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SIZE SPECIFIC FECUNDITY OF RED ABALONE (*HALIOTIS RUFESCENS*): EVIDENCE FOR REPRODUCTIVE SENESCENCE?

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ABSTRACT The fecundity of wild red abalone, *Haliotis rufescens*, was examined during four reproductive seasons (2000-2003) in northern California. A broad size range of abalone were sampled (n = 425) from Van Damme State Park and the Point Arena area. Sexual maturity was defined as the presence of sperm or mature oocytes 170–190 μm in diameter, with a jelly coat, detached from the trabeculae in the gonad. Histologic examination revealed that abalone <50 mm in shell length had not yet sexually differentiated and that 50% of the females from 105–130 mm and the males 75–95 mm had mature gametes while all larger animals were mature. Fecundity, as measured by an estimate of the number of mature eggs per female (X), increased exponentially with increasing shell length (Y) until the peak at 215 mm in shell length after which mature egg number began to decline. The largest female 260 mm (10.24 inches) had >80% necrotic eggs. The data were fit to a non-linear Gaussian curve with 3 parameters;

$$(Y) = Ae^{-(X-\mu)^2/2\sigma^2}$$

the maximum productivity (A = 2,850,000 eggs y^{-1}), size at maximum productivity (μ = 215 mm), and standard deviation (σ = 38 mm) of the distribution of maximum productivity versus size. We conclude that whereas large females in excess of 215 mm in shell length undergo some senescence (decline in egg production), these females could potentially contribute as much to reproduction as the mid-size (130–215 mm) females. This suggests that management strategies that protect large females such as marine protected areas or *de facto* reserves will help maintain egg production and that more work is needed to better understand the relationship between female size and egg necrosis.

KEY WORDS: abalone reproduction, *Haliotis rufescens*, size at maturity, necrotic eggs, molluscs, northern California

INTRODUCTION

A basic understanding of reproduction and other vital rates for red abalone, *Haliotis rufescens* (Swainson 1822), populations is necessary for both ecologic studies and fishery management of wild populations. Management strategies such as minimum legal sizes depend on reproduction occurring prior to the onset of fishing. Knowledge of size specific fecundity and size at maturity can be used in size-structured models to examine the population dynamics of wild stocks. Whether the largest oldest females contribute to reproduction, undergo partial or complete reproductive senescence has important implications for population dynamics and management.

Red abalone populations in northern California support an important recreational fishery. Unlike the southern abalone fishery, which was closed in 1996 following intensive fishing (Dugan & Davis 1993, Karpov et al. 2000), the northern fishery is very active with landings estimates ranging from 400,000 to 700,000 red abalone taken per year (CDFG unpubl data). This northern fishery is unique in several ways (1) the use of SCUBA and commercial fishing has been prohibited for more than 40 years; (2) there are few access points along the rugged coastline; and (3) there are long periods of rough ocean conditions. The fishery in the north with an estimated 40,000 fishers is also managed using a combination of a minimum size limit (178 mm), season closures (December to March and July), daily (3/day) and yearly bag limits (24/year), and closed areas. The fishery generates a yearly average of $13.2 million (1985–1989) in tourism revenue to northern coastal communities (CDFG 1997). As with many fisheries, the recreational abalone fishery highly prizes large trophy animals.

Previous abalone reproduction studies have identified a number of important features associated with wild red abalone in northern California. First, there may be a difference in the size at maturity between males and females (Giorgi & DeMartini 1977); second, red abalone are capable of being highly fecund producing more than 12 million eggs (Giorgi & DeMartini 1977); and third, necrotic eggs have been found in mature females (Young & DeMartini 1970, Giorgi & DeMartini 1977). Laboratory conditioning (feeding kelp) has been shown to reduce the size at first maturity and increase estimates of fecundity by 260%, relative to wild abalone (Ault 1985). These results suggest that reproduction studies based on laboratory (or aquaculture) reared red abalone may not be relevant for wild populations. It is unknown whether the largest females have more necrotic eggs suggesting the possibility of reproductive senescence, as has been found in some other mollusks (Downing et al. 1993).

Red abalone fecundity and size at maturity was investigated for wild animals in northern California. Red abalone populations are centered along 480 km of rocky coastline dominated by bull kelp, *Nereocystis*, in Sonoma and Mendocino Counties north of San Francisco. Samples of red abalone were collected from Van Damme State Park (n = 393) over 4 years (2000–2003) and from the Point Arena Abalone Derby (n = 32) in 2000 and 2001. For each abalone, gonad volume was determined and samples of gonad tissue were prepared for histologic assessment of reproductive condition. Histologic evaluations were conducted to determine the maturation stage of the ovaries and testes. The potential fecundity of each female was estimated by multiplying estimated gonad volume by the mean number of mature eggs enumerated per slide excluding the necrotic eggs. We discuss the relationship between abalone size, and fecundity as well as reproductive senescence and it's implications for the ecology and management of red abalone populations in northern California.

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MATERIALS AND METHODS

Collections

A total of 393 red abalone ranging in shell size from 29–224 mm were collected at Van Damme State Park, CA (lat. 39°16′08″N, long. 123°47′58″W) with 137 in April 2000, 71 in January 2001, 62 in February 2002, 123 in January 2003, and 8 in September 2003 (Fig. 1). Sublegal red abalone ranged in size from 29–224 mm in shell length from Van Damme State Park and 212–260 mm from the Point Arena Abalone Derby. Red abalone were collected using SCUBA from depths ranging between 5 and 15m.

The fecundity of the smallest animals (<150 mm) was examined using abalone collected in January and September 2003. The fecundity of the largest red abalone was examined by sampling at the annual Point Arena Derby where recreational fishers skin dive (no SCUBA) for the largest abalone from Sonoma or Mendocino County. The Derby was held August 5, 2000 (n = 18), and August 4, 2001 (n = 14). Data were not included from the Derby in August 2002, because only three abalone were entered. The Derby was not held in 2003.

Laboratory Dissection and Preparation

All animals were weighed and the length of the shell was measured then, the foot and organs were detached from the shell (shucked) and weighed. Sex was determined by visual examination of the gonad and later confirmed histologically. Mature female gonad tissue appears dark green in color whereas the male gonad is tan. The length and width of the conical gonadal appendage, including the inner digestive gland core was measured. Slices were made half way down the appendage and the height and width of the gonad/digestive cone and the height and width of the inner core of the digestive gland were measured (Fig. 2). The digestive gland is dark brown in color. Gonad dimensions for animals <125 mm shell length were measured microscopically with an ocular micrometer. Gonad volume was estimated by assuming that the digestive gland and gonad were cone shaped. The volume of the inner digestive gland cone was subtracted from the total cone volume to yield the volume of the outer gonad cone as described by Tutschulte (1976), and Tutschulte and Connell (1985). The gonad index was defined as gonad volume *100/abalone body weight.

Samples of the gonad were taken for histologic preparation from the mid-section. All gonad samples were fixed in invertebrate Davidson's solution (a formalin based fixative) (Shaw & Battle 1957) for 24 hours, then transferred to 70% ethanol. Once in alcohol the tissues were processed for paraffin histology. Deparaffinized 5-μm sections were stained with hematoxylin and eosin (Luna 1968), and mounted on slides for examination using light microscopy. Not all samples had enough gonad tissue to score and some abalone tissue sections were not quantifiable and so we report the histologic results from 86 abalone in April 2000, 62 from January 2001, 62 from February 2002 and 123 from 2003.

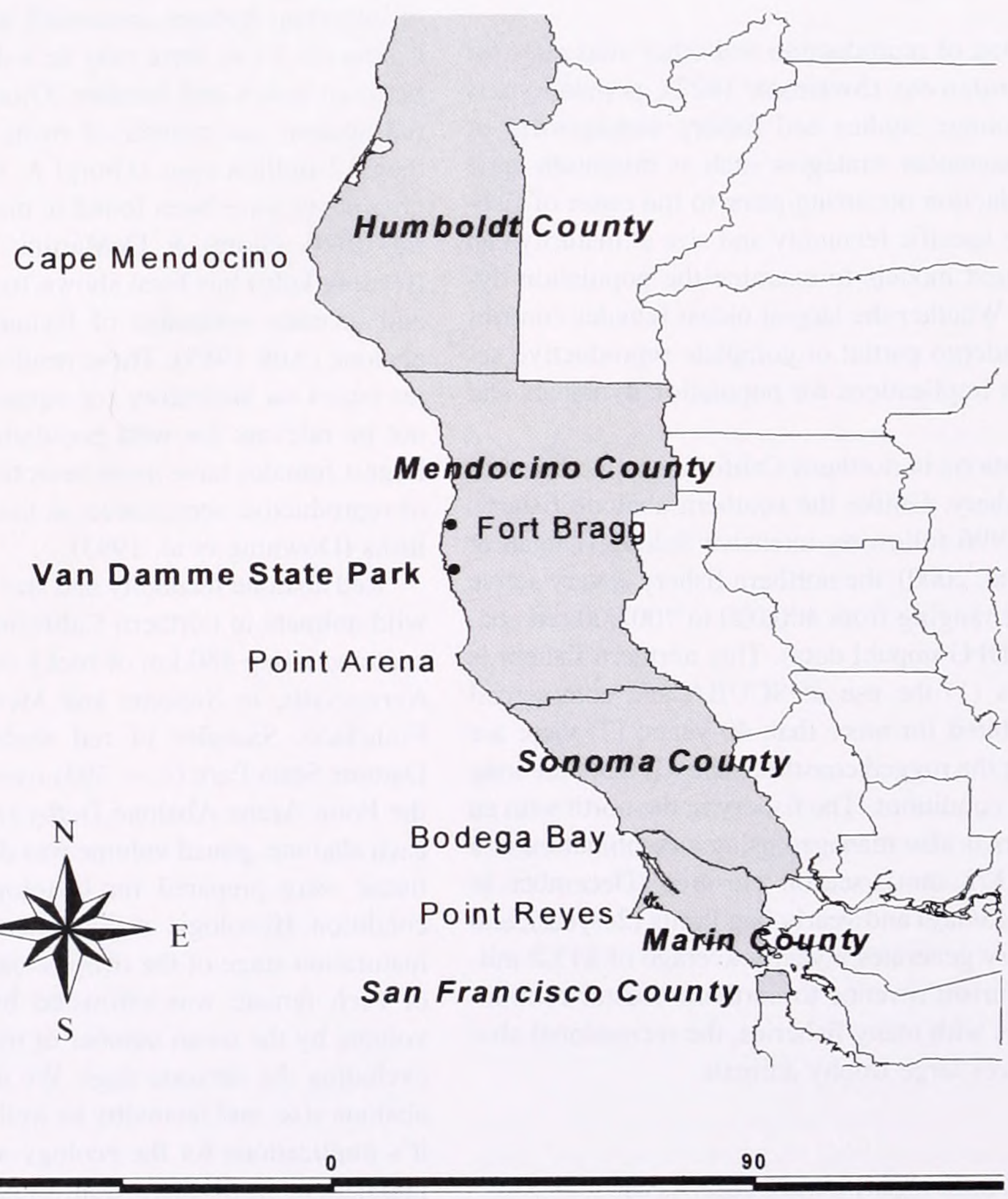

Figure 1. Map of northern California showing Van Damme State Park and Point Arena where red abalone were collected for this study.

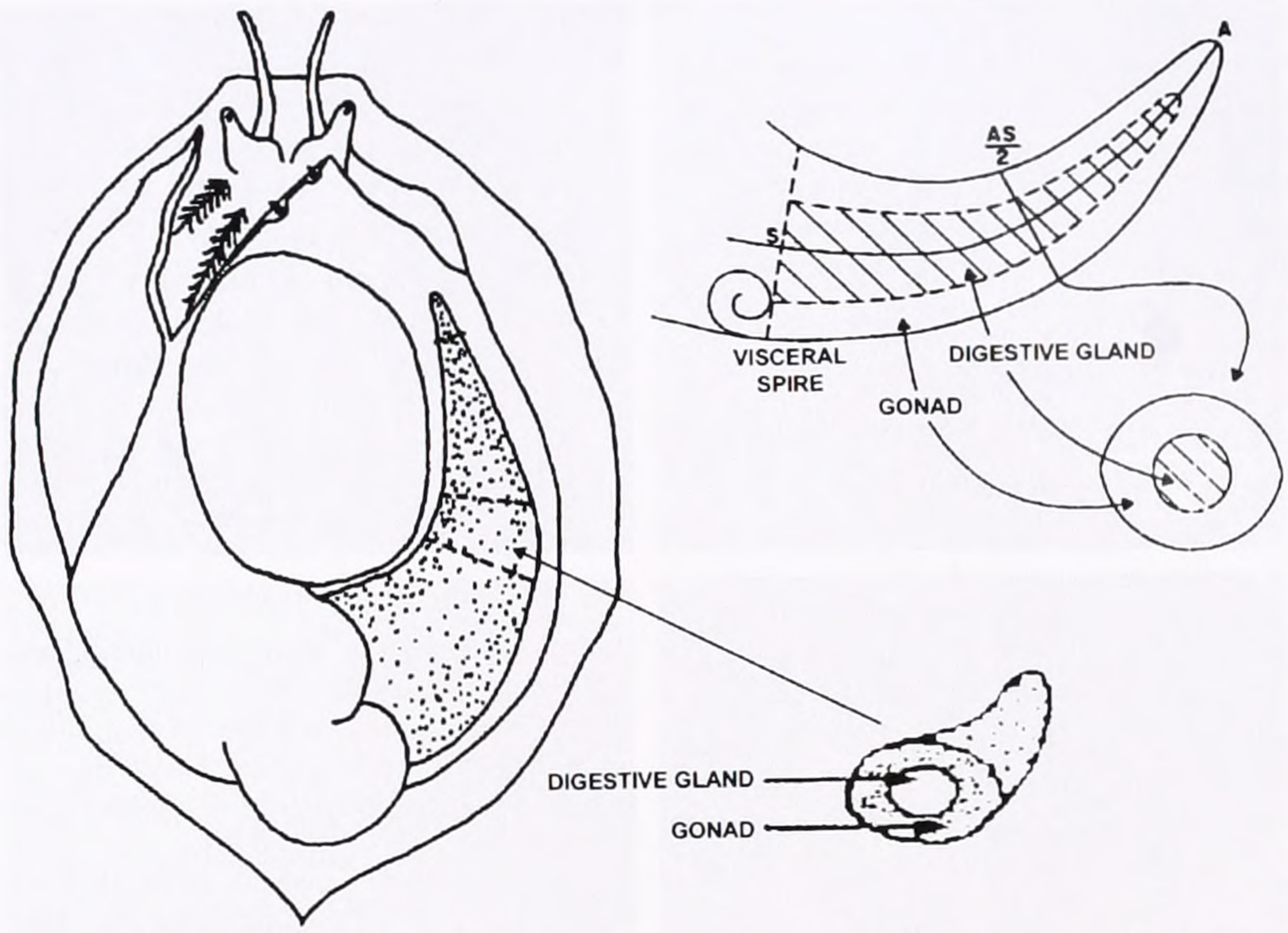

Figure 2. Diagram of red abalone anatomy showing dissection and measurements of red abalone gonad and digestive gland within conical appendage.

Classification of Oocytes

Three classes of oocytes were identified: immature, mature, and necrotic (degenerating) (Young & DeMartini 1970, Brickey 1979, Martin et al. 1983). Immature oocytes range from 5–60 μm in diameter, stain violet, and attach to trabeculae in the gonad. The larger immature oocytes, 40–60 μm diameter become pear shaped and have a distinct nucleus. Slightly larger oocytes, approaching mature size but still attached to trabeculae, were classified as immature. Mature oocytes were 170–190μm diameter and approximately circular.

They have a speckled, densely granular appearance due to a combination of colorless lipid droplets, <6 μm diameter, set in a magenta-stained yolk groundmass. Lipid droplets comprise 30% to 50% of the oocyte volume. The nucleus is usually crescent shaped. The oocytes are surrounded by three extra-cellular layers: a 1-μm vitelline layer, a chorion about 10 μm thick, and the jelly coat 10–20 μm thick. Mature oocytes are detached from the trabeculae, free to be released at spawning.

Young and DeMartini (1970) and Giorgi and DeMartini (1977) first described necrotic oocytes that appear to be autolysing residual mature oocytes. The necrotic oocytes are approximately the same diameter as mature oocytes and are composed of irregular, textureless, orange eosinophyllic masses up to 50-μm wide and set in a fine mesh of dark purple basophyllic material. Numerous vacuoles up to 30-μm diameter connect to give the oocytes a spongy, mosaic appearance. In the early stage of necrosis the oocytes are the same size and shape as mature oocytes. In more advanced stages, the oocyte wall distorts and ultimately ruptures, dispersing the cell contents into the gonad.

Fecundity Estimates

In addition to the gonad volume the total number of mature eggs was determined for each abalone. Egg number was estimated by counting all the mature eggs in 4 microscope fields (×200), dividing by the volume of the 4 fields, and multiplying by the gonad volume. The volume of a microscope field is equal to the area of the field times the thickness. The area was calculated using an ocular micrometer for field dimensions. Because a small mature oocyte section can be from an oocyte largely above or below the section plane, the thickness was defined as twice the average oocyte diameter. The average oocyte diameter was 176 μm, exclusive of the jelly layer. It was determined by measuring the diameter of 1000 of the largest, roundest oocytes in the sections, and by measuring fresh oocytes.

These methods were used to estimate the number of immature eggs in the smaller females, <125 mm and necrotic eggs in all size females. For abalone <76.6 mm all oocytes were counted. Due to the dramatic increase of the number of oocytes in abalone >76.6 mm, only larger oocytes, 40–60 μm were counted, because smaller oocytes were too numerous to count. Necrotic egg number was estimated by counting all the necrotic eggs in 4 microscope fields (×200), dividing by the volume of the 4 fields, and then multiplying by the gonad volume.

RESULTS

Size at Maturity

Abalone shell length was related to reproductive maturity (Fig. 3 and 4). The smallest female with mature oocytes capable of spawning was 106 mm long and weighed 170 g. The smallest animal that could be identified as a female with immature oocytes had a shell length of 50 mm, and a body weight of 15 g. Animals less than 50 mm did not have differentiated gonad tissue. There were 19 immature females ranging from 50–104 mm. Only 6 of 17 females between 106–126 mm had mature oocytes. All 48 females from 129–175 mm had mature oocytes.

Mature males were found at a smaller size than females. The smallest male with sperm was 75 mm and weighed 40 g. The smallest male with spermatocytes and testis structure was 64 mm, and weighed 30 g. Of eight males in the 75–91 mm size range four of them had sperm. All the males between 91–175 mm had sperm (n = 63) with three exceptions that were large males (collected April 2000) with well developed testis structure and spermato-

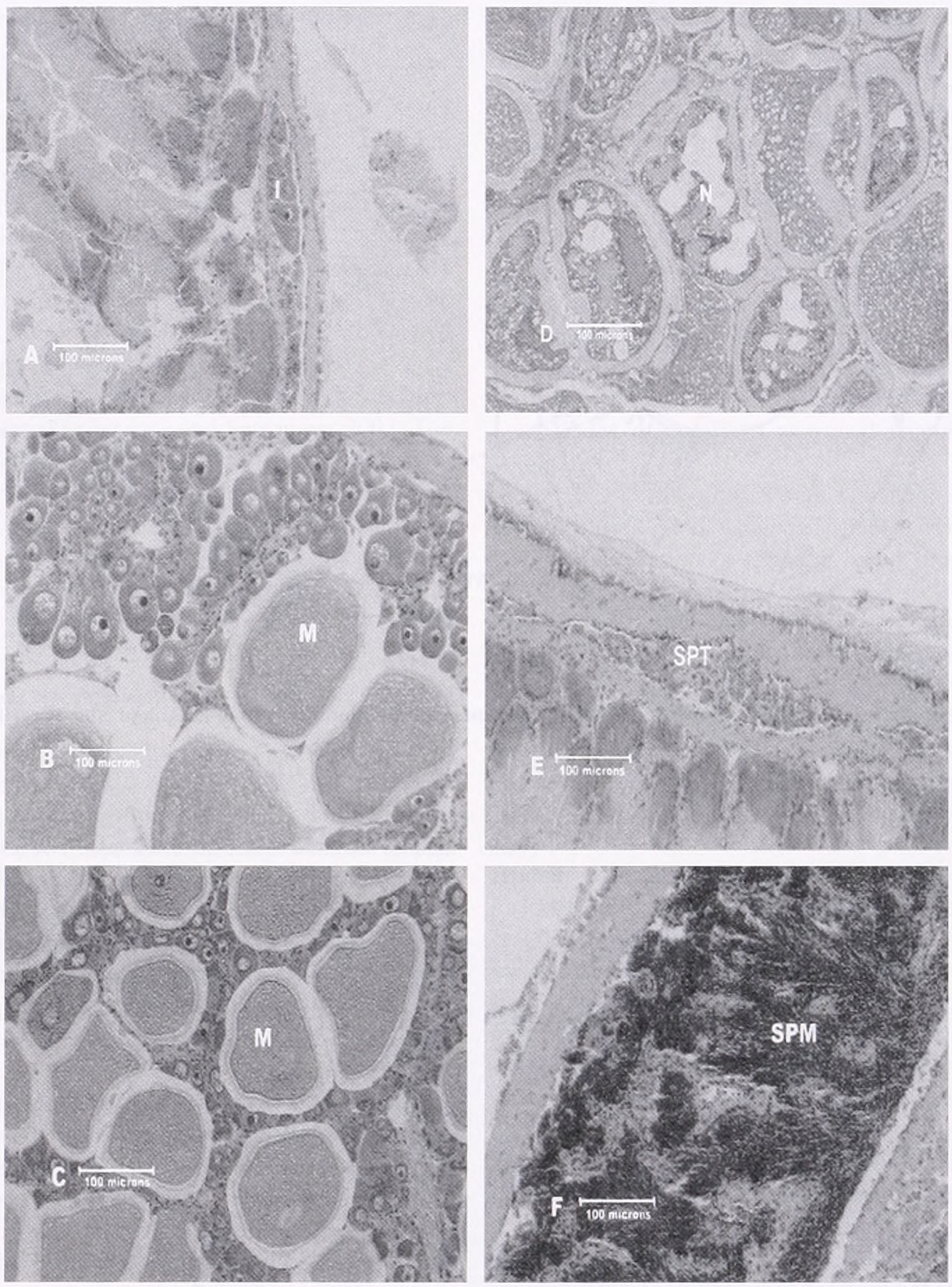

Figure 3. Photomicrographs of gonadal stages of red abalone, *H. rufescens*. A. Female with immature (I) oocytes, shell length 50mm. B. Female with mature (M) oocytes shell length 106 mm. C. Female with abundant mature oocytes shell length 130 mm. D. Female with necrotic (N) oocytes shell length 187 mm. E. Immature male with spermatocytes (SPT), no sperm shell length 75 mm. F. Mature male with abundant sperm (SPM) shell length 100 mm.

cytes, but no observable sperm, suggesting they spawned prior to collection.

Size Specific Reproduction

Gonad volume increased with increasing shell size after 50 mm shell length for females and 64 mm for males. No gonad tissue was visible for abalone smaller than 50 mm in shell length using the microscope. Gonad tissue, or tissue destined to become gonad, appeared as a thin purplish membrane around the digestive gland for animals 50–75 mm. Gonad indexes and sex for all abalone <112 mm (and some abalone in the 114–126 mm size range) with these thin membrane-like gonads were determined from the histologic sections. Abalone >129 mm were measured macroscopically during dissection. These measurements revealed that females ranging in size from 50–75 mm had very thin sections of gonad (<50 μm) with few immature eggs averaging 801 immature eggs per female ($n = 3$). For example, within the three gonad cross sections of a 65-mm female; two sections had no oocytes; whereas the third had only three immature oocytes. Females greater than 75 mm in shell length had dramatically thicker gonad tissue layers (>250 μm) accompanied by a large increase in the numbers of immature eggs averaging 725,763 immature eggs for females 75–100 mm ($n = 8$).

Egg number increased rapidly until a shell length of 215 mm when mature egg number declined (Fig. 4). The relationship between shell length (X) and egg number (Y) can be modeled using a Gaussian curve of the form:

$$(Y) = Ae^{-(X-\mu)^2/2\sigma^2}$$

where A is defined as the maximum productivity, μ is the size at maximum productivity, and σ the standard deviation describes the

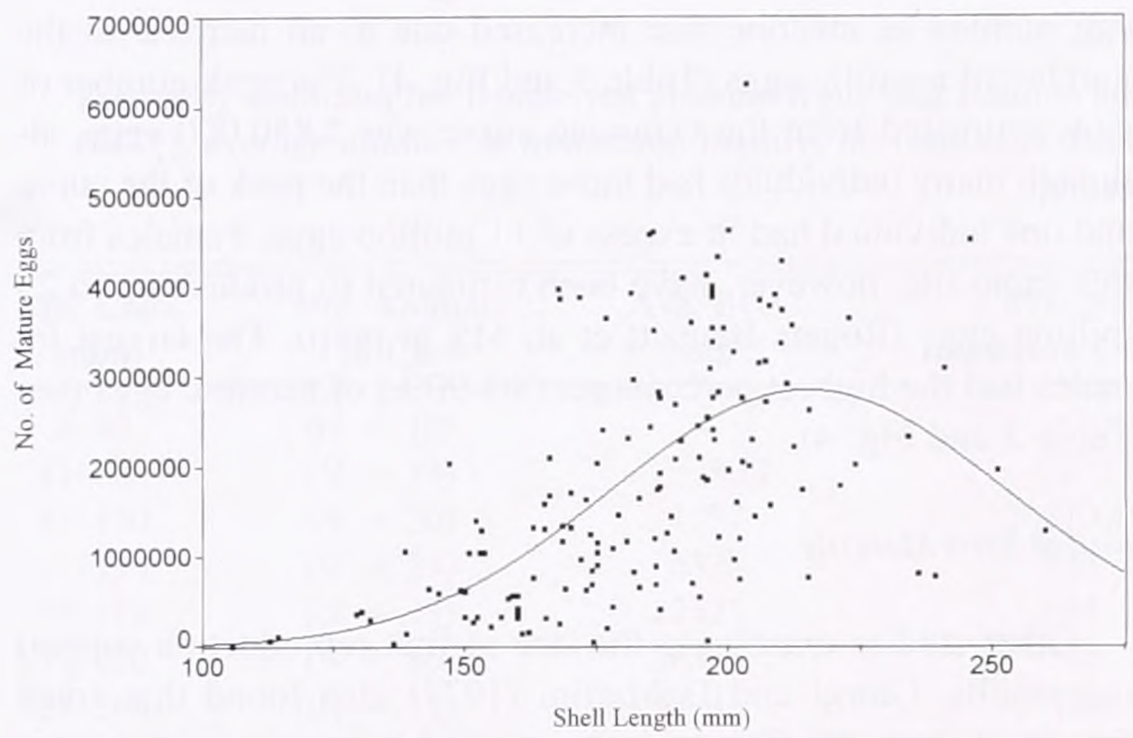

Figure 4. Graph of the relationship between mature egg number and adult female red abalone size (n = 154) from Van Damme and Point Arena in northern California modeled using a Gaussian curve. One female (233 mm length) was outside the 99.9% prediction interval with more than 11 million eggs and was excluded from the Gaussian curve fit.

width of the distribution of maximum productivity versus size. Females are subject to fishing pressures from 177 mm to 253 mm (±1 SD) and this size class is potentially responsible for 68% of the total mature egg production whereas sublegal females will produce 32% of the egg production.

The smallest mature female (105 mm) had the fewest mature eggs (≈2,400) whereas the largest females had the most eggs (Table 1). Mature egg number increased from an average of 63,000 for females ranging in size from 90–120 mm to 2.5 million eggs per female from 178–220 mm and 3 million for the largest females >220 mm. The average number of mature eggs increased per gram of body weight from 330 for females from 90–120 mm in shell length to almost 2,500 eggs per gram of body weight for females 178–220 but declined to 2,000 eggs per gram of body weight for the largest size class >220 mm. In contrast to the small females with few oocytes, the small males (75 mm), had abundant sperm (Table 2).

Necrotic Eggs

The largest red abalone had high percentages of necrotic eggs (Table 3, Figs. 3 and 4). The largest red abalone in the collection (260 mm) from the sport derby had >80% necrotic eggs. The smaller abalone (80–120 mm) had the least number of necrotic eggs.

DISCUSSION

Abalone Size and Reproduction

Histologic examination of gonad tissues revealed that reproductive stage was related to shell length (see Table 3, Fig. 3). Red abalone became sexually differentiated at approximately 50 mm when primary oocytes or spermatocytes (or sperm) are first observed in the gonad tissue. In females >75 mm in shell length, there was a dramatic increase in the thickness of the ovary tissue accompanied by an exponential increase in the number of primary oocytes (see Table 3). The smallest female with mature oocytes was 105 mm, although it was not until a shell size of 130 mm that 100% of the females had mature eggs and the number of mature eggs increased dramatically. Egg number increased to a peak at an abalone shell length of 215 mm, followed by a decrease in mature

TABLE 1.

Sexual maturity of female red abalone ranging from 28.8–150.0 mm in shell length collected from Van Damme State Park in January and September 2003. Total number of mature oocytes estimated for each female abalone. Plus signs (++) indicate the presence of immature or mature eggs while minus signs (––) indicate their absence. Not Measured, not enough tissue to measure (NM). Indeterminate Sex (IS).

Shell Len. (mm)	Body Wt. (gm)	Total No. Mature Oocytes	Immature Oocytes Present	Mature Oocytes Present
28.8	1.6	0	IS	––
36.4	4.1	0	IS	––
36.8	4.2	0	IS	––
46.3	12.0	0	IS	––
49.8	15.0	0	++	––
51.5	15.0	0	++	––
56.5	20.0	0	IS	––
57.7	21.0	0	++	––
58.0	18.0	0	++	––
58.5	14.0	0	IS	––
59.8	24.0	0	++	––
61.2	24.0	0	IS	––
61.5	25.0	0	++	––
62.5	30.0	0	IS	––
64.6	31.0	0	++	––
76.6	56.0	0	++	––
76.7	49.0	0	++	––
81.8	53.0	0	++	––
84.0	68.0	0	++	––
85.0	66.0	0	++	––
85.2	64.0	0	++	––
90.6	90.0	0	++	––
91.0	87	0	++	––
96.2	112	0	++	––
98.4	136	0	++	––
101.8	117	0	++	––
103.9	134	0	++	––
105.7	170	2400	++	++
107.1	120	0	++	––
109.2	180	0	++	––
111.4	187	0	++	––
112.8	152	74000	++	++
114.5	234	112000	++	++
116.4	182	0	++	––
118.5	163	0	++	––
118.7	232	NM	++	++
119.4	261	NM	++	++
120.1	127	0	++	––
121.1	254	0	++	––
122.0	311	0	++	––
122.0	156	0	++	––
125.0	207	0	++	––
125.0	272	NM	++	++
126.4	257	0	++	––
129.2	306	372000	++	++
130.4	262	398000	++	++
132.0	361	308000	++	++
136.3	292	33000	++	++
138.5	391	1073000	++	++
138.8	383	144000	++	++
141.0	237	NM	++	++
142.9	341	NM	++	++
143.0	528	645000	++	++
145.0	482	597000	++	++
147.0	499	2035000	++	++
149.0	499	627000	++	++
150.0	585	334000	++	++
150.0	408	606000	++	++

TABLE 2.

Sexual maturity of male red abalone ranging from 28.8–140.1 in shell length collected from Van Damme State Park in January and September 2003. Plus signs (++) indicate the presence of spermatocytes or mature sperm while minus signs (––) indicate their absence. Indeterminate Sex (IS).

Shell Len. (mm)	Body Wt. (gm)	Spermatocytes Present	Mature Sperm Present
28.8	1.6	IS	
36.4	4.1	IS	
36.8	4.2	IS	
46.3	12	IS	
56.0	17	++	––
56.5	20	IS	
58.5	14	IS	
61.2	24	IS	
62.5	30	IS	
64.4	30	++	––
72.2	40	++	––
72.3	39	++	––
74.9	40	++	++
75.8	46	++	++
78.0	71	++	––
81.6	72	++	++
82.8	60	++	––
86.3	66	++	++
90.8	78	++	––
91.0	90	++	––
94.7	104	++	++
94.9	88	++	++
99.5	102	++	++
100.8	108	++	++
102.1	143	++	++
103.8	138	++	++
104.9	130	++	++
105.6	162	++	++
105.9	127	++	++
106.9	143	++	++
111.3	154	++	++
111.3	151	++	++
113.7	213	++	++
114.7	160	++	++
115.8	207	++	++
117.6	226	++	++
120.4	280	++	++
120.4	220	++	++
123.8	242	++	++
123.9	202	++	++
127.0	347	++	++
127.8	276	++	++
129.0	291	++	++
129.3	320	++	++
129.5	275	++	++
131.7	304	++	++
132.3	323	++	++
135.0	307	++	++
135.1	282	++	++
138.0	308	++	++
138.8	300	++	++
140.1	288	++	++

egg number as abalone size increased due to an increase in the number of necrotic eggs (Table 3 and Fig. 4). The peak number of eggs estimated from the Gaussian curve was 2,850,000 eggs, although many individuals had more eggs than the peak of the curve and one individual had in excess of 11 million eggs. Females from this same site, however, have been estimated to produce up to 23 million eggs (Rogers-Bennett et al. MS in prep). The largest females had the highest percentages (80–90%) of necrotic eggs (see Table 3 and Fig. 4).

Size at First Maturity

Other studies examining the size at first reproduction support our results. Giorgi and DeMartini (1977) also found that small female abalone 40–50 mm in length had immature oocytes (see Table 3, Fig. 3), however different criteria were used to define maturity. We define maturity as requiring the presence of mature oocytes. Mature oocytes can be distinguished from immature (<50 μm in diameter) based on egg size (180 μm in diameter), having both stained yolk and lipid droplets and being detached from the trabeculae (stalk), ready to be spawned (see Fig. 3). Samples collected in this study in January and September 2003 showed that the smaller abalone 50–100 mm did not have mature oocytes. Giorgi and DeMartini (1977) also found that abalone <132 mm collected in June and July only had small (<50 μm) immature eggs. Ault (1985) collected wild red abalone and found that only female red abalone >110 and males >60 mm spawned successfully after artificial induction (using hydrogen peroxide) further supporting our conclusions.

There was a large gap in sizes between immature and mature males and females (Tables 1 and 2). Females with immature oocytes were 50 mm in shell length and those with mature oocytes were 130 mm. This suggests two alternative hypotheses: either the eggs from smaller females mature at a different time of year, which we missed with our sampling dates (January and September 2003) or it may take a few years before ovaries mature. Eggs from female frogs, *Rana temporaria,* take 3 years to mature (Grant 1953). A Gaussian growth curve has been used to estimate that it would take 3–4 years for females in northern California to grow from 50 mm to maturity at 105 mm and 1–2 years for males to mature from 50 to 75 mm (Rogers-Bennett et al. MS in review).

We found a significant difference in the size at maturity between the sexes with females maturing at a larger size than males, as was found in the southern California (Tutschulte 1976, Tutschulte & Connell 1985). Wild abalones in southern California have also been found to mature at large sizes. Tutschulte (1976) found that 4 of 19 pink abalone in the size ranges from 59–119 mm had mature oocytes, and that green abalone mature at 101 mm. More studies however, are needed on the time and food resources required for maturation of gametes in wild populations.

Oceanographic conditions are known to influence abalone reproduction and successful recruitment (Shepherd et al. 1998). For example, El Niños are associated with decreased dissolved nitrogen levels, poor kelp growth (Tegner et al. 1997), poor abalone growth (Haaker et al. 1998) and possibly decreased abalone egg production. Perhaps as a result of oceanographic conditions recruitment is highly variable in time and space (McShane & Smith 1991). If females have just a few years to spawn prior to growing into the fishery, some females may not spawn during this time if oceanographic conditions remain unfavorable. In fact, minimum size limits failed to prevent the collapse of abalone populations in

TABLE 3.

Fecundity estimates for female red abalone from Van Damme and Point Arena by size class showing average estimated gonad volume (EGV), average number of immature, mature, necrotic eggs. Percent of necrotic eggs to total number of mature and necrotic eggs per female abalone.

Size Class (mm)	No. Animals in Class	Ave. EGV mm^3	Ave. No. Immature Oocytes	Ave. No. Mature Oocytes	Ave. No. Necrotic Oocytes	% Necrotic Oocytes
0–40	(N = 10)	—	0	0	0	0
41–80	(N = 13)	80.7	37721	0	0	0
81–120	(N = 20)	1237	2027000	62959	28024	30.8
121–150	(N = 21)	6328	NM	597706	59076	9.0
151–178	(N = 49)	12623	NM	1153328	75154	6.1
179–220	(N = 80)	26362	NM	2491901	192538	7.1
221–260	(N = 11)	44746	NM	3068098	2005563	40.0

southern California (Tegner et al. 1989, Karpov et al. 2000) and elsewhere (Shepherd & Rodda 2001, Shepherd et al. 2001).

Evidence for Limited Reproductive Senescence

The largest individuals had the most (80% to 90%) necrotic eggs (Table 3, Fig. 4) suggesting the onset of reproductive senescence. On average, individuals in the largest size class had 40% necrotic eggs, the most of any of the size classes (see Table 3). Legal size abalone from this same date had less than 20% necrotic eggs. Histologic examination of female ovaries (n = 34) from VDSP indicated that in August 2001 only 12% of the eggs were necrotic, suggesting August is not a period of unusually high percentages of necrotic eggs. Few studies however, have examined reproductive senescence in mollusks, with freshwater mussels showing reproductive senescence (Downing et al. 1993), whereas marine quahog clams did not (Walker 1994).

Egg production capacity of very large female abalone (>215 mm) is still high, despite having high percentages of necrotic eggs. The size class with the greatest number of mature eggs per female abalone was the largest size class (220–260 mm) (see Table 3, Fig. 4), suggesting that even with reproductive senescence, the largest females are still capable of producing millions of eggs. It is unknown, however, if these females spawn successfully relative to smaller females or if the eggs produce viable, high quality larvae.

Egg Conservation and Reserves

One way to maintain egg production would be to exclude large females from the fishery using upper size limits or area closures. Legal size abalone (± 1 SD of the peak 215 mm) have the potential to generate 68% of the egg production (see Fig. 4). As in other recreational trophy fisheries however, where large animals are highly prized, the addition of an upper size limit may not have popular support. While reserves may benefit the fishery in the north, these areas were largely absent in the south where stocks collapsed. The south also had additional abalone fishing pressures compared with the north because much of the coast is accessible, ocean conditions are frequently favorable and the use SCUBA was permitted for abalone fishing. The few reserves in the south such as the Anacapa Island Ecological Reserve (McArdle 1997) did function to protect large abalone and was shown to have the potential for increased egg production compared with neighboring fished areas (Rogers-Bennett et al. 2002).

The fishery in the north seems to be sustainable, perhaps in part due to protection of a portion of the stock in reserve areas and a large *de facto* reserve (both at deep depths [<8.5 m] and along inaccessible portions of the coast), which may be the key for sustainability as has been suggested in other fisheries (Walters & McGuire 1996). Inside established reserves in the north more juvenile abalone have been found compared with fished areas (Rogers-Bennett & Pearse 2001). If large abalone are to be protected and allowed to spawn, then maintaining reserves will need to remain a top priority for management, recreational divers and wildlife protection.

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