specimens were still full of either spermatozoa or large oocytes (160 to 250 microns). Many of the oocytes were necrotic. By the end of autumn, up to about 90% of the oocytes in a cross-section of ovary would be necrotic, while other specimens contained several gametogenic stages. Testes contained stages from spermatogonia through spermatozoa. Ovaries contained oogonia and a spectrum of oocytes up to 250 microns in diameter. Large oocytes in some of these females were necrotic, and were probably residuals from the preceding spawning.

By winter 1972–73, all specimens contained maximum densities of either spermatozoa or large oocytes. Necrotic oocytes were present in some of the females and the quantities varied individually. Up to about 95% of the oocytes in a cross-section of ovary would be necrotic.

During spring 1973, spawning occurred in both the Point Cabrillo and Van Damme populations. As in spring 1972, only a portion of either population spawned. Of the 19 Point Cabrillo males collected from April 1973 through June 26, 1973, four contained maximum densities of spermatozoa, two lacked spermatozoa and displayed intense proliferation of early spermatogenesis and 15 displayed intense proliferation with few spermatozoa. Of the 33 females inspected during this period, 14 were ripe and the other 19 contained few large oocytes and displayed intense proliferation of small oocytes up to 40 microns. Necrotic oocytes were still present in some females. Van Damme specimens had similar gametogenic conditions.

During the summer and autumn 1973, both populations displayed the same variety of gametogenic events as were noted from the Point Cabrillo specimens in summer and autumn 1972.

By January 1974, all specimens contained maximum densities of either spermatozoa or large oocytes. Additionally, necrotic oocytes were present in some ovaries as noted for winter 1972–73. In March 1974, one female displayed spawning; all others were full of gametes.

Field observations support the histological evidence of spring and early summer spawning. We observed eight males spawning on July 17, 1972. On March 24, 1974, Steven Schultz of California Department of Fish and Game (pers. commun.) observed at least 10 males spawning in approximately 6 m (20 ft) of water at Point Cabrillo. On March 25, 1974, we observed two females spawning at Point Cabrillo at a depth of 6 m (20 ft). However, these two abalones had been tagged and measured for growth the preceding day and the disturbance may have induced spawning. On April 25, 1974, we observed three males spawning in 3.5 m (12 ft) of water at Van Damme State Park. During April 1975, we observed numerous males and one female spawning at Point Cabrillo.

The evidence from histological preparations and field spawning observations indicates that only a portion of the population spawned during the spring and

early summer, a condition not peculiar to the red abalone. In British Columbia, Quayle (1971) found that only a portion of a pinto abalone, *Haliotis kamtschatkana,* population spawned during the spring of several years. Poore (1973) also observed only a portion of a population of *H. iris* spawning during 1969.

Some members of our populations only released a portion of their gametes; and thus, spawned incompletely, as noted for other haliotids (Crofts 1929; Newman 1967; and Poore 1973). The residual gametes from incomplete spawnings could account for the varying quantities of necrotic oocytes observed during the study. A third portion of the population did not spawn at all during a given season resulting in retention of all their gametes. Virtually all unspawned large oocytes were necrotic. These three spawning patterns henceforth will be referred to as types. Type I spawning pattern is defined as complete spawning, Type II as incomplete spawning, and Type III as nonspawning. Histological evidence only allows for diagnosing of a specimen's spawning pattern during the season preceding the sampling date.

Type I Spawning Pattern

The annual reproductive cycle of Type I specimens was classified with modifications into the phases developed for the surf clam, *Spisula solidissima* (Ropes 1968), and for the gaper clam, *Tresus capax,* (Machell and DeMartini 1971).

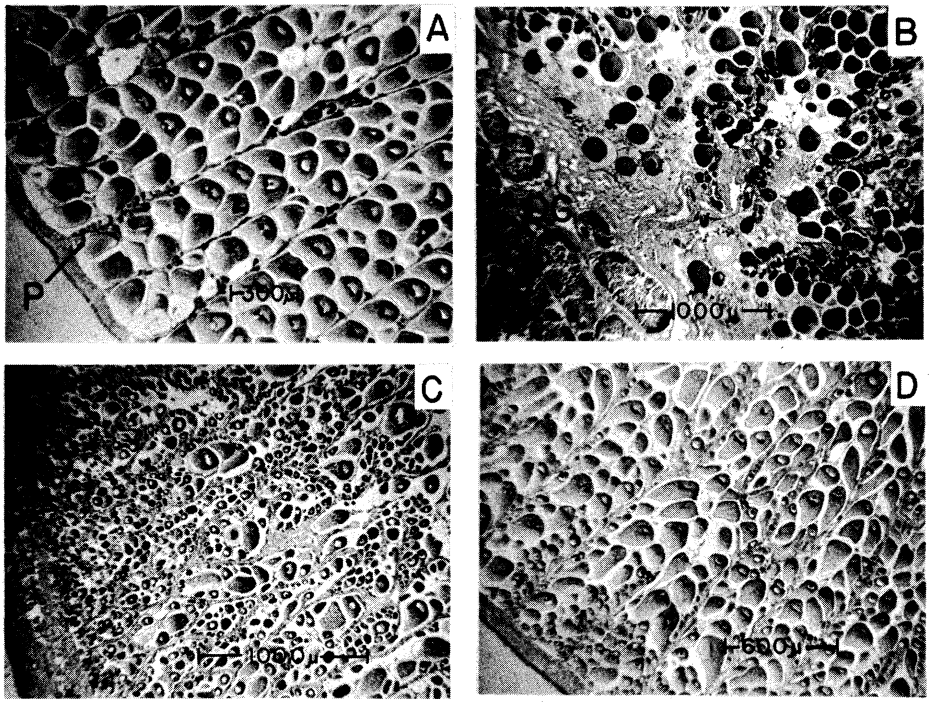

FIGURE 2. A, Ripe ovary of female displaying Type I pattern, collected March 5, 1974. P = proliferation near peripheral gonad wall. B, Partially spawned ovary of a female displaying Type I pattern, collected July 9, 1972. Note the free oocytes near the digestive gland = DG. C, Active ovary of female displaying Type I pattern, collected April 7, 1974. D, Advanced active ovary of female displaying Type I pattern, collected August 3, 1973.

Ripe Phase: An ovary was defined as ripe when virtually all primary oocytes were greater than 160 microns. Oocytes can reach a maximum diameter of about 250 microns. Slight proliferation of small oocytes less than 50 microns was still evident, especially near the peripheral wall of the gonad (Figure 2A). A ripe testis mainly contained spermatozoa. Few early gametogenic stages were present and were restricted to the area immediately surrounding the trabeculae (Figure 3A). Specimens were ripe during the winter with maximum ripeness attained in February.

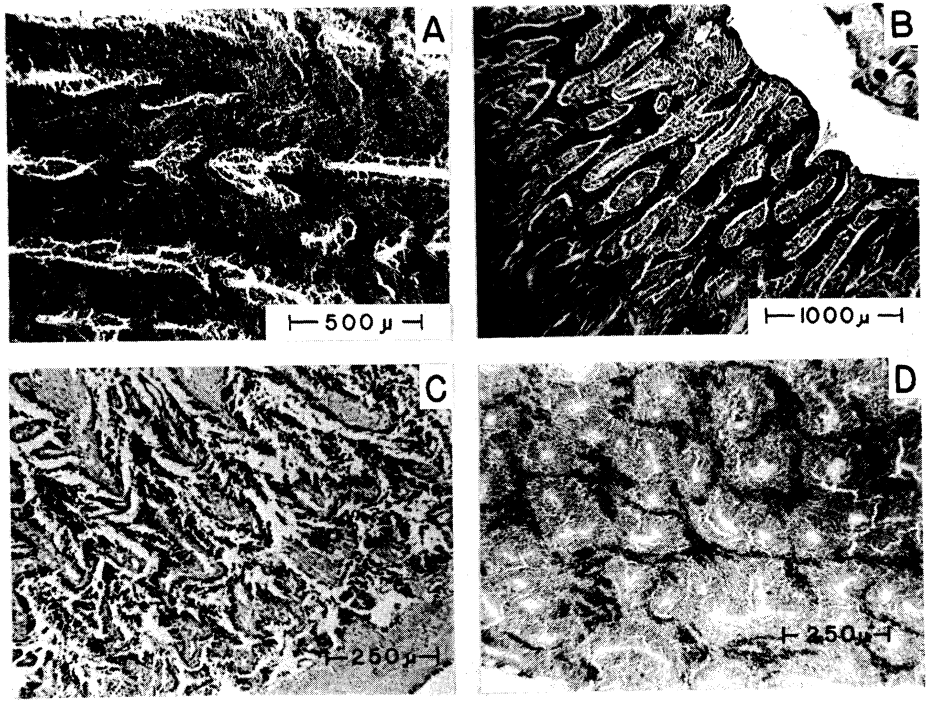

FIGURE 3. A, Ripe testis of male displaying Type I pattern, collected January 30, 1974. Trabeculae are light areas enveloped by a thin band of spermatogenic stages antecedental to spermatozoa. Spermatozoa dominate the remainder of the testis. B, Partially spawned testis of male displaying Type I pattern, collected April 3, 1973. Dark areas contain spermatozoa. C, Spent testis of male displaying Type I pattern, collected April 7, 1973. D, Active testis of male displaying Type I pattern, collected July 19, 1972.

Partially Spawned Phase: The partially spawned phase followed the ripe phase. Partially spawned gonads contained reduced densities of gametes relative to ripe gonads (Figures 2B and 3B). Histologically, partially spawned specimens could not be classified accurately as either Type I or Type II because we could not predict whether the specimen would have released all its gametes had it not been collected (Type I), or if it had finished spawning and was retaining residual, ripe gametes (Type II). The partially spawned condition was evident in specimens collected throughout the spring.

Spent Phase: The spent phase was characterized by a lack of ripe gametes and extremely slight gametogenic activity (Figure 3C). Macroscopically, the gonad was reduced greatly. The spent condition was observed only during spring. Few

spent gonads were observed indicating that few members of the population are Type I or that in most cases gametogenesis is initiated concurrently with or immediately after spawning. Webber and Giese (1969) noted initiation of gametogenesis immediately after spawning in a population of black abalone, *H. cracherodii.*

Active Phase: The active phase, which occurred during summer, is characterized by intense gametogenic activity. Ovaries contained primarily small oocytes less than 50 microns in diameter (Figure 2C). In testes, spermatogonia and primary spermatocytes dominated (Figure 3D). As the active phase progressed into autumn, oocytes continued to develop and increse in size. Later in autumn, ovaries contained a spectrum of oocytes ranging from about 10 to 250 microns in diameter in more or less equal proportions (Figure 2D). Near the end of autumn, large oocytes and spermatozoa were approaching maximum densities characteristic of the ripe phase.

Type II Spawning Pattern

The Type II pattern (incomplete spawning) followed the same annual gametogenic and spawning cycles as the Type I pattern, but differed only by a partial release of gametes. During the summer, intense gametogenic activity indicative of the active phase was evident, but additionally, numbers of large ripe oocytes were still present. The quantity of residual oocytes varied individually. As autumn approached, residual oocytes became necrotic. By winter, there was a mixture of ripe and necrotic oocytes (Figure 4A). There was no evidence of necrosis of residual spermatozoa.

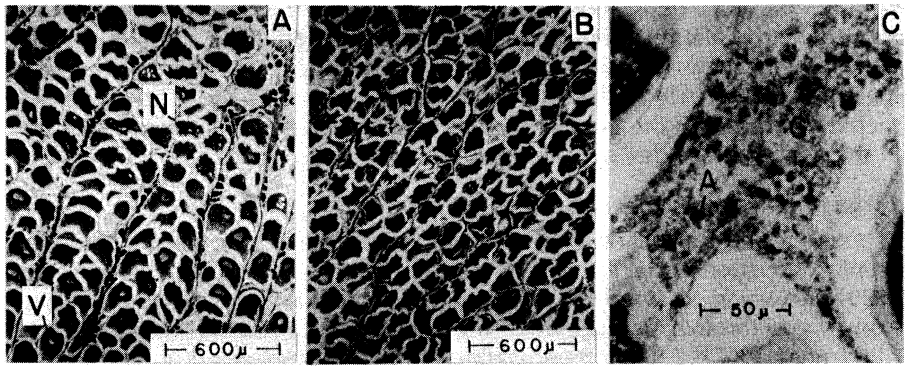

FIGURE 4. A, Ovary of female displaying Type II pattern, collected March 5, 1974. Note presence of necrotic = N and viable = V oocytes. B, Ovary of female displaying Type III pattern, collected January 28, 1973. Virtually all oocytes are necrotic. C, Female collected March 5, 1974. Granular substance = G and associated cells found among necrotic oocytes = A.

Type III Spawning Pattern

Type III specimens, nonspawners, entered the spawning season with ripe gonads but did not spawn. Specimens sampled during summer were still ripe. By late summer, early necrotic stages appeared in the ovaries. No events resembling the active phase were apparent during summer as was the case for Type I and Type II patterns. Early spermatogenic events and transformations from oogonia to primary oocytes were relatively few. Quantities of unspawned

gametes may have inhibited gametogenesis until the residual gametes were either released or reabsorbed. Throughout autumn necrosis became extensive, and by winter, up to about 95% of the large oocytes in a cross-section of ovary would be necrotic in Type III specimens (Figure 4B).

Boolootian, *et al* (1962) postulated year round spawning for a red abalone population near Pacific Grove, California. Young and DeMartini (1970) concurred on this point for red abalones collected near Fort Bragg, California, because ripe gametes were present throughout their monthly samples. Either the Fort Bragg animals did not spawn during their year of study or Young and DeMartini's (1970) sample size was too small to detect the spawning we observed. We examined Young and DeMartini's (1970) histological preparations and found no gonads resembling the partially spawned or spent conditions that we had found in spring. We believe that their specimens did not spawn during their study. Poore (1973) observed that two New Zealand species, *H. iris* and *H. australis,* did not spawn during the 1968–69 season, while they did spawn during the 1967–68 season. But, because Young and DeMartini's (1970) sample size was 10 abalones per month versus our 30 abalones per month, they may have had a sampling error. There are some records in the literature of only a few or of a single animal in a population spawning. Because of this variability among invertebrates, investigators agree that a large sample is much preferred (Giese 1959).

Incompletely spawned gonads (Type II spawning pattern) are not uncommon among other haliotids. Crofts (1929) examined the ormer, *H. tuberculata,* after spawning and noted that gonads lacked marked signs of being spent. Newman (1967) observed incomplete spawning in the Midas abalone, *H. midae,* as did Poore (1973) for a population of *H. iris* in New Zealand. Price (1974) investigated a southern California population of red abalones and found substantial variation about the mean gonadal bulk index during the spawning period. We suggest that this variation may be the result of partially spawned and (or) non-spawning members present in the population which would display little or no reduction in the gonad bulk index over the previous sampling period.

Exogenous Factors Affecting Reproduction

Intensity and fluctuation of water temperature have long been considered dominant exogenous factors affecting invertebrate reproductive cycles (Giese 1959). Spawning occurred in a population of the disc abalone, *H. discus hannai,* from August through October when water temperature was maximum, 20 C (68 F) (Tomita 1967). A French population of the ormer spawned during summer and early autumn, when water temperature was maximum, 17 C (70 F) (Girard 1972). Similarly, red abalone imported to Japan, had optimal gonadal maturation and subsequent spawning between 14 and 20 C (57 and 68 F) (Shibui 1971).

Due to a series of thermograph malfunctions, we did not generate a continuous temperature record during the study. However, our high and low recordings were 7.6 and 13.9 C (46 and 57 F), respectively. Low temperatures occurred during winter and early spring, while higher temperatures occurred during late summer and early fall. Spawning, though often incomplete, did not correlate with high water temperatures. Newman (1967) noted low-intensity spawning in areas of low water temperature fluctuation for the Midas abalone. Annual water temperature fluctuation in our areas may not be great enough to stimulate complete spawning.

Photoperiod, physical disturbance, and food abundance also are known to affect invertebrate reproductive cycles, either independently or in concert (Giese 1959). Kelps *(Alaria, Hedophyllum, Nereocytis)* are the major foods in the diet of adult red abalones found near Mendocino, and are most abundant during summer months. During late fall and winter, there is virtually no available kelp. Abundant summer kelps correlate with intense gamete production. The abundance of kelp at this time apparently provides ample nutrition for both growth and gamete production. A similar correlation between gonad growth and abundant food was noted for two South Australian haliotids, *H. laevigata* and *H. Cyclobates* (Shepherd and Laws 1974).

Necrosis

Necrotic oocytes occurred in some ovaries in all monthly samples. Necrosis was first noted in the red abalone by Young and DeMartini (1970). They observed that the nucleus became eosinophilic, the nuclear membrane then broke down and numbers of eosinophilic vacuoles appeared in the cytoplasm, and the plasma membrane convoluted and eventually ruptured. Typically, only oocytes greater than 150 microns were necrotic. The number of necrotic oocytes present is a direct result of the spawning pattern followed the preceding season. Some winter specimens contained no necrotic oocytes (Type I), while in others, necrotic oocytes were present in varying amounts (Type II) to the point where virtually all large oocytes were necrotic (Type III). We believe that necrotic oocytes were autolysing residual gametes. Observations by Arthur Giese (pers. commun.) support our assessment. He noted degenerating mature gametes in abalones late in the breeding season and believes that degeneration removes unspawned gametes. He observed less intense oocyte degeneration than we observed. The occurrence of necrotic oocytes is not limited to haliotids. Harvey (1956) found some ovaries of the sea urchin, *Arbacia punctulata,* full of both degenerate and abnormal eggs which had not been spawned the previous season. Caddy (1967) observed autolysing eggs in spent ovaries of the bivalve *Macoma balthica.* In gaper clams, Machell and DeMartini (1971) observed cytolysis of residual oocytes in spent ovaries and the presence of leucocytes in association with the necrotic oocytes. In our specimens, a yellowish staining granular substance appeared in the lumen in areas of advanced necrosis. A distinct cell type appeared among the granules and is probably associated with them (Figure 4C). Granules and these associated cells appeared not only in the ovarian lumen, but also in the digestive gland and the wall separating the digestive gland from the gonad, leading us to believe that the associated cells are resorptive. Granules and these cells were sparse in ovaries containing large numbers of viable oocytes. However, the quantities of necrotic oocytes, granules, and associated cells increased concomitantly. Neither the granules nor associated cells were observed within the cytoplasm of unruptured oocytes. The granules and associated cells were noted in the testes, but not to the extent that they appeared in ovaries. The term "leucocyte" may categorize these cells associated with the granules, but we refrain from applying the term here since the terminology and criteria used to define and classify invertebrate leucocytes can be broad and confusing (Cheney 1971).

Sex Ratio

Females of gonorchoristic molluscan species tend to be more numerous than males and may become even more numerous as the increasing population age (Fretter and Graham 1964). They postulated that this may be a result of the early death of males. Females outnumbered males in the Point Cabrillo population, but not in the Van Damme population. Two hundred sixty-nine mature specimens (109 males and 160 females) were collected at Point Cabrillo and 115 (56 males and 59 females) at Van Damme for determining a sex ratio. The hypothesis that the sex ratio was 1:1 was tested for each population. A Chi-square value of 9.66 was calculated for Point Cabrillo while Van Damme had a value of .0781 (χ^2 p.05, 1 d.f. = 3.841). Therefore, the hypothesis was rejected for Point Cabrillo and accepted for Van Damme. The degree of human predation certainly has a significant effect on the age class structure of these two populations. For years the red abalone at Van Damme have been heavily fished by sportsmen, consequently, the larger, older individuals are constantly being harvested. However, the Point Cabrillo population has been closed to fishermen for many years, possibly allowing a natural age class structure and sex ratio to develop as Fretter and Graham (1964) note for populations comprised of older individuals.

Minimum Size at Sexual Maturity

Unlike Newman's (1967) study, where only macroscopic coloration of the gonad was used to indicate sexual maturity, each of our specimens was inspected histologically. We define a sexually mature specimen as one having either spermatozoa or primary oocytes.

All specimens in size class 100.0 to 125.0 mm (3.9 to 4.9 inches) were sexually mature and females mature at smaller sizes than males (Table 1). The smallest mature female was 39.5 mm (1.6 inches), while the smallest male was 84.5 mm (3.3 inches). If both sexes have the same growth rates, then females mature earlier than males. All specimens with shucked weights greater than 100.0 g (0.2 lb) were sexually mature (Table 2).

TABLE 1. Shell Length at Sexual Maturity and Frequency of Occurrence of Male and Female Red Abalones Collected on June 12, 26 and July 26, 1973, at Point Cabrillo Lighthouse Station.

Length classes (mm)	*Number of specimens*	*Number sexually mature*	*Number males*	*Number females*	*Total % sexually mature*
0 – 25.0	2	0	–	0	–
25.1– 50.0	8	1	–	1*	12.5
50.1–75.0	14	8	–	8*	57.2
75.1–100.0	14	10	2	8*	71.5
100.1–125.0	10	10	7	3*	100.0
125.1–150.0	20	20	11	9**	100.0
150.1–175.0	8	8	2	6	100.0
175.1–	23	23	11	12	100.0
Total	99	80	33	47	

* Size classes where all oocytes were less than 50 microns.

** Size class where some specimens contained all oocytes less than 50 microns and other specimens contained oocytes both greater than and less than 50 microns.

TABLE 2. Shucked Weight at Sexual Maturity and Frequency of Occurrence of Male and Female Red Abalones Collected on June 12, 26 and July 26, 1973, at Point Cabrillo Lighthouse Station.

Shucked weight (g)	*Number of specimens*	*Number sexually mature*	*Number males*	*Number females*	*Total % sexually mature*
0 100.0	36	17	3	14	47.2
100.1–200.0	12	12	5	7	100.0
200.1–300.0	16	16	7	9	100.0
300.1–400.0	5	5	5	0	100.0
400.1–500.0	1	1	1	0	100.0
500.1–600.0	5	5	1	4	100.0
600.1–700.0	6	6	2	4	100.0
700.1–	18	18	9	9	100.0
Total	99	80	33	47	

Typically, 50 microns was the maximum diameter of oocytes present in specimens smaller than 132.0 mm (5.2 inches). Specimens greater than 132.0 mm usually contained some oocytes up to 100 microns. Because the abalones were collected in June and July when oocytes would not be maximum size, the question arises, would these small oocytes mature by the following winter? In an attempt to answer this question a small sample of 10 abalones ranging in length from 99.5 to 139.5 mm (3.9 to 5.5 inches) was collected on December 3, 1973 (Table 3). Pieces of gonad were removed and oocytes were measured with an ocular micrometer. Food availability and growth are apparently greatest from mid-spring through early fall. Thus, these winter specimens were probably shorter during the previous June. Based on our unpublished growth studies, the 99.5 mm specimen (Table 3), which contained no oocytes larger than 160

TABLE 3. Length, Whole Weight, Shucked Weight and Occurrence of Ripe Oocytes Greater Than or Equal to 160 Microns in Small Female Red Abalones Collected on December 3, 1973, at Point Cabrillo Lighthouse Station.

Length (mm)	*Whole weight (g)*	*Shucked weight (g)*	*Occurrence of ripe oocytes*
99.5	155.8	114.8	–
112.0	284.1	207.3	+
112.5	326.1	234.1	+
120.0	368.4	257.6	+
123.5	291.3	223.3	+
125.0	317.8	210.4	+
134.0	424.6	301.4	+
136.0	409.2	296.9	+
138.5	557.1	431.1	+
139.5	494.6	343.9	+

microns, may well have been 80.0 to 95.0 mm (3.2 to 3.7 inches) long in June. If so, it probably had oocytes no larger than 50 microns (Table 1) during the previous summer. Two specimens, 112.0 and 112.5 mm (4.4 inches) long contained oocytes greater than 160 microns, with many near 250 microns (Table 3). During the summer months, these abalones were probably 95.0 to 108.0 mm (3.7 to 4.3 inches). Abalones of this size range, examined during the summer, contained only oocytes smaller than or equal to 50 microns (Table 1), indicating that some females containing only oocytes smaller than 50 microns during the

summer may contribute ripe oocytes to the following season. However, none were observed spawning in the field. Larger females, 100.0 to 140.0 mm (3.9 to 5.5 inches), collected during the summer, contained very few oocytes greater than 160 microns. The lack of ripe residual oocytes from previous seasons indicates either previous spawning activity or resorption of the residual oocytes. Resorption probably occurs after necrotic oocytes have lysed. Because virtually no necrotic oocytes were evident in specimens less than 150 mm (5.9 inches), resorption seems unlikely. These small abalone which do spawn can be classified as displaying the Type I pattern.

The presence of only small oocytes during the summer and large oocytes during the winter in abalone, less than 140 mm (5.5 inches) further supports the hypothesis of the annual gametogenic cycle, i.e., ripeness is attained during the winter.

Gonadal pigmentation was always associated with the presence of either spermatozoa or oocytes, but gametes can be present in the absence of pigmentation. Nine of the 24 specimens less than 75.0 mm (3.0 inches) contained gametes when examined histologically (Table 4). Only two of the nine were pigmented. The testes of the ormer, *H. tuberculata,* were unrecognizable until males were 4 cm (1.6 inches) long, but spermatozoa were obtained from specimens 2.8 cm (1.1 inches) long; spawning probably first occurred in animals 2 to 3 years old (Stephenson 1924).

TABLE 4. Shell Length at Sexual Maturity Comparing Frequency of External Gonad Pigmentation with Occurrence of Spermatozoa or Oocytes Within Red Abalone Gonads Collected June 12, 26 and July 26, 1973, at Point Cabrillo Lighthouse Station.

Length classes (mm)	*Number of specimens*	*Number of specimens displaying macroscopic gonadal pigmentation*	*Number of specimens containing spermatozoa or oocytes*
0 – 25.0	2	0	0
25.1– 50.0	8	0	1
50.1– 75.0	14	2	8
75.1–100.0	14	5	10
100.1–125.0	10	10	10
125.1–150.0	19	19	19
150.1–175.0	8	8	8
175.1–204.5	23	23	23

We observed no histological evidence of hermaphroditism. Girard (1972) noted successive hermaphroditism in a specimen of the ormer. Murayama (1935) observed a hermaphroditic specimen of the Japanese species, *H. gigantea.*

Fecundity

As found by Newman (1967) for the Midas abalone, histological inspection prior to counting indicated that there were two broad size classes of primary oocytes. The larger oocytes, greater than 160 microns, were used for determining fecundity because these would ripen by the next spring. Additionally, precise counting of the smaller oocytes was impractical due to the smallness and adherence to the germinal epithelium.

Eight specimens with nearly the same shucked weight, approximately 800.0 g (1.8 lb) were chosen for fecundity estimates. Densities in oocytes per gram of ovary were determined for each of the three different locations on each

specimen (Table 5). The hypothesis that mean oocyte counts of different gonad locations was the same was tested by a one-way analysis of variance. An F value of 2.21 was calculated (F p.05, 2 and 21 d.f. = 3.47). Therefore, any position on the ovary can be sampled to determine total oocyte counts. We used pieces from the mid-portion for fecundity estimates. Fecundity estimates ranged from 619,000 to 12,575,000 oocytes per ovary (Table 5). Fecundity can vary substantially between specimens of the same length (Table 5). Such variability may be due to errors in technique while weighing the smaller pieces or making actual counts, but it is more likely due to individual variation. Specimens were collected in late autumn, and based on our observations of the reproductive cycle, we did not expect ovaries to contain maximum densities of large oocytes until the following winter. Thus, all specimens would not be expected to contain the same percentage of large oocytes because many were still growing. A more accurate estimate of fecundity could have been obtained by sampling just prior to spawning. Thus, our figures probably underestimate the actual fecundity.

TABLE 5. Fecundity Estimates Using Oocytes Greater Than or Equal to Approximately 160 Microns, for Female Red Abalones Collected December 3, 1973, at Point Cabrillo Lighthouse Station.

Shell length (mm)	*Body weight (g)*	*Gonad weight (g)*	*Gonad sample weight (g)*			*Oocyte counts*			*Oocytes per gram using mid-portion*	*Fecundity × 10⁶*
			Tip	*Midportion*	*Base*	*Tip*	*Midportion*	*Base*		
134.0	301.4	10.6	.039	.045	.056	4950	4340	4810	96444	1.0
136.0	296.9	7.6	.105	.043	.042	11620	3500	2710	81395	0.6
138.5	431.1	14.5	.048	.060	.048	4120	4310	4070	71833	1.1
143.5	405.1	9.6	.048	.056	.051	4590	4750	4000	84821	0.8
146.5	428.2	11.3	.064	.071	.083	4920	5110	4340	71971	0.8
148.5	417.9	17.0	.028	.059	.040	2360	3850	3910	65254	1.1
161.5	437.4	22.8	.054	.038	.040	6590	4350	3010	114473	2.6
162.0	701.2	50.6	.038	.052	.042	5190	5490	4190	105576	5.3
168.5	688.3	40.8	.041	.059	.064	4710	5860	6220	99322	4.1
169.5	652.0	55.0	.039	.055	.055	5100	5760	5660	104727	5.8
171.0	695.9	30.4	.035	.040	.039	4350	4360	4740	109000	3.3
171.5	786.9	22.5	.018	.044	.036	3150	5170	3380	117500	2.6
171.5	744.4	44.2	.039	.038	.045	4420	5350	4410	140789	6.2
172.5	580.6	32.7	.059	.061	.049	6400	5840	5040	95737	3.1
176.5	639.1	56.1	.043	.042	.062	4950	6360	6220	151428	8.5
180.5	745.6	30.2	.026	.059	.067	3750	7870	7600	133389	4.0
182.5	822.9	67.7	.039	.040	.038	5320	4330	3610	108250	7.3
185.0	836.4	48.2	.034	.045	.029	5120	3740	3700	83111	4.0
185.0	770.1	86.3	.029	.037	.044	2600	2800	3810	75675	6.5
190.5	1042.1	65.4	.044	.022	.037	4850	4230	2920	192272	12.6
192.0	887.1	60.4	.045	.061	.042	4850	6460	4840	105901	6.4
192.0	806.8	49.3	.049	.038	.071	5900	6920	6020	182105	9.0
198.0	940.9	47.1	.020	024	.023	4150	2350	3960	97916	4.6
198.5	1008.6	52.3	.038	.028	.046	4400	1910	3180	68214	3.6
198.5	1066.1	76.0	.025	.058	.044	4230	6550	4550	112931	8.6

Another factor which affects the true fecundity is the presence of necrotic oocytes. While counting, necrotic oocytes were not distinguishable from viable oocytes. Necrotic oocytes could only be detected in histological preparations. Thus, there were no means to determine accurately the percentages of necrotic oocytes per ovary.

Gonads of specimens less than 125.0 mm (4.9 inches) were so thin that accurate estimates of fecundity were not determined. Based on fecundity estimates made for larger females, we estimate that females 100.0 to 125.0 mm (3.9 to 4.9 inches) can have at least tens of thousands, if not hundreds of thousands of oocytes, at the upper end of this size range. Even though the numbers of gametes, particularly of oocytes, is relatively low for these smaller specimens, very few necrotic oocytes were observed in histologic preparations. However, in some females greater than 150.0 mm (5.9 inches), about 75 to 95% of the large oocytes viewed in a cross-section of ovary were necrotic. Consequently, these smaller abalones are contributing substantial quantities of viable oocytes to the gametic pool.

ACKNOWLEDGMENTS

This work is a result of research sponsored by Office of Sea Grant, NOAA, U.S. Department of Commerce, under Humboldt State University grant numbers, 04-3-158-26 and 04-4-158-10. We extend or appreciation to the California Department of Fish and Game and Ronald Warner for the use of their Autotechnicon.

REFERENCES

Bonnot, Paul. 1930. Abalones in California. Calif. Fish & Game., 16(1): 15–23.

Boolootian, Richard A., A. Farmanfarmaian, and A.C. Giese. 1962. On the reproductive cycle and breeding habits of two western species of *Haliotis*. Biol. Bull., 122(2):183–193.

Caddy, J. F. 1967. Maturation of gametes and spawning in *Macoma balthica* L. Can. J. Zool., 45:955–965.

Cheney, Daniel P. 1971. A summary of invertebrate leucocyte morphology with emphasis on blood elements of the Manila clam, *Tapes semidecussata*. Biol. Bull., 140(3):353–368.

Crofts, Doris R. 1929. *Haliotis*. Liverpool Mar. Biol. Comm. Mem., 29:1–174.

Croker, Richard S. 1931. Abalones. Calif. Div. Fish and Game, Fish Bull., (30):58–72.

Fretter, V., and A. Graham. 1964. Reproduction, in K.M. Wilbur and C.M. Yonge (Ed.), Physiology of Mollusca, Vol. 1. Academic Press, New York. 473 p.

Giese, Arthur C. 1959. Comparative physiology: Annual reproductive cycles of marine invertebrates. Ann Rev. Physiol., 21:547–576.

Girard, Annie. 1972. La reproduction de l'ormeau *Haliotis tuberculata* L. Rev. Trav. Inst. Peches Marit., 36(2):163–184.

Harvey, E. B. 1956. The American *Arbacia* and Other Sea Urchins. Princeton University Press. London. 298 p.

Heath, H. 1925. The abalone question. Calif. Fish & Game., 11(3): 138–139.

Leighton, David L. 1974. The influence of temperature on larval and juvenile growth in three species of southern California abalones. Fish. Bull., 72(4):1137–1145.

Machell, John R., and John D. DeMartini. 1971. An annual reproductive cycle of the gaper clam, *Tresus capax* (Gould), in south Humboldt Bay, California, Calif. Fish & Game., 57(4):274–282.

Murayama, S. 1935. On the development of the Japanese abalone, *Haliotis gigantea*. Coll. Agric. Imp. Univ. Tokyo., J., 13:227–233.

Newman, C. G. 1967. Reproduction of the South African abalone, *Haliotis midae*. S. Afr., Div. of Sea Fish, Invest. Rep., 64:1–24.

Price, Pamela. 1974. Aspects of the reproductive cycle of the red abalone, *Haliotis rufescens*. Masters thesis, San Diego State Univ. 64 p.

Poore, Gary C. B. 1973. Ecology of New Zealand abalones, *Haliotis* species (Mollusca: Gastropoda). 4. Reproduction. New Zeal. J. Mar. Freshwat. Res., 7(1,2):67–84.

Quayle, D. B. 1971. Growth, morphometry and breeding in the British Columbia abalone (*Haliotis kamtschatkana* Jones). Can., Fish. Res. Board, Tech. Rep., No. 279:1–84.

Ropes, John W. 1968. Reproductive cycle of the surf clam, *Spisula solidissima*, in offshore New Jersey. Biol. Bull., 135(2):349–365.

Shepherd, S. A., and Helene M. Laws. 1974. Studies on South Australian abalone (genus *Haliotis*) II. reproduction of five species. Aust. J. Mar. Freshwat. Res., 25:49–62.

Shibui, Tadashi. 1971. Studies on the transplantation of red abalone and its growth and development. Jap. Soc. Sci. Fish., Bull., 37(12):1168–1172.

Stephenson, T. A. 1924. Notes on *Haliotis tuberculata*. U.K., Mar. Biol. Ass., J., 8(2):480–495.

Tomita, Kyoji. 1967. The maturation of the ovaries of the abalone, *Haliotis discus hannai* Ino, in Rebun Island, Hokkaido, Japan. Hokkaido Fish. Exp. Sta., Rep., 7:1–7.

Webber, H. H., and A. C. Giese. 1969. Reproductive cycle and gametogenesis in the black abalone *Haliotis cracherodii* (Gastropoda: Prosobranchiata). Mar. Biol., 4:152–159.

Young, James S., and John D. DeMartini. 1970. The reproductive cycle, gonadal histology and gametogenesis of the red abalone, *Haliotis rufescens* (Swainson). Calif. Fish & Game., 56(4):298–309.

Δ75712—800 3-77 600 OSP